The Late Neogene elephantoid-bearing faunas of Indonesia and their palaeozoogeographic implications

A study of the terrestrial faunal succession of Sulawesi, Flores and Java, including evidence for early hominid dispersal east of Wallace's Line

Gert D. van den Bergh

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Gert D. van den Bergh, Marine Chemistry and Geology, Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands.

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The stratigraphic framework of the Neogene fossil vertebrate bearing formations of the Indonesian islands Sulawesi and Flores is established and the sediments are dated by means of marine micropalaeontological and/or palaeomagnetic methods. The results allow comparison of the fauna evolution on these islands with the better known fauna succession of Java. On both Sulawesi and Flores remains of large mammals and reptiles were excavated from fossil-rich layers, documenting the composition of large vertebrate faunas fairly well. For Sulawesi this procedure allows distinction of separate fauna units which formerly had been lumped together. Both on South-Sulawesi and Flores 3 successive faunas can be distinguished. The oldest terrestrial faunas have recorded ages of 2.5 Ma and 0.9 Ma, respectively. On both islands intermediate faunas have a Middle Pleistocene age, while the youngest faunas are subrecent to Recent.

Elephantoids (*Stegodon* and *Elephas*) showing various degrees of dwarfing are important constituents in all non-subrecent/Recent faunas. Their dental, cranial and postcranial remains are described in detail and their taxonomic positions are discussed. A new species (*Stegodon sondaari* sp. nov.) is described from Flores. Geological/tectonic data and the nature of the impoverished and highly endemic faunas from Sulawesi and Flores both indicate longlasting isolation from the southeast Asian mainland and from Java.

On Flores and probably also on South Sulawesi fauna turnovers with extinction and immigration of elephantoids occurred around the Early to Middle Pleistocene transition. On both islands the total disappearance of elephantoids presumably took place before the onset of the Holocene. On Flores the Middle Pleistocene faunal assemblage is associated with a palaeolithic industry, which is tentatively ascribed to *Homo erectus*. Early hominids appear to have been able to cross water barriers and successfully colonize Flores as far back as 0.6 Ma ago. They may have been in part responsible for the observed faunal turnover on the island, but alternatively, extinctions may have been caused by a volcanic catastrophe.

The existing biostratigraphic framework of Java is discussed and some additions concerning elephantoid taxa are given. Following the emergence of Java above sea-level from the Late Pliocene until c. 1.5 Ma, mammalian dispersal to the island was limited. This is illustrated by impoverished faunal assemblages and the occurrence of various dwarfed elephantoids in this time interval, indicating isolated conditions. Further uplift and volcanic activity in combination with episodes of moderate low sea-level led to an increasing accessibility of the Java region until c. 0.8 Ma, though the faunas from this time interval remain somewhat impoverished, suggesting filter dispersal. *Stegodon elephantoides* is for the first time recorded from Java, originating from a layer correlated with this time interval. Corridor dispersal to Java occurred for the first time at around 0.8-0.7 Ma, and can be tied to marked glacio-eustatic sea-level lowerings starting at 0.8 Ma. This period of low sea-level may also have triggered the faunal turnovers observed on Sulawesi and Flores, by enhancing the chance for a second (overseas) dispersal wave to

these islands, and perhaps exchange between Sulawesi and Flores. However, superficial similarities between various island stegodonts must be ascribed to parallel evolution in most cases. Common adaptive trends that can be recognized are dwarfing and increase in hypsodonty.

On Java local evolution is documented by the recognition of three successive subspecies of *Stegodon trigonocephalus*. On Java the extinction of *Stegodon* and the first recording of *Elephas maximus* concurs with environmental changes from an open woodland biotope to a rainforest biotope, which took place after the penultimate glacial maximum at 125 ka. On South Sulawesi the Recent fauna presumably entered after the connection with the remaining part of Sulawesi had been established.

De rijke biodiversiteit van het enorme eilandenrijk gelegen tussen het vasteland van zuidoost Azië en het Australische continent, dat onder andere het gehele Indonesische territorium omvat, is in grote mate te danken aan de complexe geologische geschiedenis. Daarbij heeft isolatie op eilanden een grote rol gespeeld. Fossiele landvertebraten-voorkomens van de eilanden Java, Sulawesi en Flores vormen het uitgangspunt van de huidige studie. De diverse fossiele faunas van deze eilanden zijn in een litho- en chronostratigrafisch kader geplaatst, waardoor een bijdrage is geleverd om de complexe zoögeografische evolutie van de regio te reconstrueren.

Soorten behorende tot de superfamilie der Elephantoidea, waartoe ook de recente olifanten behoren, zijn zeer goed vertegenwoordigd in de fossiele faunas. Vertegenwoordigers van deze groep hebben zich gedurende de laatste 2,5 miljoen jaar met groot succes kunnen verspreiden binnen het gebied. Fossiele vindplaatsen met één of meerdere Elephantoidea, zijn bekend van de eilanden Sumatra, Java, Borneo, Sulawesi, Sangihe, Flores, Sumba, Timor, Luzon en Mindanao. In een recenter verleden is de grote verscheidenheid aan olifanten grotendeels weer verdwenen, niet alleen regionaal, maar wereldwijd. Vanwege het relatief veelvuldige voorkomen van fossiele olifanten resten, ook op eilanden waar de meeste andere zoogdieren niet konden komen, is de nadruk in dit proefschrift komen te liggen op de olifanten (in de ruimste betekenis van het woord).

In het eerste hoofdstuk worden de achtergrond en doelstellingen van het onderzoek geïntroduceerd. Ook wordt de gevolgde taxonomische classificatie van de Proboscidea uiteengezet, gevolgd door een beschrijving van de opgravingsprocedures en een verklaring van de gebruikte terminologie en meetmethoden.

Het tweede hoofdstuk handelt over een aantal nog niet eerder beschreven elephantoïden resten van Java, die voor zover mogelijk in het bestaande biostratigrafische kader worden geplaatst. De landfauna-veranderingen die zich gedurende het Pleistoceen op Java hebben afgespeeld waren in grote lijnen bekend, en daarom is het biostratigrafisch kader van Java van groot belang als referentie voor de vergelijking met de fauna opeenvolgingen op de eilanden Sulawesi en Flores. Het huidige onderzoek laat zien dat wat de olifanten betreft de evolutionaire opeenvolging op Java complexer is geweest dan aanvankelijk werd aangenomen.

Sinds Java gedurende het laat Plioceen ten gevolge van vulkanische en tectonische activiteit boven de zeespiegel is uitgerezen, is er een toename in het totaal aantal soorten grote zoogdieren opgetreden tot zo'n 800.000 jaar geleden. Een van de eerste elephantoïden die Java bereikte was *Sinomastodon bumiajuensis*. Deze mastodont is geassocieerd met de 2 tot 1,5 miljoen jaar oude Satir Fauna, welke slechts een beperkt aantal soorten omvat, waaronder een nijlpaard, herten en een reuzenschildpad, hetgeen duidt op eiland omstandigheden. Vertegenwoordigers van deze taxa hebben Java waarschijnlijk bereikt door een zeebarrière over te steken (sweepstake route). De ongeveer 1,2 miljoen jaar oude, maar slecht bekende, Ci Saat Fauna was oorspronkelijk gedefiniëerd door het eerste voorkomen op Java van *Stegodon*. Door de relatieve zeldzaamheid van fossielen uit dit tijdinterval was de overgang tussen de Satir Fauna en de Ci Saat Fauna nauwelijks bekend. Een nog niet eerder beschreven onderkaak met een ouderdom van tussen de 1,2 en 1,3 miljoen jaar, wordt hier aan *Stegodon elephantoides* toegeschreven. Deze zeldzame soort was tot nog toe alleen bekend uit Myanmar. Opvallend is dat enkele meters boven de laag met *S. elephantoides* nog een reuzenschildpad aangetroffen is, hetgeen erop lijkt te wijzen dat de overgang tussen de Satir en Ci Saat Fauna een geleidelijke is geweest.

Twee jongere faunas, de 0,9 miljoen jaar oude Trinil Haupt-Knochenschicht Fauna en de 0,8-0,7 miljoen jaar oude Kedung Brubus Fauna, zijn veel beter bekend. De Trinil H.K. Fauna is een enigszins verarmde Zuidoostaziatische vasteland fauna, met als enige elephantoïde *Stegodon trigonocephalus*, terwijl in de Kedung Brubus Fauna daarnaast ook een echte olifant, *Elephas hysudrindicus* voorkomt. De Kedung Brubus Fauna is een evenwichtige continentale fauna. De laat-Pleistocene Ngandong Fauna lijkt qua samenstelling veel op de Kedung Brubus Fauna, met dit verschil dat vele soorten op subspecies niveau verschillen, waaronder *S. trigonocephalus*. Vergelijking van *Stegodon* materiaal afkomstig uit diverse vindplaatsen, waaronder nog niet eerder beschreven kiezen uit Ngandong, toont aan dat er drie opeenvolgende subsoorten van *S. trigonocephalus* kunnen worden onderscheiden, van oud naar jong *S. t. praecursor* (Ci Saat Fauna?), *S. t. trigonocephalus* (Trinil en Kedung Brubus Faunas) en *S. t. ngandongensis* subsp. nov. (Ngandong Fauna).

Verder is vast komen te staan dat er meerdere verdwergde *Stegodon* vormen op Java hebben geleefd, maar hun precieze inpassing in de tijdsschaal is tengevolge van onvoldoende stratigrafische gegevens moeilijk vast te stellen. Belangrijk is ook dat het voorkomen van *Elephas maximus* op Java voor het eerst met zekerheid kon worden aangetoond. *E. maximus* moet na de voorlaatste IJstijd in Sundaland zijn onstaan of vanuit zuidoost Azië zijn binnengekomen. Aan het einde van het tweede hoofdstuk wordt getracht de belangrijkste fauna-veranderingen op Java te koppelen aan glacio-eustatische zeespiegel fluctuaties en klimaatsveranderingen.

In het derde hoofdstuk worden de stratigrafie en terrestrische fauna opeenvolging van Sulawesi behandeld. Zowel fossiele als Recent nog voorkomende landvertebraten zijn in het verleden van Zuidwest Sulawesi beschreven. Daarnaast is er ook een paleolithische industrie uit hetzelfde gebied bekend, die met zogenaamde terrassen geassocieerd zou zijn. Het was echter niet duidelijk of de diverse fossiele taxa dezelfde ouderdom hadden, en of de stenen werktuigen al dan niet met primaire fossielvoorkomens geassocieerd waren. Ook bestond er onenigheid over de manier waarop de landvertebraten op Sulawesi terecht waren gekomen, over zee of via voormalige landverbindingen. Om die laatste probleemstelling te benaderen is een uitgebreide literatuurstudie gemaakt van de regionale geologie en tektoniek, waaruit blijkt dat de Makassar Straat gedurende het Midden Eoceen is ontstaan. Mogelijk is er tijdens het Oligoceen nog een landverbinding geweest, maar voor alle latere verspreidingen naar Sulawesi moeten er een of meerdere zeebarriéres zijn genomen. Ook voormalige landverbindingen tussen Noord Sulawesi en Mindanao zijn zeer onwaarschijnlijk. Het huidige stratigrafisch en geologisch onderzoek heeft uitgewezen dat er geen sprake is van terrassen maar dat de fossielhoudende lagen, behorende tot de fluvio-estuariene Beru Member van de Walanae Formatie, locaal is opgeheven in een breukbegrensd gebied, zonder dat er noemenswaardige scheefstelling is opgetreden. Dit impliceert dat de paleolithische werktuigen, indien afkomstig uit deze afzettingen, een veel grotere ouderdom kunnen hebben dan de Laat Pleistocene ouderdom die tot nog toe werd aangenomen.

De samenstelling van de terrestrische fauna uit de Beru Member, Walanae Fauna genoemd, duidt op eiland-omstandigheden. De oudste, beschreven associaties van de Walanae Fauna zijn afkomstig uit het Boven Plioceen en zijn ca. 2,5 miljoen jaar oud, hetgeen ouder is dan de oudste (ei)land fauna van Java. De jongste lagen met Walanae Fauna hebben waarschijnlijk een vroeg-Pleistocene ouderdom. De fauna bevat de volgende elementen: een uitgestorven dwergolifant (*"Elephas" celebensis*), een dwergstegodont (*Stegodon sompoensis*), een reuzeschildpad (*Geochelone atlas*), een varkenssoort (*Celebochoerus heekereni*), *Crocodylus* spec. en Trionychidae gen. et sp. indet. Fragmentarische oppervlakte vondsten wijzen erop dat in een later stadium mogelijk ook een grote *Stegodon* soort deel uitmaakte van de Walanae Fauna. Aangetoond kon echter worden dat de Walanae Fauna géén grote zoogdiersoorten bevat die recent nog voorkomen. De Walanae Fauna leefde geruime tijd geïsoleerd en vast is komen te staan dat bij het meest voorkomende element, *Celebochoerus*, in de loop der tijd een verkorting van de metapoden is opgetreden als aanpassing aan het eilandmilieu.

Onverwachts is nog een tweede, jongere fossiele fauna ontdekt, die Tanrung Fauna is genoemd naar de Tanrung Formatie waarin deze fauna is aangetroffen. In de Tanrung Formatie zijn in situ fossielen van een middelgrote tot grote stegodont (*Stegodon* sp. B) aangetroffen en van een kleinere *Celebochoerus* soort. Behalve het laatstgenoemde taxon zijn geen resten van andere elementen uit de Walanae Fauna in de Tanrung Formatie gevonden. De Tanrung Fauna heeft een (geschatte) midden Pleistocene ouderdom. Oppervlakte vondsten in het gebied waar de Tanrung Formatie dagzoomt omvatten resten van *Anoa* sp. en van *Sus celebensis* (beide Recent nog voorkomende soorten), en van een geavanceerde hoogkronige *Elephas* soort, waarvan waarschijnlijk alleen de laatsgenoemde uit de Tanrung Formatie afkomstig is. De andere soorten zijn zeer waarschijnlijk afkomstig uit jongere kustafzettingen, die met een erosief contact op de Tanrung Formatie zijn afgezet. Vermoedelijk gedurende het Vroeg of Midden Pleistoceen is er een fauna omslag in Sulawesi opgetreden. In ieder geval moeten er meerdere, in de tijd verspreide elephantoïden immigraties naar Zuidwest Sulawesi zijn geweest. *Stegodon* sp. B is ook aangetroffen op het eilandje Sangihe. Vermoedelijk pas in het Laat Pleistoceen zijn olifanten geheel uit Zuidwest Sulawesi verdwenen. De Recente fauna van grote zoogdieren, inclusief *Babyroussa* en *Anoa*, is waarschijnlijk vanuit Centraal Sulawesi naar Zuidwest Sulawesi verspreid nadat een landverbinding tussen beide delen tot stand was gekomen. *Babyroussa* leefde mogelijk al sinds het Oligoceen in Centraal Sulawesi.

Het vierde hoofdstuk behandelt de paleontologie van de elephantoiden van Sulawesi. *Stegodon sompoensis* is een verdwergde eilandvorm en behoort tot de groep stegodonten waartoe ook *S. trigonocephalus* (Java) en *S. ganesa* (Indiase sub-Continent) behoren. *"Elephas" celebensis* is eveneens een dwergvorm, die over een aantal unieke schedelkenmerken beschikt. Deze soort stamt mogelijk af van de vroegste *E. planifrons* populaties van het vasteland, maar kan ook uit meer archaïsche Elephantidae zijn ontstaan. *Stegodon* sp. B is een middelgrote tot grote stegodont, die mogelijk nauw verwant is aan *S. florensis* uit vroeg midden-Pleistocene afzettingen op het eiland Flores. De identiteit van enkele schaarse *Elephas* resten kon niet nader worden vastgesteld, maar duidelijk is dat deze olifant nauw verwant moet zijn geweest met een geavanceerde midden- of laat-Pleistocene *Elephas* soort, waarschijnlijk *E. namadicus*. Hiermee is het aantal elephantoïden soorten die ooit op Sulawesi hebben geleefd op minimaal 4 soorten komen vast te staan.

Het vijfde hoofdstuk richt zich op de stratigrafie en fauna opeenvolging van het fossielrijke Soa Bekken in Flores. De ± 0,9 miljoen jaar oude Fauna A afkomstig uit de onderste Member A van de Ola Bula Formatie, bevat een dwerg stegodont (*Stegodon sondaari* sp. nov.), een reuzen landschildpad (*Geochelone* sp.), een kleine krokodil en resten van de recent nog voorkomende Komodo varaan (*Varanus komodoensis*). De jongere Fauna B is geassocieerd met de fluviatiele Member B van de Ola Bula Formatie en heeft een ouderdom van tussen de 0,7 en 0,6 miljoen jaar. Fauna B bevat geen *S. sondaari* noch reuzenschildpad, maar wel een middelgrote stegodont (*S. florensis*) en een reuzenrat (*Hooijeromys nusatenggara*). Zowel Fauna A als Fauna B duiden wederom op geïsoleerde eiland omstandigheden. De faunaomslag op Flores vertoont gelijkenis met die van Zuidwest Sulawesi in timing en karakter. Op beide eilanden treden belangrijke faunaveranderingen op rond de overgang van Vroeg naar Midden Pleistoceen en komen de kleinste dwerg elephantoïden voor in de oudere fauna. Bewezen kon worden dat op Flores de jongere Fauna B geassocieerd is met een primitieve lithische industrie. Deze kan gezien de hoge ouderdom (gebaseerd op paleomagnetische analyse) niet worden toegeschreven aan *Homo sapiens*; gedacht wordt dan ook dat *Homo erectus* de maker van de werktuigen is geweest. Deze gegevens suggereren dat *H. erectus* in staat zou zijn geweest om zeestraten over te steken. Tot nog toe werd algemeen aangenomen dat *H. sapiens* de eerste zeevaarder was, maar uit de huidige gegevens zou afgeleid kunnen worden dat *H. erectus* al zo'n half miljoen jaar eerder de zee is opgegaan. Dit zou weer verstrekkende gevolgen hebben voor interpretaties betreffende de technische en geestelijke vermogens van *H. erectus*. Hoewel voorzichtigheid is geboden, is de hoge ouderdom van de artefact-houdende laag inmiddels al wel bevestigd door middel van alternatieve dateringsmethoden.

Het zesde hoofdstuk geeft een paleontologische beschrijving van de stegodonten uit Flores. *Stegodon sondaari* is de kleinste tot nu toe bekende dwergstegodont en verschilt duidelijk van dwergstegodonten uit Sulawesi en Timor. Kiezen van *S. sondaari* vertonen enkele primitieve kenmerken, hetgeen suggereert dat deze dwergsoort afstamt van een archaïscher soort dan *S. trigonocephalus*. *S. sondaari* kan mogelijk al sinds het laat Plioceen op Flores vertegenwoordigd zijn geweest. Geconcludeerd wordt dat de stegodont uit fauna B van Flores op soortsniveau verschilt van *S. trigonocephalus*, en als *S. florensis* aangeduid dient te worden. Kiezen van *S. florensis* vertonen overeenkomsten met die van *Stegodon* sp. B uit de Tanrung Fauna van Sulawesi.

De hoofdstukken 7 en 8 geven een aantal paleozoogeografische en paleobiologische beschouwingen naar aanleiding van de resultaten op de diverse eilanden. De elementen van de Walanae Fauna zijn waarschijnlijk vanuit het Indiase Subcontinent via Burma en Sundaland in Zuidwest Sulawesi terecht gekomen door de zeeëngte tussen Zuidwest Sulawesi (dat toen een apart eiland vormde) en het Sundaplat over te steken. Dit is waarschijnlijk tijdens het Laat Plioceen gebeurd, toen belangrijke glacioeustatisch-bepaalde zeespiegel laagstanden optraden waardoor de totaal overzee te overbruggen afstanden geringer waren dan in de recente situatie. De oudere landfaunas van Java zijn eveneens voor het grootste deel afkomstig uit het Indiase Subcontinent. Aanvankelijk is het verspreidingsmechanisme naar Java sweepstake- en filter-verspreiding geweest. Vanaf het Sunda Plat konden sommige soorten zich verder verspreiden naar Sulawesi. De latere maximale verspreiding naar Java vond plaats via een corridor rond 0,8 miljoen jaar geleden. In Japan en Taiwan komen dan ook voor het eerste continentale faunas binnen, terwijl in Sulawesi en Flores slechts enkele nieuwe soorten binnenkomen. Deze observaties zijn in overeenstemming met gegevens omtrent eustatische zeespiegelfluctuaties, waaruit blijkt dat vanaf 0,8 miljoen jaar geleden de zeespiegel gedurende langere periodes lager kwam te liggen dan in het tijdsinterval daarvoor, waardoor het Sunda platform meerdere malen geheel droog kwam te liggen. Waarschijnlijk was deze laagstand ook bepalend voor de fauna-omslagen op de eilanden Sulawesi en Flores. Het is zeer wel mogelijk dat de voorouder populatie van *S. florensis* niet vanuit Java maar vanuit Sulawesi op Flores terecht is gekomen, hoewel een landverbinding tussen beide eilanden uitgesloten kan worden.

Op Java valt pas in de laat-Pleistocene Punung Fauna een duidelijke relatie met zuid-Chinese faunas te onderscheiden. Wederom vond verspreiding via een corridor plaats. Vooralsnog zijn er geen eenduidige aanwijzingen dat Chinese elementen ook Sulawesi en Flores hebben bereikt via de Philippijnen. Het is echter niet uit te sluiten dat een of meerdere elephantoïden de route Philippijnen-Sulawesi-Flores hebben gevolgd.

Vast staat dat de dwerg elephantoïden van Sulawesi, Flores en Timor verschillen op soortsniveau. Deze vormen moeten onafhankelijk van elkaar onstaan zijn, terwijl oppervlakkige gelijkenissen kunnen worden toegeschreven aan paralelle evolutie. Zo lijkt er naast de algemene trend van verdwerging ook een evolutionaire trend te zijn geweest die er toe leidde dat de dwarsrichels op de kiezen van eiland stegodonten geleidelijk aan hoogkroniger werden, waardoor in sommige gevallen sterke gelijkenis met de kiezen van de eerste echte olifanten optrad. Deze toename in hypsodontie moet gezien worden als een aanpassing aan het eilandmilieu. Algemeen wordt gedacht dat verdwerging van grote zoogdieren op eilanden in de eerste plaats het gevolg is van de combinatie van een geringer voedselaanbod en het ontbreken van carnivoren. De kleinste elephantoïde uit de regio, *Stegodon sondaari*, had een geschat volwassen lichaamsgewicht van tussen de 200 en 500 kg. Opvallend is dat de elephantoïden uit de jongere, midden-Pleistocene eilandfaunas van Flores en Sulawesi weliswaar kleiner zijn dan vasteland soorten, maar desalnietemin grotere afmetingen hebben dan de verdwergde vormen uit de voorafgaande laat-Pliocene — vroeg-Pleistocene faunas. Op Flores kan deze geringere verdwerging van de "tweede golf" elephantoïden mogelijk toegeschreven worden aan de aanwezigheid van een warmbloedige predator, namelijk *Homo*. Voor Sulawesi zijn er vooralsnog geen aanwijzingen in die richting, tenzij in de toekomst bewezen zou kunnen worden dat de paleolithische werktuigen van de Tjabenge Industrie dezelfde ouderdom hebben als de Tanrung Fauna.

Een leeftijdsprofiel van *S. sondaari* gebaseerd op de slijtpatronen van kiezen toont aan dat de aangetroffen fossiel-accumulatie het gevolg is van niet-selectieve massale sterfte. Combinatie met sedimentologische gegevens duidt erop dat de massale sterfte het gevolg moet zijn geweest van een vulkanische uitbarsting. De reconstructie van leeftijdsprofielen voor andere associaties van elephantoïden leidde tot minder eenduidige resultaten.

In het laatste hoofdstuk worden een aantal conclusies die voortvloeien uit het huidige onderzoek samengevat.

Contents

1. Introduction

Indonesia: a transitional zoogeographic region

During his extensive journeys throughout the Malay Archipelago (in the area now known as Indonesia) from 1854 to 1862, the British naturalist Alfred Russel Wallace collected more than hundred thousand insects, birds and mammals from the enormous variety of species that inhabit the numerous islands of this tropical region. While still in the East Indies, his findings led him to the conclusion that there had to have been isolation and evolution, in order to explain the faunal distribution observed on the different islands. Wallace reached this conclusion independently from Charles Darwin, whose name is so firmly associated with the evolution theory. The island of Celebes, now called Sulawesi, particularly caught Wallace's attention, as this island seemed, contrary to what would be expected from its central position in the Archipelago, 'to be at once the poorest in the number of its species, and the most isolated in the character of its productions, of all the great islands in the Archipelago.' In 1868, six years after his return to Great Britain, Wallace wrote: '...Celebes must be one of the oldest parts of the Archipelago. It probably dates from a period not only anterior to that when Borneo, Java and Sumatra were separated from the continent, but from that still more remote epoch when the land that now constitutes these islands had not risen above the ocean. Such an antiquity is necessary to account for the number of animal forms it possesses, which show no relation to those of India or Australia...'.

Wallace thought that most faunal elements of Sulawesi had been isolated for a long period of time and therefore had gone their own evolutionary pathways leading to distinct endemic, or 'peculiar' as he puts it, productions. A good example was the babirusa, or 'pig-deer', an extant inhabitant of Sulawesi with pig-like features, and yet, with its large recurved upper canines and long and slender legs, so distinct from all other pig species in the world. The zoogeographic boundary separating Sundaland (comprising the larger islands Borneo, Sumatra, Java and Bali) in the west from Celebes and Lombok in the east was first drawn on a map in a paper Wallace published in 1863 (Fig. 1). Huxley (1868) extended Wallace's Line northwards between Borneo and the Sulu Archipelago, across the Sulu Sea and further through the Mindoro Strait west of the Philippines. Wallace considered the Philippine realm as Asiatic and did never agree on this northern extension of his line. Though Huxley called it Wallace's Line, it should thus be referred to properly as Huxley's Line (Fig. 1), corresponding more or less with the edge of the southeast Asiatic continental shelf as far as Mindoro Strait (Simpson, 1977).

Wallace also seemed unsatisfied with the course of his original boundary west of Sulawesi and doubted weather this island should be included in the Oriental Region or not (George, 1981). In his last comment on the subject (Wallace, 1910, in George, 1981) he had changed his mind and argued that Sulawesi was really an outlier of the Asiatic continent but was separated at a much earlier date. He concluded that Wallace's Line should be drawn east of Sulawesi.

Many more lines were drawn based on the distribution of different groups of animals (Simpson, 1977). The most significant as it seems now was Lydekker's Line (Fig. 1), which delineated the boundary between the Australian Region and the Austro-Malayan Region. The latter was considered a transitional zoogeographic zone between the Oriental and Australian Regions and with its western boundary corresponding with Wallace's Line (thus east of the Philippines). Lydekker's Line corresponds with the western edge of the Sahul Continental shelf and thus forms the eastern counterpart of Huxley's Line.

The many islands and seas in between Sunda and Sahul have been given the name Wallacea, a name first applied by Dickerson in 1928 for the island region in between the Sunda and Sahul shelves, including the Philippines. As discussed by Simpson (1977), too many zoogeographic boundaries have been drawn, because most researchers have based their ideas not on the whole fauna but put most weight on limited groups, such as birds, landsnails, mammals, or bats. The dispersal ability or the potential to cross water barriers is not the same for every group of organisms, and can be different even amongst members of one group. By delineating absolute boundaries between the Oriental and Australian regions it seemed impossible to please all zoogeographers at the same time. Simpson therefore proposed to keep the Oriental Faunal Region bounded by the Sunda Shelf (Huxley's Line) and the Australian Region bounded by the Sahul Shelf (Lydekker's Line) and proposed to give up attempts to assign the intervening islands to any subregion or intermediate zone.

While Wallace, as a pioneer in zoogeography, had based his findings entirely on extant species distributions and didn't have the disposal of geological data, the situation has greatly changed nowadays. The plate tectonics theory and the increased geological and geophysical data from the SE Asian region have greatly improved our ideas on the formation of the present day configuration of islands and landmasses. Seen in this light there is much to say now in favour of delineating the continental shelf edges as the major boundaries of the Oriental and Australian regions. Though it seems that there is no real objection to designate the whole island region in between the Sunda and Sahul Shelves as a transitional zone, with influences from both neigh-

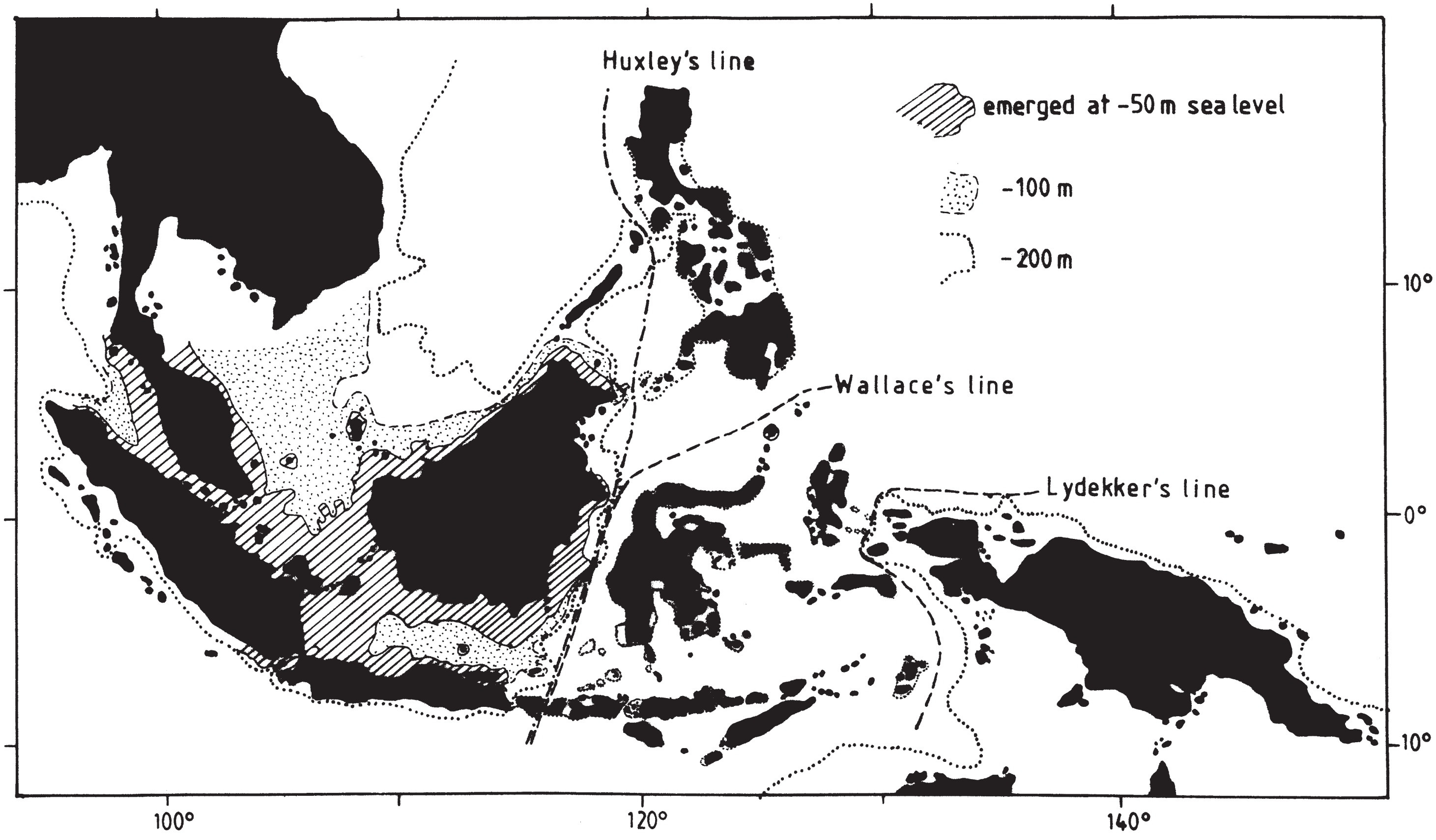


Fig. 1. Map showing the Sunda and Sahul landmasses in the west and east, respectively. These landmasses correspond with broadly uniform faunal regions, the Oriental and Australian faunal region, respectively. The transitional region between the zoogeographic boundaries known as Huxley's line in the west and Lydekker's line in the east is also referred to as Wallacea.

boring faunal regions and with local radiations and dispersals, it is true that the fauna on each island, with its particular composition, affinity, history, and ecology should be studied on its own. The latter standpoint will be the starting principle in this thesis. As a matter of convenience, the term 'Wallacea' will be used sometimes to refer to the island area in between Huxley's and Lydekker's Line, thus including the Philippine realm.

The first known fossil faunas: Java

Before the Second World War practically nothing was known concerning the prehistoric faunas from the Wallacean islands. On Java however, fossil mammals of Pleistocene age had been known since the middle of the nineteenth century (Theunissen et al., 1990). Amongst others the Javanese painter and naturalist Raden Saleh (1867) described fossils he had collected at two localities in east Java. Dubois started the first systematic excavations on Java in 1890 after having worked in west Sumatra since 1888, collecting fossil mammals from several caves in the Padang Highlands (Theunissen, 1989; Storm, 1995). In Java he started collecting near Kedung Brubus and Trinil. Soon afterwards he discovered the famous remains of *Pithecanthropus erectus* (now *Homo erectus*) in 1891-92 at the latter locality. In 1895 Dubois returned to The Netherlands, while the excavations were continued until 1900 by his assistants. No more remains of *Pithecanthropus* were reported, but many vertebrate fossils were collected, which were sent to Leiden, where they were stored in the National Museum of Natural History (Coll. Dubois). Most of the fossil material had to await detailed studies for over 50 years, until Dirk Albert Hooijer, curator of the Dubois Collection, started to work on it.

Between 1906 and 1908 more systematic work was carried out at Trinil during the Selenka expedition. In the late 1920s and 1930s the geological work on Java got a great impulse through the exploration for oil and mineral resources under the responsibility of the Dutch East Indies Geological Survey. One of the tasks was the geological mapping of Java. The Dutch mining engineer L.J.C. van Es, who had become interested in the *Pithecanthropus* findings of Dubois, published in 1931 his thesis entitled 'The age of *Pithecanthropus*', concluding that still many questions concerning the geology and age of the fossil vertebrates remained unanswered. At that time the Geological Survey of the Dutch East Indies had started systematic excavations at many known and new fossil vertebrate-bearing sites, and van Es concluded that they all had to be considered of Pleistocene age, except some younger fossil remains collected at the banks of the Tjitarum River in West Java.

The Dutch geologist W.F.F. Oppenoorth in 1932 described hominid remains excavated along the Solo River near the village Ngandong. The hominid remains, 11 fragmented skulls designated as *Homo soloensis*, originated from a terrace along the NS transect where the Solo River cuts trough the EW trending Kendeng Hills. They were found associated with over 20000 fossil vertebrate remains, and Oppenoorth indicated that a comparison of these fossils with those from other localities might provide better insight in the Javanese faunas of the Pleistocene. In 1930 G.H.R. von Koenigswald was contracted on the post of vertebrate palaeontologist at the Dutch East Indies Geological Survey, in order to carry out the task of erecting a subdivision of the Pleistocene vertebrate faunas of Java. In a series of papers (von Koenigswald, 1933, 1934, 1935a,c,d) he set forth his ideas concerning the biostratigraphy of Java, for a large part based on guide fossils. He distinguished from old to recent 8 terrestrial faunas: Tji Sande, Tji Djulang, Kali Glagah, Jetis, Trinil, Ngandong, Sampung, and Recent. The oldest Tji Sande Fauna, which was based on only one rhinoceros molar, was considered as Late Miocene.

Much later, von Koenigswald's biostratigraphical scheme would appear to be incorrect. It appeared that fossils from different localities had been lumped in single faunal units. Also the use of guide fossils by von Koenigswald to define his biozonation scheme, as was common practice in those days, appeared to be of little use because these guidefossils often represented isolated findings of very rare species (de Vos et al., 1982; Braches & Shutler, 1982). After ascertaining that the origin of the fossil material of the Dubois Collection was reliable (de Vos & Sondaar, 1982), during the 1980s a new biostratigraphic scheme was established for Java to replace the classical biozonation of von Koenigswald. This new scheme was based on the fossil contents of single localities (de Vos et al., 1982; Sondaar, 1984) and litho- and chronostratigraphical work that had been carried out between 1976 and 1979 by a joint Indonesian-Japanese project (Watanabe & Kadar, 1985; Aimi & Aziz, 1985). Leinders et al. (1985) combined both results and attached absolute ages to the successive faunas. More work has since been carried out by other workers in the area (amongst others: Sémah et al., 1986; Hyodo et al., 1993; van den Bergh et al., 1996). For Java the faunal succession throughout the Quaternary is roughly known now and the new standard biostratigraphical scheme of Java of Sondaar (1984) will serve as a basis for comparison with the other islands. It must be stated however, that much details of the faunal succession and dating remain to be resolved. Some new data concerning the biostratigraphy of Java will be dealt with in the second part of this thesis.

The fossil vertebrates from Sulawesi (Celebes)

While fossils from Java had been known already for a long time, it was not until 1947 that the first fossil vertebrates were discovered in Wallacea, viz. in southwest Sulawesi. The fossils were collected by van Heekeren, who was employed by the Archaeological Service in Indonesia. He found the fossils in what he recognized as a number of terraces along the eastern side of the Walanae Valley near the village of Beru. Besides vertebrate fossils these deposits also seemed to yield primitive artefacts, which were to become known as the Cabenge (old spelling: Tjabenge) Industry (van Heekeren, 1957a, 1958). The fossils, and successively collected fossil material from other localities in the same area (Sompoh, Celeko), were sent to Leiden and described by Hooijer in a series of publications entitled 'Pleistocene vertebrates from Celebes' (Hooijer, 1948a-c, 1949, 1953a-c, 1954a-c,e, 1964a, 1969b). The fauna appeared to be a mixture of marine and terrestrial vertebrates. The terrestrial elements were represented both by still extant endemics and by species totally unrelated to the modern Sulawesi fauna, but all clearly of Asiatic origin.

In 1950 van Heekeren was forced to leave the area because of political instability, and it was not until 1970 when van Heekeren, now together with Hooijer, could visit the area again. New fossil findings from the already known and some newly discovered localities, like Calio, Marale and Ciangkange were reported subsequently (Hooijer, 1972b).

Amongst the fossil material described by Hooijer were remains of a pygmy elephant, *Archidiskodon celebensis* Hooijer, a pygmy stegodont *Stegodon sompoensis* Hooijer, a giant tortoise, *Geochelone atlas* Falconer & Cautley, and the most abundant of all, a now extinct suid, *Celebochoerus heekereni* Hooijer. Besides these extinct species, Hooijer reported on a number of fossils from still extant mammals from the same area, namely *Anoa depressicornis* Hamilton Smith and *Sus celebensis* Müller & Schlegel, *Crocodylus* sp., and some marine vertebrates: sharks and stingrays. In 1972 also a large *Stegodon* cf. *trigonocephalus* was added to this assemblage. Hooijer stated that it might have co-occurred with both pygmy elephantoids known from the area.

The whole assemblage of fossil species from several localities and different stratigraphic levels was to become known as the *Archidiskodon-Celebochoerus* Fauna. In 1948 Hooijer already had suggested that there were at least two geological horizons based on an examination of matrix adhering to some of the fossils. In 1975 Hooijer again declared that there was no proof that all species inhabited southwest Sulawesi at the same time, but the fossil species from the Cabenge area are sometimes still considered as a single faunal unit (e.g. Whitten et al., 1988).

Musser (1987) ends his paper on the mammalian fauna of Sulawesi with stating that still many questions remain concerning the fossil fauna in South Sulawesi. He puts forward the hypothesis that the Pliocene (or Early Pleistocene) elephantoids and *Celebochoerus* were part of an island fauna, unbalanced, free of major predators, and unrelated to the real Sulawesi fauna (that is the extant endemic fauna of Sulawesi); and further that the anoa (the extant endemic dwarf buffalo of Sulawesi, placed by him in the genus *Bubalus*) and *Sus celebensis* are from much later sediments and lived at a later time. He calls to the necessity of careful fossil collecting under tight stratigraphical control in Sulawesi and other regions of the island, which only can provide the information to either support or falsify this hypothesis (Musser, 1987).

The Lesser Sunda Islands: fossil vertebrates from Flores, Timor and Sumba

On the island Flores fossil stegodont remains were first discovered in 1956 at a place called Ola Bula. Theodor Verhoeven, a Dutch priest stationed at the Roman Catholic Seminary of Mataloko immediately understood the importance of these findings, and took care that they were sent to the NNM at Leiden. Hooijer (1957a) examined the collected material and attributed it to *Stegodon trigonocephalus florensis* Hooijer, a new subspecies of the then wellknown *S. t. trigonocephalus* Martin from Java. The Flores subspecies was characterized by a slightly smaller size and a higher degree of hypsodonty. Throughout the years more fossil material was found in the same region, amongst it a pair of dP_3's of very small size, which were attributed to a real dwarf stegodont, about half the size of *S. trigonocephalus* (Hooijer, 1964c). In 1964 Verhoeven made a fieldtrip to the island of Timor, and also there he found pygmy stegodont material, which was named *Stegodon timorensis* by Sartono (1969). In 1979 Sartono announced the occurrence of a *Stegodon* on Sumba and as also elephantoid remains had been found on Sulawesi earlier, it gradually became clear that elephantoids had been able to colonize various islands from the Indonesian Archipelago, like they had also been able to colonize the Mediterranean islands in the past.

In 1970 Hooijer himself visited Timor, Flores and Sulawesi and collected more elephantoid fossils from these islands. However, the two dP_3 described in 1964 remained the only dwarf stegodont specimens from Flores (Hooijer, 1972a). The insular faunas from the Lesser Sunda Islands appeared very poor in species, and apart of stegodonts only remains of endemic rodents, tortoises and a varanid were amongst the Pleistocene fossils encountered there (Hooijer, 1957b, 1972c; Musser, 1981; Brongersma, 1958; Sondaar, 1987). However, from Flores also primitive looking stone tools were reported from the same layers that had yielded *Stegodon trigonocephalus florensis*, and it was speculated that Solo Man might have reached Flores during the Middle or Late Pleistocene (Maringer & Verhoeven, 1970).

Overseas dispersal or land connections?

Until short after the 1970 expedition to Flores, Timor and South Sulawesi in which Hooijer participated, he held the opinion that the SW Sulawesi faunal elements evolved locally on Sulawesi in geographic isolation from the surrounding islands. In 1971 Hooijer described giant tortoise material collected on Timor and he concluded that the Timor and Sulawesi tortoises belonged to the same species, *Geochelone atlas*, also known from the Indian subcontinent. The spreading of this species beyond Wallace's Line was thought to have been the result of overseas dispersal (Hooijer, 1971). Subsequently, he presented the description of a complete M_3 of a pygmy stegodont from the locality Calio (old spelling: Tjalio) in South Sulawesi (Hooijer, 1972b: 7-9). Though this molar resembled the M_3 of *Stegodon timorensis* from Timor, he preferred to attribute it to *Stegodon sompoensis*, reasoning that it was highly probable that the Sulawesi and Timor pygmy stegodonts both evolved in geographic isolation and that the similarity should be explained as due to parallel evolution.

In a following paper co-authored by the geologist Audley-Charles, former land-connections between Flores, Timor and Sulawesi were postulated, based on geological data (Audley-Charles & Hooijer, 1973). These landconnections would have disappeared subsequently as the result of tectonic movements in the area during the Middle to Late Pleistocene. The postulated landmass connecting these three islands was given the name "Stegoland" (Hooijer, 1975), and at that point Hooijer seems to have abandoned the idea that the pygmy stegodonts evolved independently on the various islands, and he designates them with the name first used for the Sulawesi dwarf, *Stegodon sompoensis*. The concept of "Stegoland" was criticized by Simpson (1977) and Sondaar (1981), arguing that the recent and fossil faunas of Sulawesi, Flores and Timor are very different and that small and large stegodonts have also been encountered in far-off Mindanao. Others (e.g. Azzeroli, 1996) have accepted the former existence of landconnections.

Faunal analysis — Grooves (1976) was the first to make a detailed analysis of the mammalian faunas of Sulawesi, both extant and fossil. He concluded that the ancestors of these faunas originated predominantly from Asia and Sundaland and argued that most of the ancestral species had reached Sulawesi at some period in the Late Tertiary owing to a narrowing of the Makassar Strait or perhaps even a brief landbridge between Java and Sulawesi, and became isolated and evolved along different pathways compared to the mainland faunal elements (vicariance). The isolation resulted in highly endemic Pleistocene and Recent faunas. Faunal links with the Philippines were discarded in the same paper.

More recently, the Earl of Cranbrook (1981), has given a detailed analysis of not only the mammalian distribution, but also of freshwater fishes, amphibians, reptiles, and birds. Based hereupon, he concluded that the evidence of all vertebrate groups present in the Sulawesi fauna strongly suggests that since its (most) recent emergence there has been no direct, unbroken subaerial connection between Sulawesi and the principal landmasses of the Sunda shelf. Nevertheless, in the Sulawesi fauna species of Asiatic origin greatly outnumber those of Australian affinity in all the groups studied, suggesting that immigration from the east has been less easy than from the west. The closeness with which the Sulawesi fauna is related to the Sundaic (Oriental) one varies with the dispersive abilities of the different taxonomic groups, and especially for freshwater fish the Makassar Strait appears to have been an insurmountable barrier.

Musser (1987) basically agrees with the conclusions of Cranbrook (1981) and put forth the hypothesis that the Pliocene or Early Pleistocene fauna lived on a separate island, free of major predators and unrelated to the extant fauna of Sulawesi.

Swimming elephants — Those who adhere to the land-bridge concept in order to explain the presence of terrestrial mammals on Sulawesi and other Wallacean islands often seem to base their ideas on the erroneous assumption that elephants can not swim very well. Considering extant elephants, its has been shown that in fact these animals are excellent swimmers, and are inclined to swim short distances in search for food. Besides they have the potential to survive for longer periods in water (e.g. Sondaar, 1977, Johnson, 1978). Under extreme circumstances they are capable of swimming 48 km and surviving three days in the water (Johnson, 1978). Stegodonts were probably equally well adapted for swimming, and there is no reason to believe that they couldn't have reached Sulawesi overseas. Fifty kilometers corresponds with the distance that would have to be crossed between the eastern edge of the Sunda Shelf and the west coast of Sulawesi at times of low sea level (Mammerickx et al., 1976). An important factor is also the fact that elephants live in herds and have also been observed swimming in herds (Johnson, 1978). Carnivores on the other hand are usually not fond of entering water and even if they do, like tigers, they lead a solitary life, which diminishes greatly their potential to establish a population on offshore islands. In addition, large mammalian carnivores need a large territorial area and many islands are therefore too small to carry a healthy population of carnivorous mammals.

Other vertebrates that are very frequently present in island faunas, extinct and extant, are giant tortoises. Giant tortoises are said to be able to float and survive long periods in sea-water, and the giant tortoises could have drifted to the various oceanic islands where they once occurred and still occur (Sondaar, 1981).

The hypothesis of landconnections facilitating overland dispersal of some terrestrial vertebrate groups has been largely abandoned now for the islands east of the Sunda shelf. Indeed, with such an assumption it would be difficult to explain why other fossil and extant genera than the 'good swimmers' are not shared between these islands. The extant vertebrate fauna of Java can illustrate such a situation that would be expected in case of landconnections with the Asian mainland: though Java is an island now, it bears a fauna with a clear mainland stamp reminiscent of the time when Java was connected with SE Asia during the last glaciation. The same can also be said of the early Middle Pleistocene Kedung Brubus Fauna and the Late Pleistocene Punung Fauna from Java, which constitute balanced faunas including a wide range of herbivore and carnivore taxa closely related to faunal elements from the Siwaliks, Birma and China (Sondaar, 1984; de Vos, 1995). Theoretically Sulawesi, with an overall size larger than Java and with a wide range of different habitats, should therefore be able to sustain a balanced and complete mammalian fauna if it were connected with the mainland once. This is not the case, however. For example large mammalian carnivores are fully absent on Sulawesi and the niche of large predators is filled by reptiles only (Cranbrook, 1981).

The earliest human occupation of Sulawesi

As mentioned briefly before, van Heekeren had also found stone implements in what he called 'terraces' in the same area near Beru (East of Cabenge) in South Sulawesi where also the vertebrate fossils originated from. Although reportedly all fossils and artefacts were surface-finds, he considered it highly probable that they were of the same age (van Heekeren, 1958), a view to which he remained inclined until after the 1970 expedition (van Heekeren, 1972). Van Heekeren distinguished seven terraces, the lowest two corresponding with the banks of the Walanae River. The third and fourth from the bottom corresponding with the 50 and 75 m contours east of the Walanae River in the surroundings of Beru, were said to be fossiliferous. Most stone artefacts were said to be collected from the 50 m terrace.

Bartstra (1977) assumed a different age for the artefacts and fossils contrary to the beliefs of van Heekeren. He postulated the presence of at most four terraces, instead of the seven originally distinguished by van Heekeren, though he gave no detailed information on the local stratigraphy. He considered the fossil fauna as Late Pliocene or Early Pleistocene, whereas the terraces, in which, according to him, both artefacts and reworked vertebrate fossils occur, were considered Late Pleistocene in age. He stated that the vertebrate remains occur in situ in the top-sediment of the bedrock of the region, which around Beru consists of partly consolidated sandstones and conglomerates. He explained the association of artefacts and vertebrate fossils as being due to the fact that the Walanae River had cut the bedrock so that fossils were reworked into the terrace fills. This view is maintained in the later publications of Bartstra et al. (1991, 1992, 1994).

Sartono (1979b) was the first to try to clarify the lithostratigraphy of the fossil-bearing deposits in more detail. He estimated a Late Pliocene age for the vertebrate fossils, based on foraminifera samples taken from marine layers underlying or interfingering with the vertebrate-bearing strata, whereas the terraces with artefacts were considered Late Pleistocene. Sartono (1979b) gave some accounts on the sedimentary sequence and presented a schematic stratigraphic scheme, however without indications from which levels his foraminifera samples and fossil vertebrates were derived precisely. Further, there were no indications given on which grounds the fossil-bearing conglomerates were distinct from the terrace gravels associated with artefacts.

One of the problems that remains with the terraces mentioned by van Heekeren, Bartstra and Sartono, is that it is not clear what is exactly meant with it. Distribution maps are not given, but it seems that the two main terraces seem to correspond with the 50 and 75 contour levels. In the most recent paper on this subject Bartstra et al. (1994: 4) speak of: 'scattered remnants of riverterrace gravel, all Pleistocene in age, and overlying the Beru Member of the Walanae Formation on the west-facing slope of the first [= Sengkang] Anticline. This gravel is implementiferous, (Palaeolithic Cabenge Industry ....), and is mainly found between the localities of Beru and Lakibong.'

Here the suggestion is made that the artefacts occur in situ in the gravels remnants which they designate as riverterraces. But, as Bartstra et al. (1991: 320) commented earlier: 'It must be emphasized that the excavations of 1970 did not provide any conclusive evidence that stone artifacts occur in situ in the high terrace gravels or finer clastics. Their distribution was not uniform, the finds appearing to be concentrated on the surface of the high westward-protruding edges of the 75-m and 50-m levels. It looked as if people occupied and manufactured their implements on terrace treads already in existence, and this general impression has not basically changed as a result of reconnaissance trips and the digging of new test pits (albeit small ones) in the Beru area in 1978 and thereafter.'

The latter remarks seem to be in contradiction with the suggestion that the terrace gravels contain stone implements in situ. Our own examinations of the excavations of van Heekeren in the area, have not yielded any in situ stone-artefacts either, though artefacts (mostly flakes as also reported by van Heekeren, 1958) can indeed be picked up from the surface at places where coarse gravels and conglomerates are exposed. This has been confirmed by Mr M. Anwar Akib, curator of the Museum of Prehistory at Calio (MPC) and caretaker of the Prehistorical Reservation near Beru. He knows the area as his own pockets and guided us in the area during our fieldwork.

As will be shown in this thesis, one of the major problems in recognizing terraces in the Beru area is that the layers of the Walanae Formation, including conglomeratic layers from the uppermost interval, have a horizontal orientation in the Beru area, and are separated from the west-dipping layers of the Sengkang Anticline to the East by a fault. This has not been taken into account by earlier workers and if no distinction can be made on other criteria than elevation alone, it would thus be extremely difficult to separate remnants of former alluvial plains from the fluvial conglomeratic layers of the Walanae Formation. Sometimes the amount of consolidation is mentioned as a criterion (Bartstra et al., 1991), but as will be shown later, this also does not seem to be unambiguous. In this thesis such other criteria, like gravel composition, clast diameter etc. have been studied, in an attempt to distinguish between coarse clastic terrace fills, if present, and conglomerates of the Walanae Formation.

Homo erectus on Flores?

In Sulawesi evidence for an Early or Middle Pleistocene human occupation is inconclusive at most. Flores is another island east of Wallace's Line, where claims have been made that that island was inhabited by Middle or Late Pleistocene humans. In 1970 Maringer and Verhoeven reported the discovery of primitive looking stone artefacts in association with remains of *Stegodon* at the localities Mata Menge and Boa Leza on Flores. Based on the association with *Stegodon*, identified as a subspecies of *S. trigonocephalus* from Java by Hooijer (1957a, 1972a), these artefacts, described as a number of pebble tools and retouched flakes mostly made of volcanic rock, were thought to be Middle or Late Pleistocene in age. It was speculated that Solo Man might have reached the Lesser Sunda Islands. However, the evidence presented by these authors is generally considered as inconclusive and it has been argued that it is not known when *Stegodon* became extinct (Bellwood, 1985; Allen, 1991). New geological investigations were seemingly required to ascertain the age of the artefact-bearing layers, something that the present thesis tries to meet with.

Conclusion and aim of this thesis

As depicted in the above paragraphs, still many questions remain to be solved concerning the detailed study of the stratigraphy, sedimentology and taphonomy of the terrestrial vertebrate- and artefact-bearing strata of South Sulawesi. Neither detailed stratigraphic sections nor small-scale geological maps of the area have been presented for the Beru area in South Sulawesi by earlier workers. Generally, fossil localities are indicated with the name of the nearest geographic feature while no, or only limited, stratigraphical information is given. In Flores the local stratigraphy of the fossil-bearing layers was unraveled to some extent by Hartono (1961), but detailed sections were not given.

It has been argued (Roth, 1992) that the study of island vertebrates can contribute greatly to develop evolutionary models not only for island mammals, but for evolutionary processes in a more general way. Islands have allowed natural evolution experiments in which the number of variables was limited because of the relatively simple nature of island ecosystems.

On most islands with fossil vertebrates, however, stratigraphic control and dating are inaccurate, and many fossil remains have been derived from scattered cave deposits with a complicated stratigraphy, which hampers their arrangement into a time-sequential order. In Sulawesi the fossil-bearing sequence is over 100 m thick, and has been shown to be very rich in vertebrate fossils. The area in Flores that yielded abundant vertebrate remains has a relatively simple geological structure. Therefore, the islands Sulawesi and Flores present good opportunities to study evolutionary changes of large vertebrates in an island environment through time.

Another topic to be dealt with in this thesis is the interaction between humans and their environment. Van Heekeren was once convinced that *Homo erectus* had lived on Sulawesi. The idea that humans once lived in Sulawesi during the Middle or Early Pleistocene is now generally abandoned (e.g. Bartstra, 1992; Keates & Bartstra, 1994; Allen, 1991), but recent evidence from the island Flores (Aziz, 1993; Sondaar et al., 1994; van den Bergh et al., 1996) proves that that island was occupied by humans relatively early at the beginning of the Middle Pleistocene. As will be shown in the next chapters, on both South Sulawesi and Flores a similar fauna turn-over pattern can be observed. On both islands there is an older insular fauna with a giant tortoise and one or two pygmy elephantoids, and a younger insular fauna with medium to large-sized elephantoids and no tortoises nor true pygmy elephantoids. It has been argued that the arrival of early hominids (presumably *Homo erectus*) on Flores led to the extinction of the tortoise and pygmy *Stegodon* there (Sondaar, 1987). The similar fauna turn-over pattern observed on both island throws new light on this matter.

The purpose of this study is to construct a litho-, bio- and chronostratigrapic scheme of the Pliocene-Pleistocene fossil vertebrate-bearing deposits of Sulawesi and Flores. These data can then be compared with the faunal succession of nearby Java, which is the best studied faunal succession in the region. The second chapter will deal with Java, where some new data can be added to the existing biostratigraphic scheme.

Stratigraphical, sedimentological and petrographical studies were used to construct lithostratigraphic correlations in the Sengkang Basin in South Sulawesi (chapter 3) and the Soa Basin in Flores (chapter 5). Using micropalaeontological, palaeomagnetic and ESR dating methods in combination with vertebrate palaeontological data, an attempt was made to obtain ages for the various lithostratigraphic units. Based on these age assessments of the various vertebrate-bearing units in Sulawesi and Flores, and combining them with the roughly dated faunal succession of Java and of the SE Asian mainland, a reconstruction of the regional palaeozoogeography is discussed in chapter 7. For Sulawesi also the identification problems concerning the terrace stratigraphy will get ample attention (chapter 3).

Palaeontology

The palaeontological chapters of this thesis (Sulawesi: chapter 4; Flores: chapter 6) will focus on the fossil elephantoids. This restriction had to be made because of the large quantities of collected fossil material, too large to treat it all in a thorough way. Because of their high potential to reach islands by means of overseas dispersal, elephantoids are found on many islands in the Wallacean region and form an excellent opportunity to study evolutionary trends under isolated conditions. A new species of pygmy *Stegodon* from Flores will be described in chapter 6. Besides the macromorphological aspects also dental enamel microstructure will be treated. Comparison with other stegodont species appeared to justify the erection of a new species: *Stegodon sondaari* sp. nov.

The palaeontology of the collected non-elephantoid fossil material will be discussed in a more general way when dealing with the faunal successions of both islands (Sulawesi: chapter 3; Flores: chapter 5). Taphonomic aspects of the fossil sites will be treated. In addition, some new data concerning the fossil elephantoids of Java will be presented. Important fossils of old and new collections from Java that have not properly been described yet, will be treated, and they will be placed within the existing biostratigraphical framework. For Java the succession of fossil elephantoids appears more complicated than was thought so far.

The remaining part of this introductionary chapter gives a short explanation of the taxonomic classification of the Proboscidea, the fieldmethods followed, and the measuring procedures on fossil material used. After that a refinement of the Javanese biostratigraphy and a description of some new elephantoid fossils from Java will be presented (chapter 2). Chapters 3 & 4 deal with the results obtained in Sulawesi. Chapter 3 starts with a short historical overview concerning the palaeontological research in South Sulawesi. Then the geology and stratigraphy is discussed, followed by an account on the faunal succession and the taphonomy of the most important sites. A systematic description of the fossil elephantoid material from Sulawesi is given in chapter 4. The same order is kept in the next chapters 5 & 6, dealing with the data obtained in Flores. The thesis is concluded with an account on the regional palaeozoogeography and on dispersals of elephantoids in the Indonesian Archipelago during the Plio-Pleistocene (chapter 7). Also some palaeobiological aspects such as estimated body weight and age profiles of fossil elephantoid assemblages will be discussed (chapter 8).

Systematics of the Proboscidea

An important element of most Indonesian fossil terrestrial vertebrate faunas is the Elephantoid *Stegodon*. Members of this genus were widespread throughout Asia during the Plio-Pleistocene and appear to have been excellent island colonizers. Stegodonts are recorded as far East as the Philippines and various Wallacean islands in the Indonesian Archipelago (Sulawesi, Sangihe, Flores, Sumba, and Timor), as well as the main Japanese islands. They were confined to regions with tropical, subtropical or warm temperate climates. In Africa rare *Stegodon* molar remains are recorded from Lower Pliocene sediments in the Afar region, East Africa, and from sediments in Uganda of at most Early Pleistocene age (Cooke & Coryndon, 1979; Kalb & Mebrate, 1993). In the Levant various Pleistocene sites have yielded stegodont remains (Hooijer, 1960, 1961; Tchernov et al., 1994), but stegodonts never seem to have reached Europe nor were they able to penetrate into the New World. The phyletic position of the stegodonts is still a matter of debate.

True elephants, including the genera *Mammuthus*, *Loxodonta* and *Elephas*, originated in Africa during the Late Pliocene. They were more adaptable to various climates and environments and reached a much wider distribution than the stegodonts. During the Pleistocene elephants reached various islands in the Indonesian realm, namely Java, Sumatra, Borneo, and Sulawesi. Only for reaching the latter island the crossing of a sea-barrier was required however.

History

Originally, stegodonts were regarded as intermediate between mastodonts (sensu lato: in early times including both Mammutidae and Gomphotheriidae) and elephants and this view was basically maintained until fossil remains from Africa became better known (Falconer, 1857; Weithofer, 1888; Gaudry, 1888; Soergel, 1912; Simpson, 1945). Schlesinger (1917) founded the genus *Stegolophodon* on *Mastodon latidens* Clift (1828), from the Lower Pleistocene of Burma. Initially, Osborn (1918) included both *Stegolophodon* and *Stegodon* in the Elephantidae, sticking to an ancestry of the latter for the elephants, but two decades later (Osborn, 1936, 1942), when it became clear that *Stegodon* was too evolved to be the ancestor of the elephants, he transferred *Stegolophodon* to the Mastodontidae and placed *Stegodon* in its own family, the Stegodontidae. Though *Stegolophodon* was not known from Africa at that time, he proposed an African origin for the Elephantidae from an early *Stegolophodon*, the latter genus which was also thought to hold the ancestor of the Stegodontidae. Around that time the first *Stegodon* fossils from Africa became known from the Kaiso Series in Uganda (Hopwood, 1939). This led Arambourg (1942) to suggest that *Stegodon* could be the ancestor of *Loxodonta*, whereas an Asiatic origin was suggested for *Elephas*. In the following years also supposed *Stegolophodon* remains were described from Africa (Singer & Hooijer, 1958; Hooijer, 1963), which strengthened the idea that *Stegolophodon* was ancestral to the elephants. However, the fragmentary evidence turned out to be unconvincing and some of these remains have subsequently been attributed to *Mammuthus subplanifrons*, others to *Primelephas* (Aguirre, 1969; Maglio & Hendey, 1970), a then newly discovered primitive elephant, which is until now considered as ancestral to the elephants (Maglio, 1970, 1973). Nowadays, it is commonly agreed upon that there is no evidence for the occurrence of *Stegolophodon* in Africa, though a poorly known stegodont, referred to as *Stegodon kaisensis*, happens to be rare in Lower Pliocene to at most Lower Pleistocene deposits in Ethiopia and Uganda. A molar fragment from Tchad, referred to as *Stegodon korotorensis* sp. nov. by Coppens (1965) is included into *Primelephas* by Maglio (1970). The latter genus is also known from the same beds in Ethiopia, which yielded cf. *Stegodon kaisensis* remains (Kalb & Mebrate, 1993).

Based on the findings of certain primitive elephants from Africa, *Stegotetrabelodon* and the already mentioned *Primelephas*, both possessing a molar morphology intermediate between those of the longirostrine tetralophodont gomphotheres and the true elephants, it was Maglio (1970, 1973) who proposed to remove the Stegodontidae (including the genera *Stegolophodon* and *Stegodon*) from the ancestry of the elephants. Maglio & Henday (1970) considered the Stegodontidae as an offshoot from the Mammutidae instead. The genus *Stegodibelodon* Coppens 1972 from Central Africa, still characterized by an elongated mandibular symphysis but lacking lower incisors, was added to the group of primitive elephants, but the exclusion of the stegodonts from the elephantids was followed by most authors in the following years (Tobien, 1975, 1976; Coppens et al., 1978), until cladistics had their entry in the phylogenetic research. Based on cladistic analysis Tassy (1982, 1983) questioned the classification of stegodonts and zygodont mastodonts together in the suborder Mammutoidea, and stated that the family Elephantidae should include gomphotheres (bunodont mastodonts) and stegodonts. Saegusa (1987), who studied the cranial characters of various *Stegodon* species, distinguished 3 monophyletic groups within the stegodonts, all with defining characters not shared with the elephants. However, he stated that the Stegodontinae as a whole may be a sister group of the Elephantidae because some derived characters are shared by both groups. At the present state of knowledge it now seems that the stegodontidae were not derived from the Mammutidae but from the tetralophodont gomphotheres, like the Elephantidae (Tassy, 1988; Tassy & Shosani, 1988). However, the precise differentiation and the position of early stegodontids relative to early elephantids remains still unresolved (Tassy & Darlu, 1986, 1987; Tassy & Shosani, 1988; Kalb & Froehlich, 1995; Shoshani, 1996). Tassy (1994, 1996) and Saegusa (1996) retain *Stegolophodon* and *Stegodon* as a monophyletic group, the Stegodontidae. Of particular importance is the recently described Early Miocene *Stegolophodon nasaiensis* from northern Thailand, considered to be the most primitive *Stegolophodon* known to date (Tassy et al., 1992). *S. nasaiensis* presumably shares the presence of lower tusks with a piriform or oval to round cross section with the gomphotheres and Late Miocene elephants such as *Stegotetrabelodon* (however, as noted by Tassy et al., 1992, the possibility remains that the isolated lower tusks, found in association with *Stegolophodon* molar fragments at the locality Mae Teep, belong to an other species).

Kalb & Mebrate (1993), Kalb & Froelich (1995) and Kalb et al. (1996) believe that

Stegolophodon and *Stegodon* are part of a paraphyletic series, informally called "stegomorphs", which in addition include the genera *Stegotetrabelodon* and *Stegodibelodon*. In their opinion *Stegolophodon* is the sister taxon of all other elephantids, whereas *Stegodon* is considered as the sister group of the elephantines.

An alternative view has been advocated by Taruno (1985) and Kamiya & Taruno (1986). *Stegolophodon* is treated by them as a member of the family Gomphotheriidae, whereas *Stegodon* is retained within the family Stegodontidae, together with the Miocene genus *Eostegodon* Yabe, 1950, exclusively known from Japan. The latter genus is considered as intermediate in molar structure between bunodont gomphotheres (*Stegolophodon*) and the lophodont stegodonts. This intermediate position of *Eostegodon* seems to be confirmed by a recent study of occlusal motion in various elephantoids, based on striae patterns on the enamel of occlusal wear surfaces (Saegusa, 1996b). It was found that *Eostegodon pseudolatidens* and *E. tsudai* (included in *Stegolophodon* by Saegusa, 1996b) already had developed a palinal mode of mastication (characterized by a disto-mesial direction of jaw movement and horizontal shearing), similar as in the stegodonts and elephants. On the other hand, the pattern found in the more primitive *Stegolophodon nasaiensis* suggested that the plesiomorphic condition of lateral movement during the occlusal motion was still retained, though the results were still rather equivocal. Factors that hamper the assessment of the precise systematic position of the stegodonts and stegolophodonts are the lack of good adult skull material of both stegolophodonts and early elephantids from Africa, as well as the lack of large molar samples of single species, from a mammalian order that is widely known to possess comparatively the largest intraspecific variabilities in molar structure (e.g. Roth, 1992; Metz-Muller, 1995). Furthermore, *Stegolophodon* is a poorly defined genus including various species primarily based on isolated molars of which the stratigraphic position is poorly known (see Tassy, 1983 for an historic review of the genus).

Classification used

In the present thesis the stegodonts will be treated as a monophyletic group, the Stegodontidae (including the genera *Stegolophodon*, *Stegodon*). The Elephantidae include the subfamilies Stegotetrabelodontinae (including the genera *Stegotetrabelodon* and *Stegodibelodon*) and Elephantinae (including the genera *Primelephas*, *Loxodonta*, *Elephas,* and *Mammuthus*). The two families, Stegodontidae and Elephantidae are both believed to have been derived from longirostrine tetralophodont gomphotheres. The possibility that the earliest elephantines were derived from *Stegolophodon* is not fully excluded however.

The Sulawesi dwarf elephant, which was originally named *Archidiskodon celebensis* Hooijer 1949, has been subsequently placed in the genus *Elephas* (Maglio, 1973). It was believed to be closely related to *Elephas planifrons*. The skull morphology of *celebensis* differs markedly from that of *Elephas* and also its molar morphology shows some primitive traits, which makes its generic position uncertain. The possibility remains that its sister group should be sought in the primitive African genus *Primelephas* or in one of the Stegotetrabelodontinae. As no skull material is known of these taxa, the generic position of the Sulawesi dwarf will be preliminary indicated as *"Elephas" celebensis* in the present thesis.

Sinomastodon bumiajuensis (van der Maarel, 1932) from Java has bunodont molars, with trilophodont intermediates, and is further dibelodont and brevirostrine (Saegusa, 1995). The genus *Sinomastodon* was erected by Tobien et al. (1986) based on material from the Yüshe Basin, Shansi Province, Northern China. The combination of characters encountered in this genus is only shared with some South American genera, but seen in the light of the poor knowledge of this genus the taxonomic relationships are poorly understood. Tobien et al. (1986) included *Sinomastodon* amongst the Gomphotheriidae, a classification followed here.

Study methods

Sulawesi

In 1985 a project was started by Fachroel Aziz of the Geological Research and Development Center (GRDC) at Bandung, to place the fossils from southwest Sulawesi in a lithostratigraphic framework. From 1989 onwards the research continued as a collaboration between the GRDC, the National Museum of Natural History at Leiden (NNM; participants J. de Vos and R. van Zelst) and the Institute of Earth Sciences at Utrecht (IESU; participants P.Y. Sondaar and G.D. van den Bergh). The fieldwork was coordinated and carried out by G.D. van den Bergh and F. Aziz.

The study area lies between 4°05′S and 4°26′S and 119°55′E and 120°08′E on the eastern margin of the Walanae depression (Fig. 2). The most conspicuous structural feature in the study area is a north-south trending ridge, the Sengkang Anticline. The Sengkang Anticline and adjacent areas in South Sulawesi were mapped using aerial photographs (Bakosurtanal, Jakarta, false colour, scale 1:60 000, run SULSEL 122-113F (1982); Topographic Service of The Netherlands, black & white, scale 1:50 000, run 2CS-5MC118-2), followed by the recording of various stratigraphic sections and mapping in the field. The resulting geological maps are presented in Enclosures A and B. The fieldwork in Sulawesi during the years 1989, 1990, 1991, and 1993 revealed many new data on the litho-, bio- and chronostratigraphy of the area. The sedimentology of the fossil vertebrate-bearing sequence was studied in detail, and petrographic studies were carried out on thin sections of sandstone samples (pointcounts of 100 grains per sample) and by means of pebble counts in conglomerate outcrops and gravel deposits (200 pebbles larger than 1 cm were counted at each site).

Numerous new fossil vertebrate localities in the surroundings of van Heekeren's sites were discovered, apart from several new fossil localities at large distances from the original sites, some in different lithological and/or structural units. Vertebrate fossils were excavated in situ as much as possible in order to collect relatively large samples from single horizons. Two localities, one south of the Lakibong River and one near the village of Lonrong (Fossil Vertebrate Localities = FVL No. 5 and 24 respectively in Enclosures A and B), appeared to be particularly rich in vertebrate remains, providing important information about the faunal composition and about the variabilities of fossil species within geologically speaking short time intervals. The various fossil vertebrate localities were correlated with the measured sections, as far as the generally poor outcrop conditions allowed for. Some of the measured sections have been sampled for palaeomagnetic and micropalaeontological dating in order to provide accurate ages.

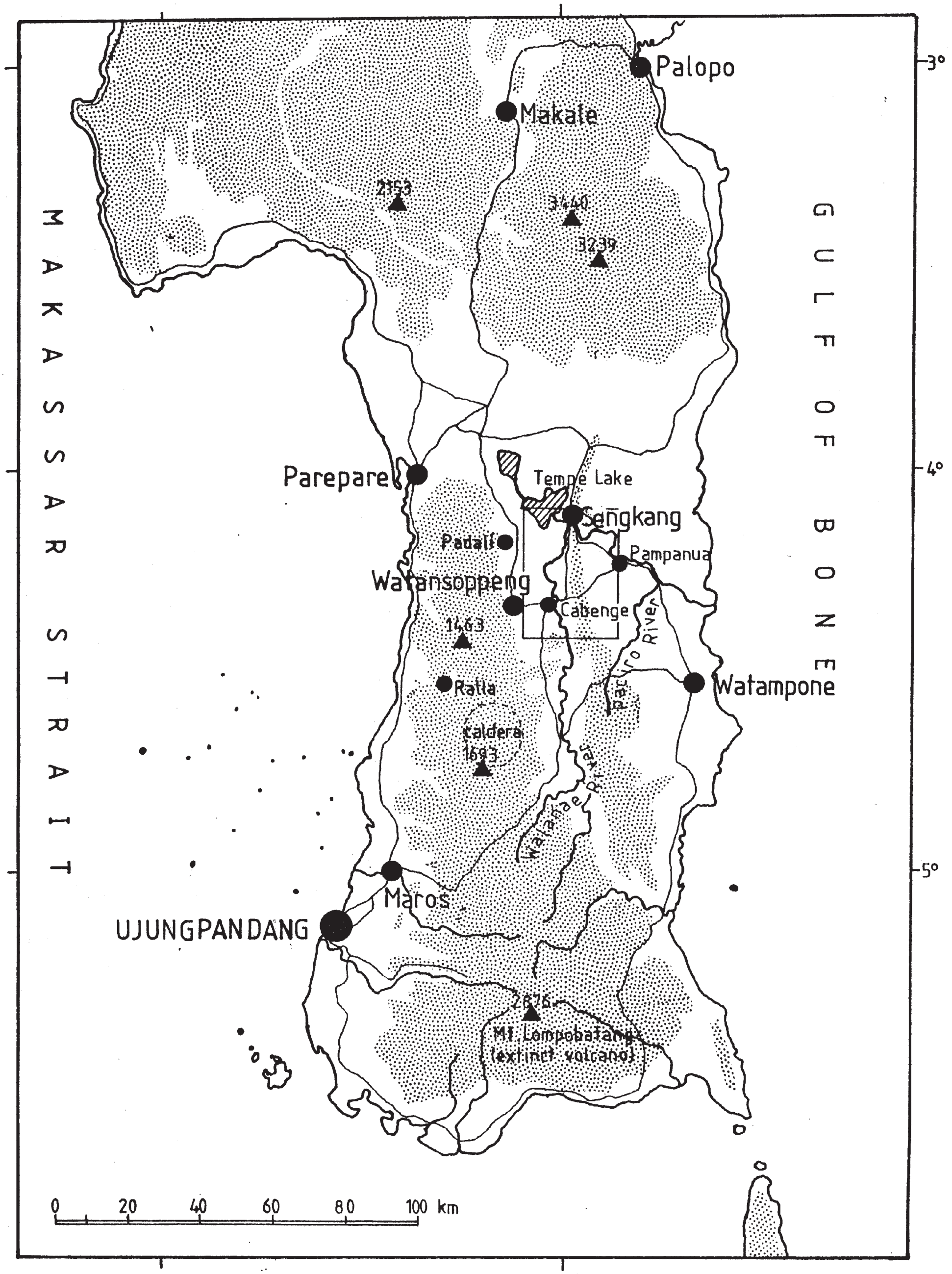


Fig. 2. Map of South Sulawesi showing the location of the study area. Stippled areas represent mountainous terrain, blank areas represent coastal lowlands and alluvial plains.

Flores

In 1991 the fieldwork program was extended to Flores. In November 1991 and 1992 and in April 1994 GRDC-NNM-IESU joint expeditions were organized to the Ola Bula area. The Flores study area (Fig. 3) falls administratively under the Ngada District, west Central Flores, and lies between 8°40′ and 8°45′S latitude and between 121°0′ and 121°15′E longitude. A preliminary geological map covering the study area, published by the GRDC in 1981 (Ruteng Quadrangle, scale 1:250 000), could be used, but of greater help was a topographic and geological map of the study area on a scale of 1:25 000, prepared by Hartono (1961). Black and white aerial photographs consulted at the GRDC only covered the southern margin of the study area. In Flores the aim was to 1) clarify the stratigraphic relationships amongst the various known sites, 2) check the earlier claims of Verhoeven concerning the in situ stone artefacts at Mata Menge and Boa Leza, 3) collect more fossil material, particularly of the dwarf stegodont, and 4) sample the various sections for palaeomagnetic dating. The previously mentioned sites were (re)discovered and some new fossil localities were found as well.

Excavation procedures

Due to time constraints the position and orientation of the excavated fossils were not recorded in detail in most sites, except for the archaeological site Mata Menge on Flores. After recoverage the fossils were put in a sample bag on which the date and location was written, and whether they were found on the surface or excavated in situ. Each excavator had his excavation area assigned with a letter code, which was also recorded on the bags. Excavated surfaces were photographed with the fossil remains still in place as much as possible. Large lumps of sediment were fragmented into small pieces, but the sediments were not sieved. Very small fossils might therefore have selectively escaped attention, though for example isolated teeth of *Varanus komodoensis* were recovered from the locality Tangi Talo in Flores using this excavation method.

Sediment samples were also taken for study in the laboratory. The fossils were further prepared, numbered and catalogued in the Quaternary Geology Laboratory (pertaining to the GRDC) in Bandung.

The locations of isolated fossils encountered on the surface or in situ were plotted on the map and recorded with data concerning the local stratigraphy, locality name, collecting conditions and date.

Terminology

For the nomenclature used in this thesis for molars of Stegodontidae and Elephantidae the reader is referred to Fig. 4A-C. The transverse lophs of stegodontid molars are wedge-shaped and are referred to as ridges, whereas the plate-like transverse lophs of elephantid molars are referred to as lamellae or plates. The shape of the valleys in between the molar ridges or lamellae has often been used to distinguish the Stegodontidae from the Elephantidae. Osborn (1942: 807) states that the bottom of the valleys in between adjacent lammellae are closed or V-shaped in what he considered as the superfamily Stegodontoidea, whereas they are open or U-shaped in the Elephantoidea. Later it appeared that the more primitive elephants like *E. planifrons* may

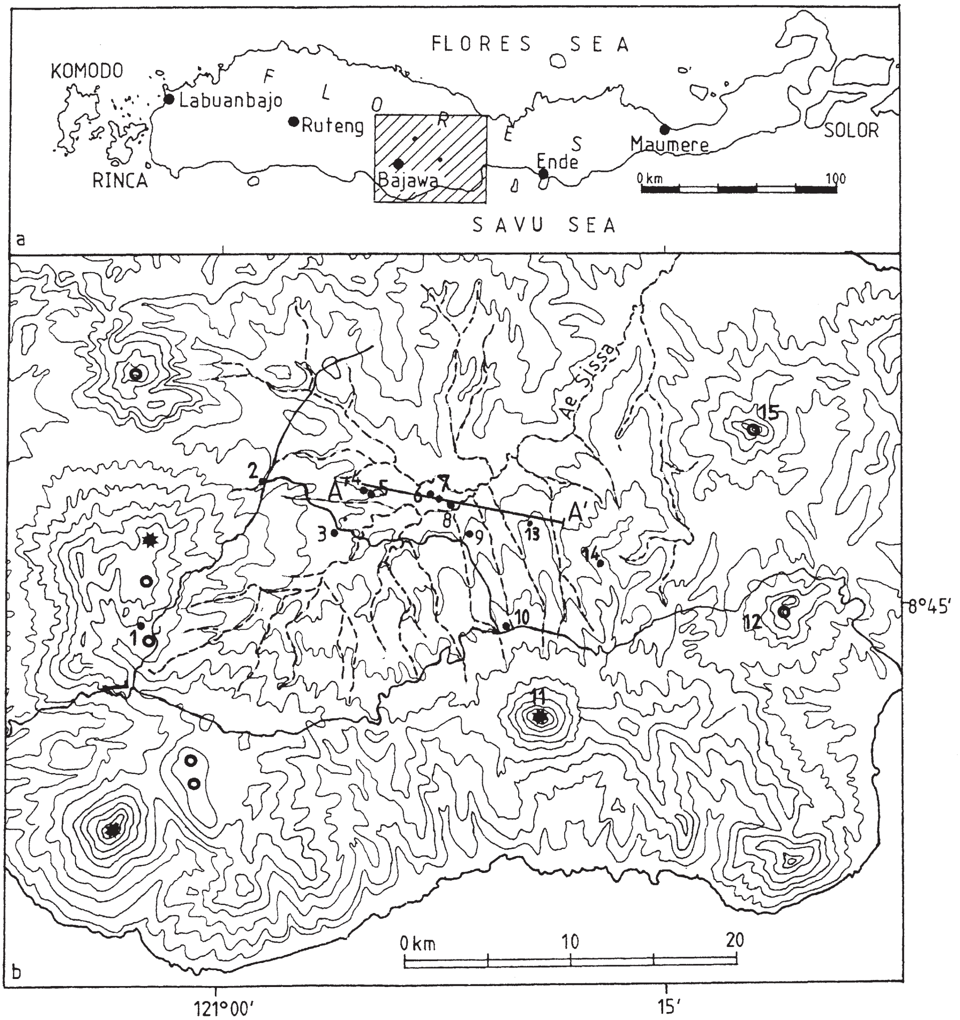


Fig. 3. Topographic map of the Soa Basin in west Central Flores, showing the various localities and volcanoes discussed in the text. Circles: extinct volcanoes; Stars: active volcanoes; 1 = Bajawa, capital of the Ngada District; 2 = Soa; 3 = Menge Ruda; 4 = Mata Menge; 5 = Boa Leza; 6 = Ola Bula; 7 = Tangi Talo; 8 = Bhisu Sau; 9 = Ola Kile (abandoned village); 10 = Boawae; 11 = Ambulobo Volcano; 12 = Kelindora Volcano; 13 = Dozo Dhalu; 14 = Gero (abandoned village); 15 = Kelilambo Volcano. The line A-A′ is the WNW-ESE profile shown in Fig. 64. Contour interval 200 m.

show V-shaped valleys as well, and Hooijer (1964b, 1974) and Maglio (1973) considered the presence of Y-shaped valleys as typical for the Stegodontidae. As pointed out by Sondaar (1984) and van den Bergh et al. (1992), the shape of the valley in between the lamellae is not always a usefull distinguishing character. Firstly, because a fossil has to be cut through and besides a single molar with median pillars developed may exhibit Y, V or U-shaped valleys depending on where the section is taken. Secondly,

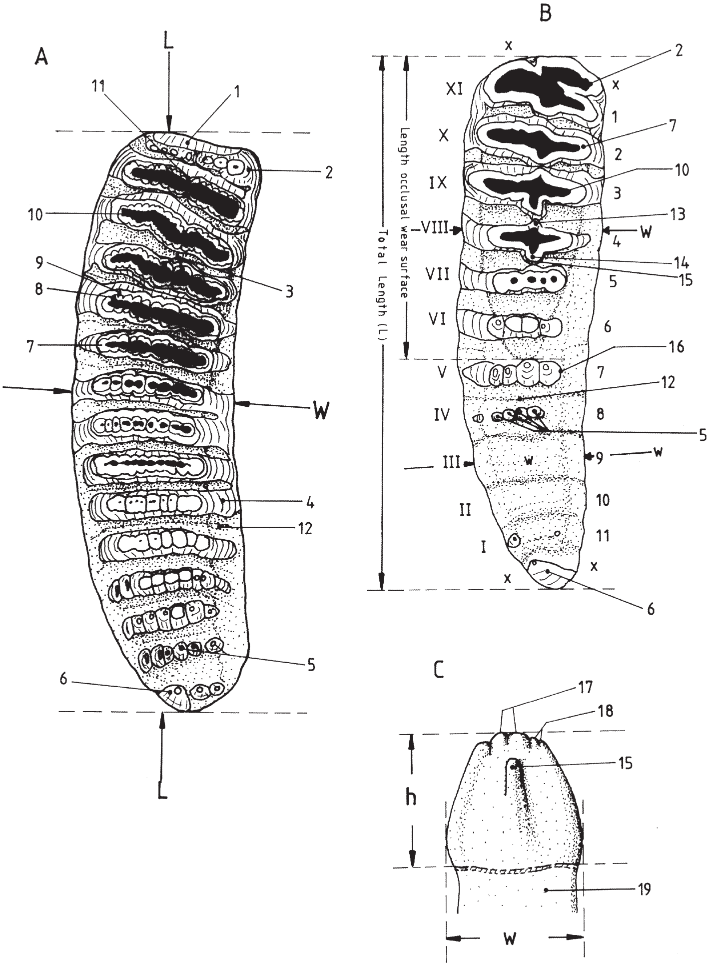


Fig. 4. Terminology and biometric parameters used in this thesis to describe Elephantoidea molars. A: Stegodontidae lower molar, occlusal view. B: Elephantidae lower molar, occlusal view. C: Elephantidae molar lamella, anterior view. Molar lamellae or ridges are counted with arabic numbers when counting from anterior in posterior direction and with roman numbers when counting from posterior in anterior direction, as indicated in fig. B.
L = maximum length; W = maximum width of molar; w = width measured at the nth lamella; h = unworn heigth measured at the nth lamella (not shown is H, which is the maximum unworn heigth of a molar, measured at the highest ridge or plate in the same way as h); 1 = contact facet with preceding molar; 2 = anterior halfridge (in Stegodontidae) or anterior halflamella (in Elephantidae); 3 = double median expansions of enamel loop; 4 = molar ridge (only in Stegodontidae); 5 = apical digitations of molar ridge; 6 = posterior halfridge (in Stegodontidae) or posterior halflamella (in Elephantidae); 7 = completed enamel wear pattern or enamel loop of occlusal surface; 8 = inner enamel layer (only in Stegodontidae); 9 = outer enamel layer (only in Stegodontidae); 10 = dentine; 11 = median cleft or median sulcus; 12 = transverse valley filled with cementum; 13 = anterior median sinus of enamel loop; 14 = posterior median sinus of enamel loop; 15 = median pillar; 16 = molar lamella or plate (only in Elephantidae); 17 = median digitations; 18 = lateral digitations; 19 = root.

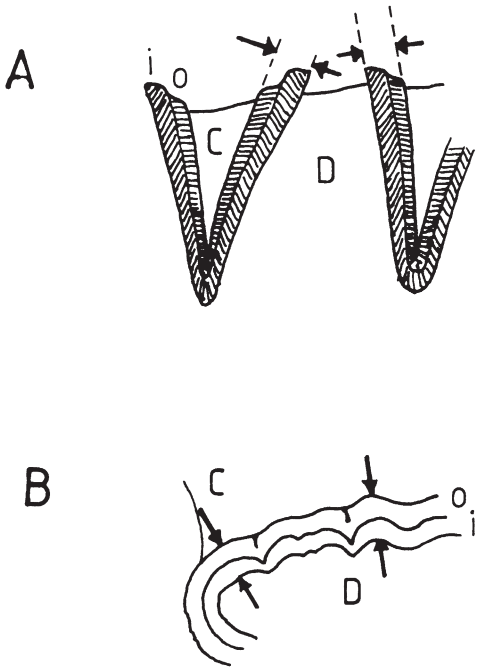


Fig. 5. A: Stepwise wear or 'Stufenbildung' developed at the occlusal surface of the enamel in *Stegodon* molars. The stepwise morphology is due to the differential resistance to wear of the inner and outer enamel layer. Shown also is the method for measuring the total enamel thickness (ET) in *Stegodon* molars (A and B). The ET is measured perpendicular to the anterior or posterior enamel surface of the ridges (A). The measurements are taken in worn ridges with completely formed enamel loops, but not in ridges which are worn down more than two-third of the molar height, because the ET tends to decrease rapidly adjacent to the transverse valley bottoms. D = dentine; C = cement; i = inner enamel layer; o = outer enamel layer.

in case of the insular stegodonts from the Indonesian islands a tendency towards increased hypsodonty results in a more "*Elephas*"-like appearance of the ridges and valleys. The shape of the valleys should only be used in addition to other criteria such as the presence or absence of median expansions in the enamel wear patterns or median pillars on the anterior or posterior faces of the ridges or the morphology of the enamel. Morphology of the enamel is a very useful character for distinguishing between molars of *Stegodon* and Elephantidae. In molars of *Stegodon* the relatively thick enamel consists of two well differentiated layers of approximately equal thickness. The outer layer, in which the parallel bundles of enamel prisms are oriented more or less horizontally (parallel to the occlusal wear surface), wears down more rapidly than the inner enamel layer, in which the enamel prism bundles are plaited in a complex manner and on average approaching the wear surface obliquely. The outer layer is less resistant to wear, which leads to a stepwise morphology of the enamel at the grinding surface (Fig. 5A). This step-wise morphology has been called 'Stufenbildung' by Janensch (1911). Characteristic for *Stegodon* molars is also the fact that the inner enamel layer is more heavily wrinkled than the outer enamel layer. This type of folded enamel has been called 'scalloped' enamel by Coppens et al. (1978). In the thick unfolded enamel of *Stegolophodon* the two enamel layers are also present, but the transition between outer and inner enamel is less well delineated and more gradual (Kamiya & Taruno, 1986), not leading to the stepwise wear morphology seen in *Stegodon*.

In Elephantidae the outer enamel layer with parallel prism bundles is largely reduced and constitutes less than one third of the total enamel thickness. A stepwise morphology of the enamel at the grinding surface is not developed in elephantidae molars.

In Stegodontidae and in the more advanced Elephantidae there sequentially appear 6 successive molars in each halfjaw. Biologists sometimes designate these 6 molars with the roman numbers I to VI. Among palaeontologists they are usually considered homologous with dP2, dP3, dP4, M1, M2, and M3, respectively in other mammals, which designation I follow here. The 6 molars are replaced horizontally, and there are never more than 2 of them in use at the same time in a single half-jaw. In the primitive *"Elephas" celebensis* the 3 milkmolars are replaced vertically by premolars, indicated with P2, P3 and P4 in this thesis. In the more advanced Elephantidae and in *Stegodon* premolars have been totally lost.

Measurements

Molars — The method for measuring morphological and biometrical parameters of elephantoid teeth is largely based on the methods of Maglio (1973) and Beden (1979). These methods were originally applied to fossil and recent Elephantidae, but are also well suitable for stegodont molars. Most lettercodes used by Beden (1979) for the biometrical parameters were derived from the French language, and have been altered here. Some modifications to the methods referred to above were applied in the present study. The biometrical parameters used here are:

P: Number of ridges (in the following the term ridges will be used, meaning both the stegodontine ridges and the elephantine plates or lamellae) present in one molar. A "-" in front or behind the ridge number P indicates incompleteness of the molar. In such a case P does not represent the total amount of ridges originally present. If a ridge is incompletely preserved in a certain specimen, a number "$^1/_2$" or "$^1/_4$" is put in front or behind "-". Thus, "$4^1/_2$-" indicates a molar fragment of which the anterior 4 ridges plus the anterior half of the 5th ridge remain. The fractions do nót designate the posterior and anterior halfridges, such as in the ridge formula notation used by Osborn (1943). Halfridges at the anterior or posterior extremities of a molar are not counted; they are indicated with "x". A halfridge was considered as a halfridge only when its width and height were 25% less than its succeeding or preceding ridge. In some transitional cases where this definition could not be applied, two alternative ridge formulas are given (e.g. x6x or x7).

In some cases the total number of ridges in incomplete molars can be deduced from the alveolar outline or the preserved rootmass: in such cases the estimated number of ridges missing is given between brackets (e.g. (x?2)8x means that of a molar fragment with 8 ridges and a posterior halfridge remaining, two ridges and possibly an anterior halfridge are lacking at the front).

L: Maximum length of the molar (Fig. 4), measured along the longitudinal axis at right angles to the planes of the intermediate ridges, conform method C of Maglio (1973: 11).

W: Maximum width of the molar, measured on the widest ridge of the molar, parallel to the anterior and posterior surfaces of the ridge (Fig. 4).

w: Width of individual molar ridges, measured in the same way as W.

H: Maximum height of a molar, measured vertically on the lateral side of the highest ridge, between the crown base and the apices of the digitations. H values are only given for unworn ridges. Values taken on slightly worn ridges are indicated with "+" behind the measured value.

h: Height of individual molar ridges, measured similarly as H (Fig. 4C).

LF: Laminar frequency, representing the number of ridges that occur in 10 cm along the longitudinal plane of the molar at the level of the transverse valley bottoms. LF values represent the averages of the medial and lateral laminar frequencies along the crown base. This method differs from that used by Maglio (1973), who takes as LF the average of 4 measurements, including a buccal and a lingual measurement along the wear surface. In strongly vertically curved molars, such as the M3, the value of the lamellar frequency measurements along the wear surface depend on the amount of wear, and thus leads to incomparable data between molars in different wear stages. If lamellar frequencies are discussed other than according to the above given definition, the lettercode LF will not be used, but instead they will be referred to with terms such as "buccal lamellar frequency" or "lamellar frequency of the occlusal surface".

The LF values were obtained by measuring the distances between two valley bottoms separating three or four successive ridges, both on the lingual and buccal side of the molar. If these distances are indicated with d_l (lingually) and d_b (buccally), and the number of ridges between the two measuring points with n, than the LF was calculated using the formula:

$$LF = \frac{n*100/d_l + n*100/d_b}{2}$$

It is well known that the number of ridges increased through time in several elephantoid lineages, resulting in a closer spacing of the ridges and thus an increase in LF. Note however, that a decrease in molar size, such as in dwarfing lineages, also results in increased LF values. Therefore, the ratio between the LF and a parameter defining molar size, such as L and W, is more indicative for the evolutionary stage of a certain species. As L measurements can often not be obtained from incomplete molars, the LF/W ratio will be given in several cases.

ET: Enamel thickness. ET is measured perpendicular to the anterior or posterior enamel surface of molar ridges (Fig. 5). Within one molar the enamel thickness is not constant and maximum and minimum value are given if possible. As the enamel usually decreases in thickness towards the base of the ridges, only measurements are included, which could be taken in ridges that are worn less than two-third. In unworn but broken molar fragments the ET could be obtained on vertical broken enamel surfaces.

h/w: Hypsodonty index, in which the height of individual ridges is expressed as a percentage of the width (h*100/w). As the h/w indices of individual ridges may differ slightly within one molar, a range of h/w indices is usually given for single dental elements. This method is preferred above the one in which a single index between the maximum height (H) and width (W) of the molar is given, because in many molar fragments or halfworn molars the H or W values could not be taken. In practice, the range of h/w indices of intermediate ridges includes the value of the H/W index of the same molar. However, at the posterior and anterior extremities of a molar hypsodonty indices tend to show aberrant values, sometimes differing more than 20% from those obtained on intermediate ridges. Therefore, the given ranges for a certain molar or molar fragment, or the h/w ranges given in the various tables with summary measurements, exclude h/w indices of the most anterior ridge and the most posterior ridge (and halfridges), and in case of the posteriorly tapering M3's, exclude the three most posterior ridges.

L/W: Ratio between the maximum length (L) and the maximum width (W).

EF: Frequency of the enamel folding. EF represents the number of folds present in a transverse distance of 10 mm along the enamel-dentine junction (Fig. 6). Notation is like in Beden (1979): 12 means 1 to 2 folds per 10 mm; 13 means 1 to 3 folds per 10 mm; 24 means 2 to 4 folds per 10 mm; etc. EF values are only given for molars in which one or more ridges are worn to such extend that single enamel loops have been formed.

EA: Relative amplitude of the enamel folds (measured along the enamel-dentine junction; Fig. 6) given as a percentage of the enamel thickness (ET): 1: EA < 33% of total ET; 2: EA = 33-67% ET; 3: EA = 67-100% ET, 4: EA = 100-133% ET, etc. If the EA values in a single molar range between two or more of the arbitrary chosen classes mentioned above, the EA value is represented by two successive numbers: e.g. "12" means EA = 0-67% ET. EA values are only given for molars with sufficiently worn ridges in which single enamel loops are completely formed. The EA is measured similar to the method of Beden (1979), but the EA class boundaries are distinct.

Dig: Amount of digitations per individual ridge or lamella. "-" indicates variation observed among ridges of individual teeth (for example 8-10 indicates that there are between 8 and 10 digitations in the various ridges of one molar). The given ranges exclude counts on anterior and posterior halfridges.

Measurements on incomplete molars or bones are followed by "+" indicating that the value of the original element was larger than the recorded value. If a measurement represents an estimated value (for example the length of a broken molar based on the alveolar outline), that value is succeeded by "e". The h and w values taken on molar ridges completely covered with cementum are succeeded by "c".

Specific ridges or lamellae of a molar are indicated with an Arabic number when counted from anterior in posterior direction (Fig. 4B), and with a roman number when counted from posterior in anterior direction (in molars that are incomplete in front).

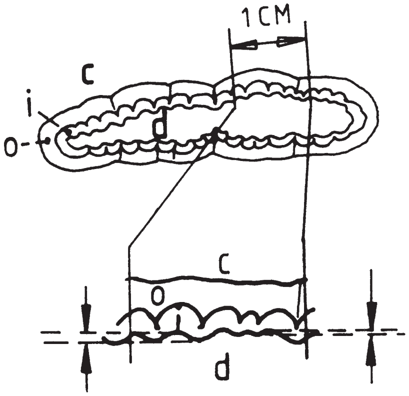


Fig. 6. Enamel Frequency (EF) and Enamel Amplitude (EA) measurements taken on enamel wear surfaces of Elephantoidea molars. EF represents the amount of enamel folds in 10 mm (transversely) along the dentine/enamel junction. In Stegodontine molars only the folds of the inner enamel layer are counted, as shown in A. The EA is expressed as a percentage of the total enamel thickness (ET).

Skeletal elements — The same biometric parameters for elephant skulls used by Beden (1979: 168, fig. 34) were used here for measuring cranial material (Fig. 7). Additional measurements that were taken if the material allowed so are: Ha′ = height from summit occipital crest to dorsal border of foramen magnum (basion); lw = width of fossa incisiva measured proximally; lx = width of fossa incisiva measured distally; Lm = length of fossa incisiva; Ak = depth of fossa incisiva.

For the mandibles the definition of the measurements used here is the same as that of Beden (1979: fig. 46), though indicated with different lettercodes (Fig. 8). For the postcranial elements the biometric parameters are indicated in Figs. 9 (atlas), 10 (cervical and thoracic vertebrae), 11 (scapula), 12 (humerus), 13 (ulna), 14 (radius), 15 (metapodals), 16 (pelvis), 17 (femur), 18 (tibia), and 19 (fibula).

Diagrams — Scatter diagrams were prepared using Harvard Graphics software. Morphological comparisons between two or more skulls or mandibles are visualized by plotting the standard measurements of each specimen in log-ratio diagrams. For each log-ratio diagram one specimen (usually the most complete one) is chosen as reference. Specialists who make use of log-ratio diagrams usually plot the average value of various standard measurements that are taken on specimens in a certain assemblage and believed to belong to the same species. However, because of the generally limited number of specimens for comparison, the values of single specimens are separately plotted in the log-ratio diagrams. The standard measurements are plotted on the horizontal axis. On the vertical axis are plotted the logarithm of the ratio between that measurement in a certain specimen and the same measurement taken on the reference specimen. The various log-ratio values of the measurements taken on a single specimen are indicated with the same symbol. The values of successive measurements from a single specimen are connected by lines. In this way differences in proportions between the reference specimen and the other specimens can be visualized. For example, if the proportions in a certain specimen would be exactly the same as in

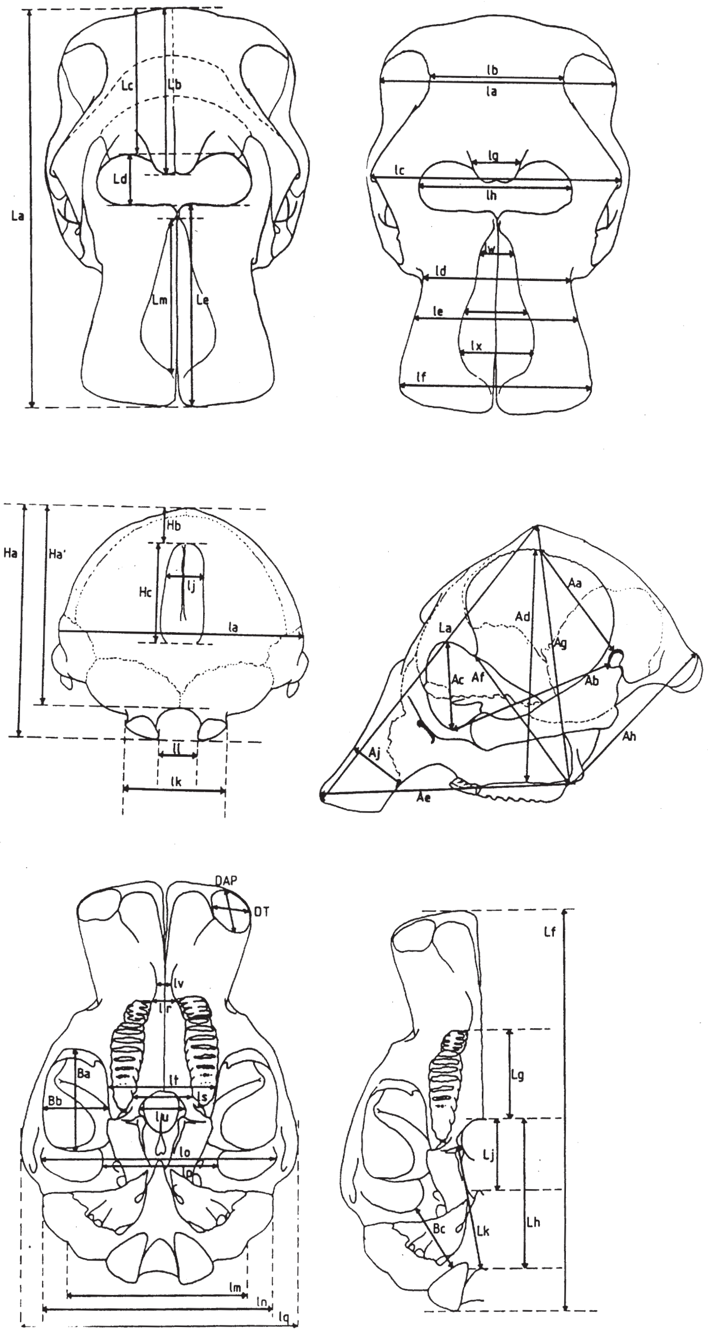


Fig. 7. Size measurements taken on Elephantoidea skulls. Most measurements are taken after Beden (1979: 168-169). Additional measurements are: Ha′ = height from summit occipital crest to dorsal border of foramen magnum (basion); lw = width of fossa incisiva measured proximally; lx = width of fossa incisiva measured distally; Lm = length of fossa incisiva; Ak = depth of fossa incisiva.

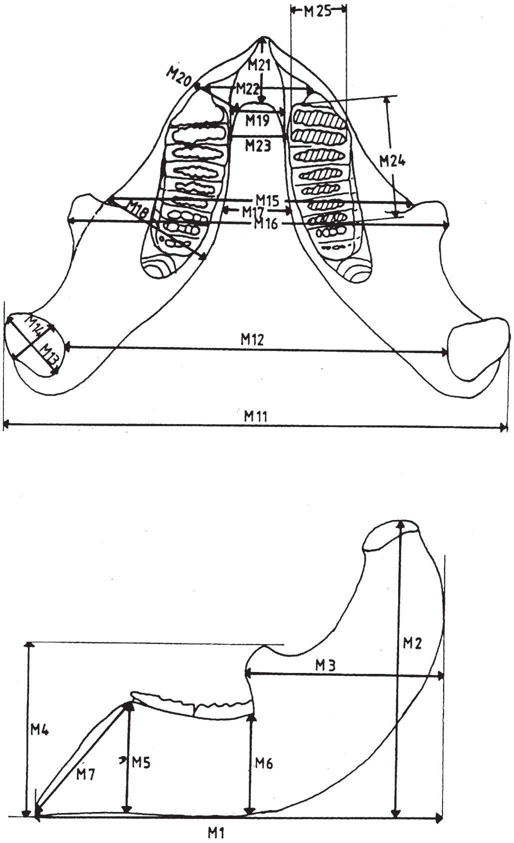


Fig. 8. Measurements taken on Elephantoidea mandibles: M1 = maximal length of mandible in a plane defined by the basal points of support and parallel to the median plane; M2 = total height of the mandible perpendicular to its basal plane; M3 = total length of the ascending ramus; M4 = height between the basal plane and the coronoid apophyses; M5 = height of the horizontal ramus measured at the level of the anterior border of the dental alveoles; M6 = height of the horizontal ramus measured at the level of the anterior onset of the ascending ramus; M7 = length of the interalveolar crest; M8 = height between the inferior border of the mandibular foramen and the base of the mandibular condyle; M9 = horizontal distance of the ascending ramus posteriorly of the posterior border of the mandibular condyle; M11 = maximal width of the mandible measured between the external borders of the condyles; M12 = width between the internal borders of the condyles; M13 = largest (transverse) diameter of the condyle; M14 = smallest (antero-posterior) diameter of the condyle; M15 = width of the mandible at the level of the onset of the ascending ramii; M16 = width of the mandible between the external borders of the coronoid apophyses; M17 = distance separating the internal borders of the horizontal ramii at the level of the onset of the ascending ramii; M18 = maximum transverse diameter of the horizontal ramus; M19 = distance separating the internal borders of the horizontal ramii at the level of the anterior border of the dental alveoli; M20 = minimum transverse diameter of the horizontal ramus; M21 = antero-posterior length of the diaphysis; M22 = distance between the superior terminations of the interalveolar crests; M23 = minimum distance between the internal borders of the horizontal ramii; M24 = length of the occlusal wear surface; M25 = maximum width of the occlusal wear surface.

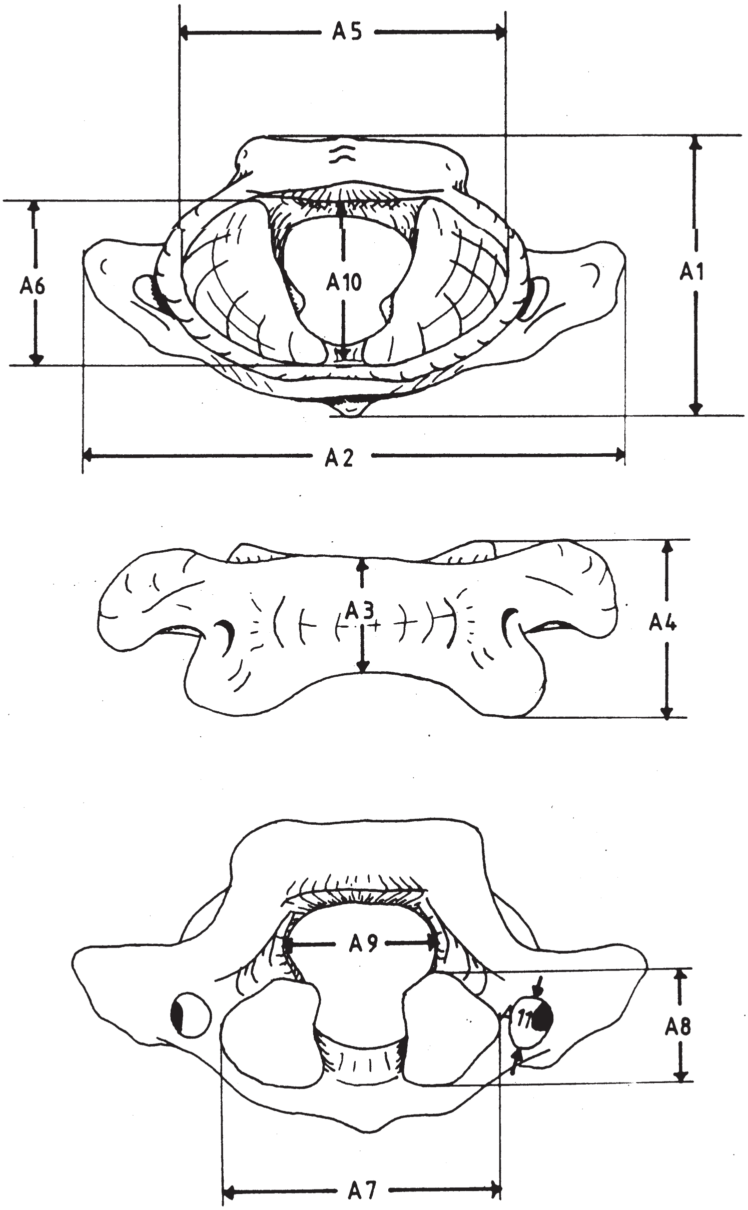


Fig. 9. Measurements taken on the Elephantoidea atlas: A1 = maximum vertical diameter; A2 = maximum transverse diameter over processus transversalis; A3 = anteroposterior diameter over arcus; A4 = anteroposterior diameter of corpus at the level of the processus transversalis; A5 = transverse diameter of the facies articularis cranialis; A6 = vertical diameter of the facies articularis cranialis; A7 = transverse diameter of the facies articularis caudalis; A8 = vertical diameter of the facies articularis caudalis; A9 = transverse diameter of the foramen vertebrale (measured caudally); A10 = vertical diameter of the foramen vertebrale (measured cranially); A11 = maximum diameter of the foramen transversarium.

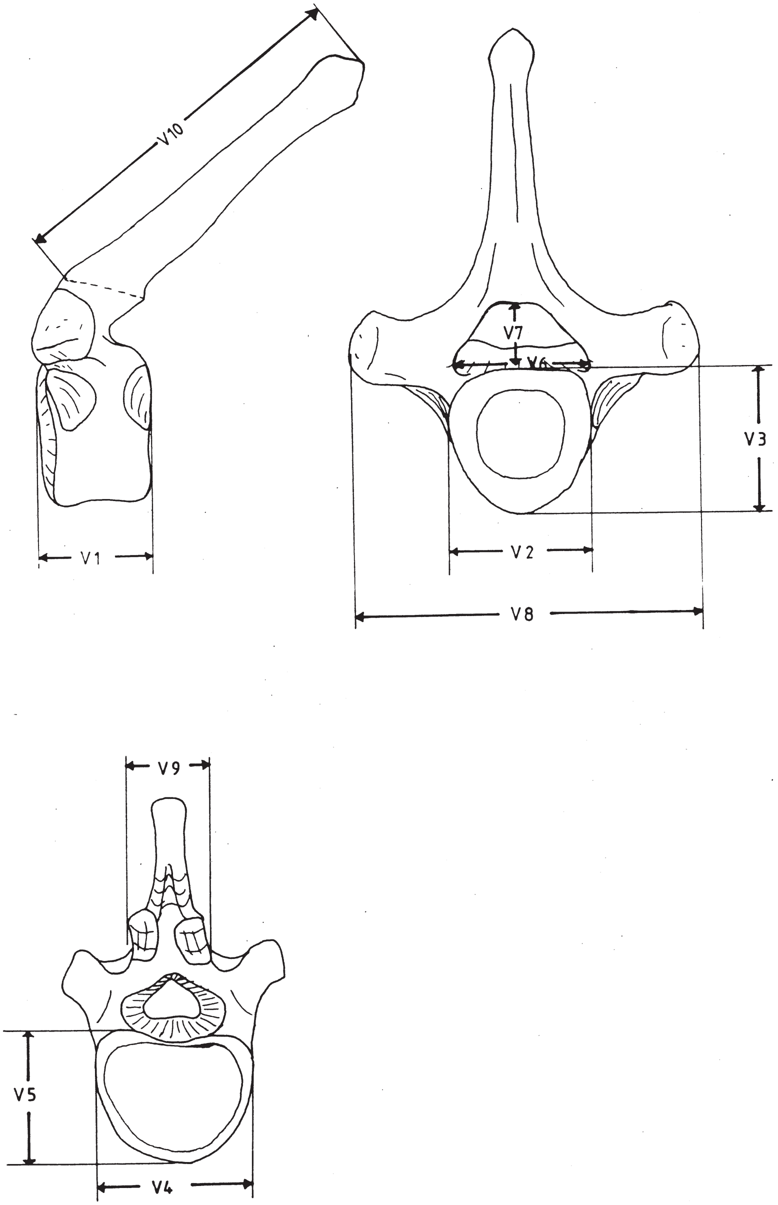


Fig. 10. Measurements taken on Elephantoidea cervical and thoracic vertebrae: V1 = maximum anteroposterior diameter of the corpus; V2 = transverse diameter of corpus at the cranial articulation fovea; V3 = dorso-ventral diameter of the corpus at the cranial articulation fovea; V4 = transverse diameter of the corpus at the caudal articulation fovea; V5 = dorso-ventral diameter of the corpus at the caudal articulation fovea; V6 = transverse diameter of the foramen vertebrale (measured cranially); V7 = dorso-ventral diameter of the foramen vertebrale (measured cranially); V8 = maximum width of vertebra over the processi transversali; V9 = maximum width of the processi articulares caudales (only in vertebrae of the caudal part of the vertebra column); V10 = length of processus spinosus over the anterior surface, starting at the ventral border of the arcus.

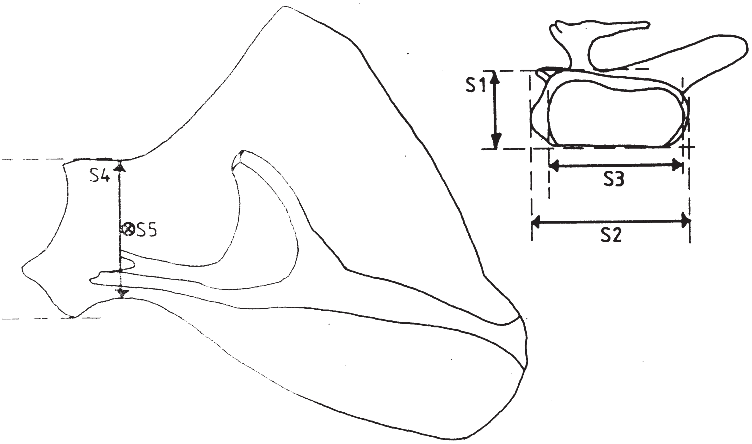


Fig. 11. Measurements taken on Elephantoidea scapulae: S1 = maximum distal transverse diameter; S2 = maximum distal anteroposterior diameter; S3 = maximum anteroposterior diameter of glenoid; S4 = minimum anteroposterior diameter of collum scapulae; S5 = minimum transverse diameter of collum scapulae.

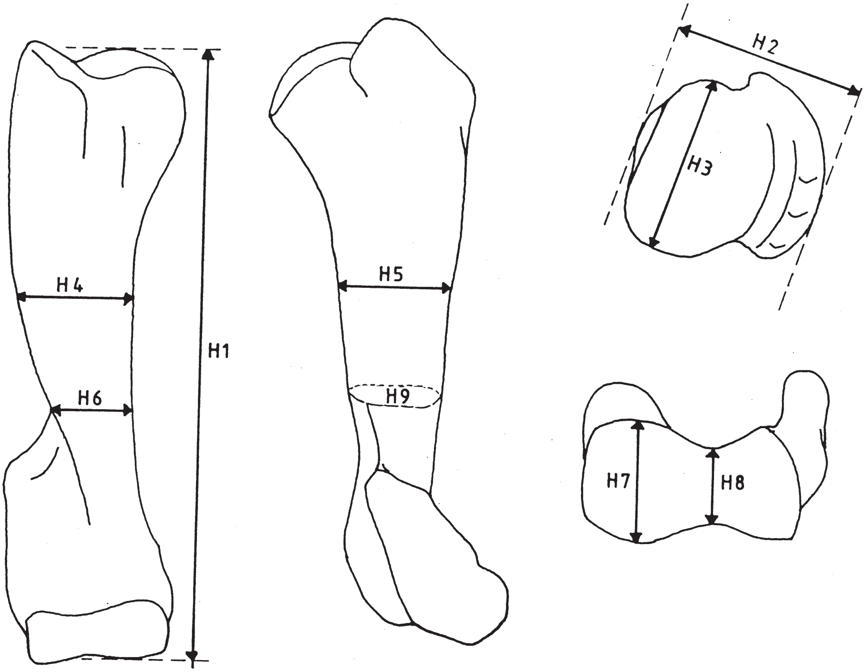


Fig. 12. Measurements taken on Elephantoidea humeri: H1 = total length from caput to medial condyle; H2 = proximal transverse diameter over caput and posterior part of the lateral tuberosity; H3 = anteroposterior diameter of caput; H4 = transverse diameter of diaphysis over distal end of deltoid tuberosity; H5 = anteroposterior diameter of diaphysis at same level as H4; H6 = smallest transverse diameter of diaphysis; H7 = maximum anteroposterior diameter of medial condyle; H8 = minimum anteroposterior diameter of trochlea; H9 = minimum circumference of diaphysis.

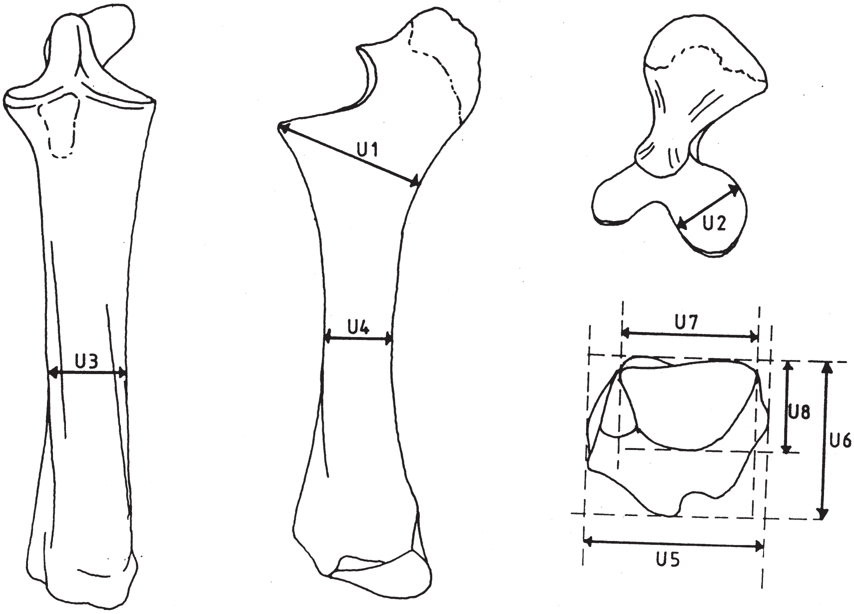


Fig. 13. Size measurements taken on Elephantoidea ulnas: U1 = maximum anteroposterior diameter proximally (over medio-anterior protrusion of humeral articular surface); U2 = transverse diameter of medial portion of humeral articular surface; U3 = minimum transverse diameter of shaft; U4 = minimum anteroposterior diameter of shaft; U5 = maximum transverse diameter of distal epiphysis; U6 = maximum anteroposterior diameter of distal epiphysis; U7 = transverse diameter of articulation facet for triquetrum; U8 = anteroposterior diameter of articulation facet for triquetrum.

the reference specimen, though its absolute size would be larger, its log-ratio values would show on a horizontal line parallel to but below the x-axis (the latter corresponding with the values of the reference specimen). For convenience the log-ratio scale to the left of each log-ratio diagram has been transformed to a multiplication factor scale to the right of the diagrams, so that absolute size differences between the values of the specimens and the reference specimen can be rapidly seen.

Large-sized elephantoids continue growing during most of their lifespan, which leads to marked size differences even among sexually mature animals. These size differences are shown off in the log-ratio diagrams. For each mandible or skull the dental wear stage is always given, so that specimens of comparable ontogenetic stage can be compared amongst each other and with specimens of different ontogenetic stages.

Calculations for preparing log-ratio diagrams and statistical parameters were made using LOTUS 123 software.

Enamel microstructure

Of some fossil molar fragments the enamel microstructure was examined using SEM and light microscopy. The samples were embedded in araldite and cut with a diamond saw. Thin sections were prepared for study under the polarizing light microscope. Horizontal and longitudinal sections were made of both samples. In

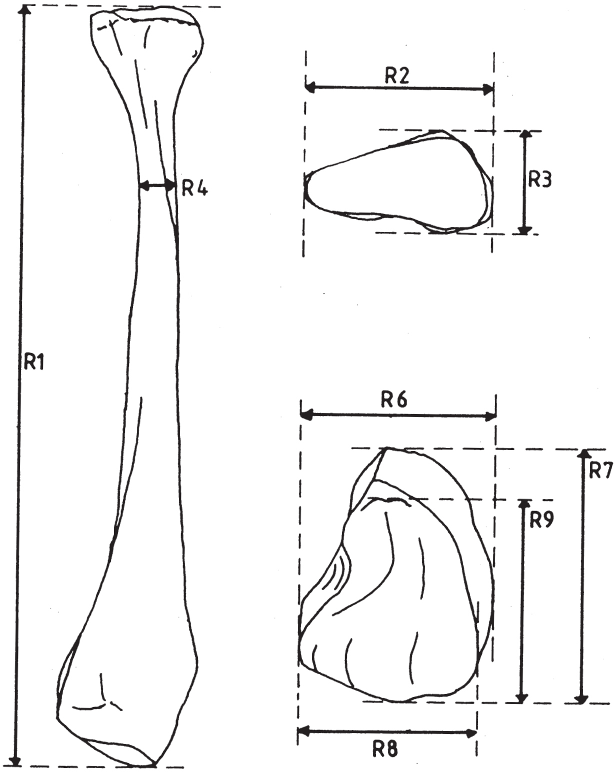


Fig. 14. Size measurements taken on Elephantoidea radii: R1 = total length; R2 = maximum transverse diameter of proximal epiphysis; R3 = maximum anteroposterior diameter of proximal epiphysis; R4 = minimum transverse diameter of shaft; R5 = minimum anteroposterior diameter of shaft; R6 = maximum transverse diameter of distal epiphysis; R7 = maximum anteroposterior diameter of distal epiphysis; R8 = maximum transverse diameter of articulation facet with lunatum; R9 = maximum anteroposterior diameter of articulation facet with lunatum.

addition, tangential and horizontal sections were prepared for study under the SEM (Hitachi S-2700). The SEM samples were ground on wetstone and successively polished with 5, 1 and 0.25 µm diamond paste (Struers), washed and etched for 10 seconds with 1% HCl. Then they were coated with a Paladium/Gold mixture using an Eiko IB5 ion coater and ready for SEM. In this way enamel samples of molar fragments of the following species were examined: *S. sondaari* sp. nov. (one isolated molar ridge not yet fully completed and a posterior fragment of either an M^1, M^2 or M^3); two samples of *S. trigonocephalus* (one M^1 and one dP_4 fragment); a lower molar fragment of *S. sompoensis*; an M^1 fragment of *S. florensis*; a molar fragment of *"Elephas" celebensis*; and an M^3 fragment of *E. planifrons*. Other samples of *S. elephantoides*, *S. aurorae* and *S. shinshuensis* were kindly provided by Dr Y. Kozawa for examination.

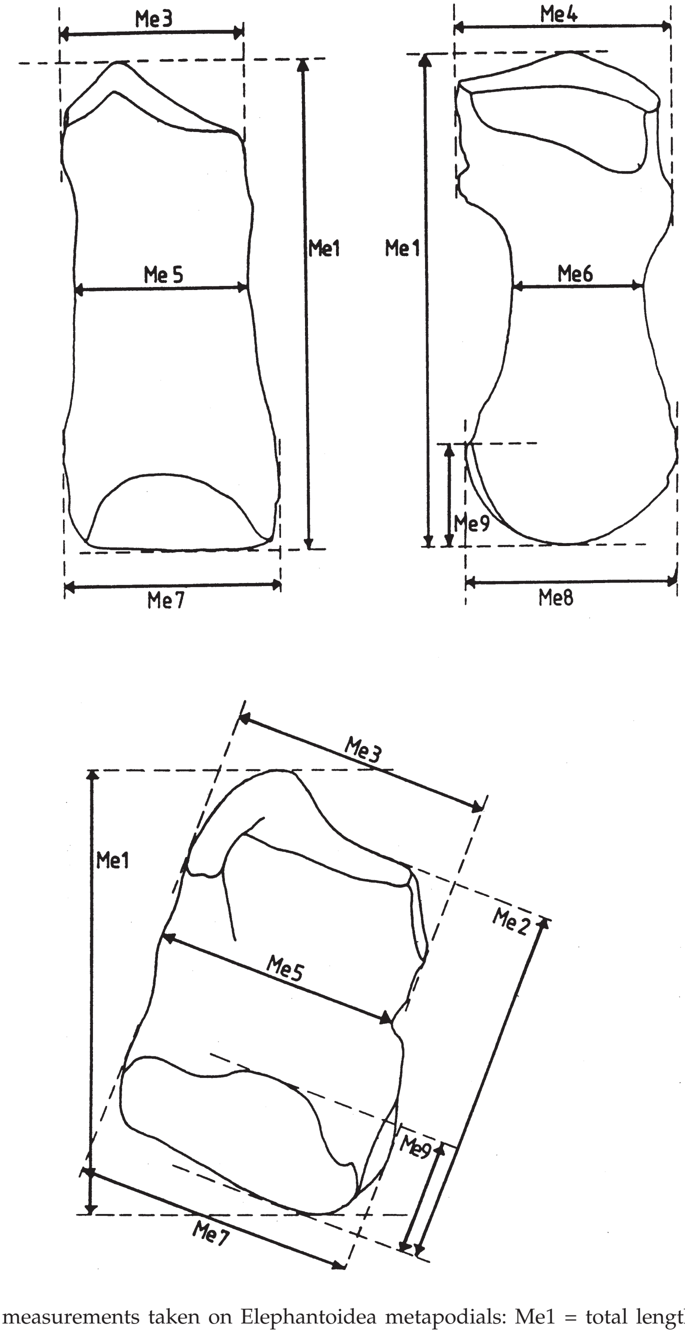
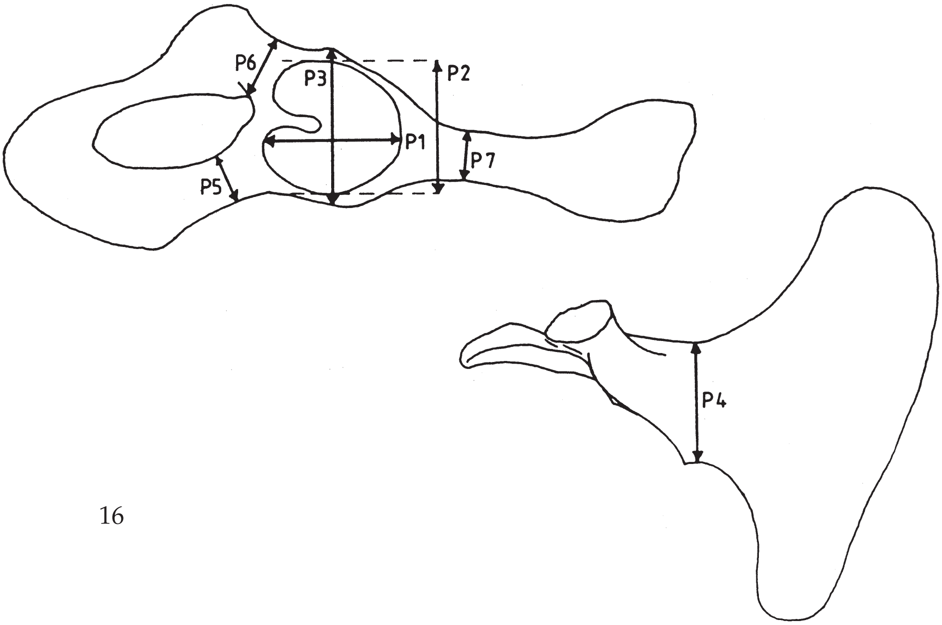


Fig. 15. Size measurements taken on Elephantoidea metapodials: Me1 = total length; Me2 = length (diagonal) of lateral metapodials in natural position; Me3 = maximum proximal transverse diameter; Me4 = proximal anteroposterior diameter; Me5 = minimum transverse diameter of diaphysis; Me6 = minimum anteroposterior diameter of diaphysis; Me7 = maximum distal transverse diameter; Me8 = maximum distal anteroposterior diameter; Me9 = vertical height of distal articulation surface, measured posteriorly; Me10 = idem, measured anteriorly.



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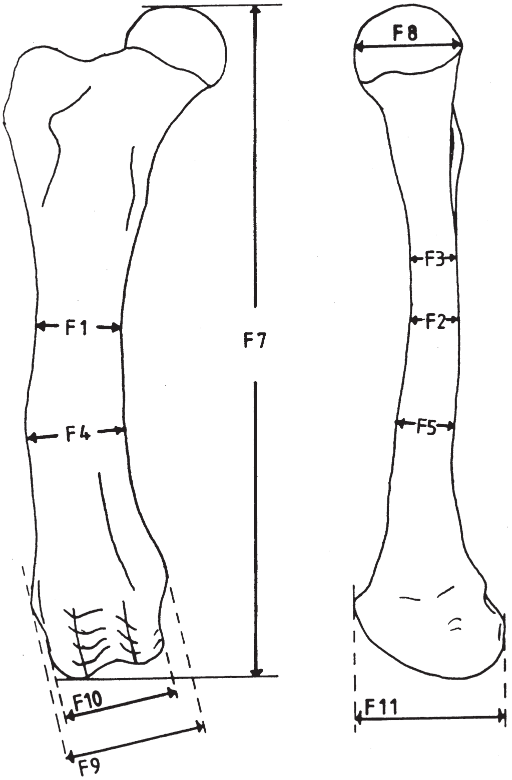

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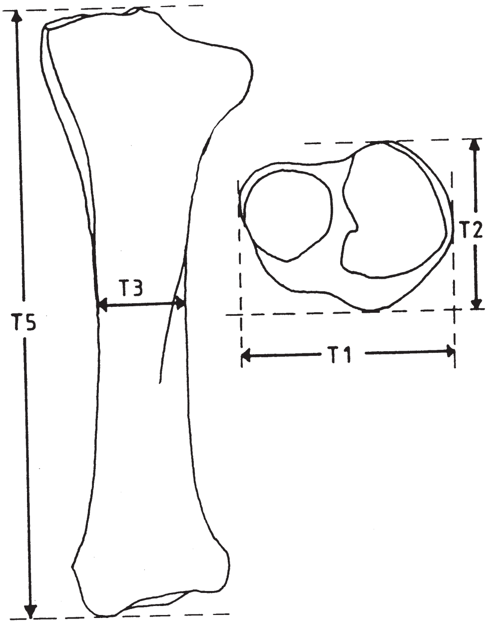


Fig. 18. Size measurements taken on Elephantoidea tibiae: T1 = maximum proximal transverse diameter; T2 = maximum proximal anteroposterior diameter; T3 = minimum transverse diameter of diaphysis; T4 = minimum anteroposterior diameter of diaphysis; T5 = total length.

Fig. 16. Size measurements taken on Elephantoidea pelvis fragments: P1 = anteroposterior diameter of acetabulum; P2 = dorsoventral diameter of acetabulum; P3 = dorsoventral diameter of acetabulum between the outer margins; P4 = minimum transverse diameter of ilium; P5 = minimum transverse diameter of ischium; P6 = minimum anteroposterior diameter of pubis; P7 = minimum dorsoventral diameter of ilium at the level of P4.

Fig. 17. Size measurements taken on Elephantoidea femora: F1 = minimum transverse diameter of diaphysis; F2 = anteroposterior diameter of diaphysis at level of minimum transverse diameter; F3 = minimum anteroposterior diameter of diaphysis; F4 = transverse diameter at distolateral tuberosities on diaphysis; F5 = anteroposterior diameter at the same level as F4; F6 = minimum circumference of diaphysis; F7 = total length of femur between caput and lateral condyle; F8 = anteroposterior diameter of caput; F9 = maximum transverse diameter of distal epiphysis; F10 = maximum transverse diameter of distal condyles; F11 = anteroposterior diameter of distal epiphysis, medial side; F12 = anteroposterior diameter of distal epiphysis, lateral side.

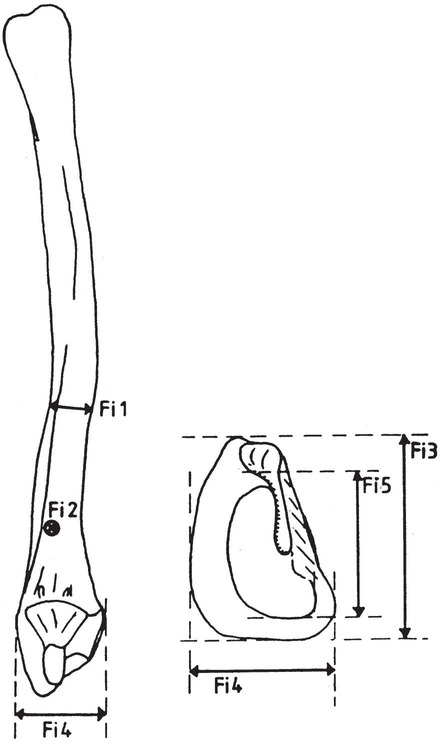


Fig. 19. Size measurements taken on Elephantoidea fibulae: Fi1 = minimum transverse diameter of shaft; Fi2 = minimum anteroposterior diameter of shaft; Fi3 = maximum anteroposterior diameter of distal epiphysis; Fi4 = maximum transverse diameter of distal epiphysis; Fi5 = maximum anteroposterior diameter of concave distal articulation facet.

Abbreviations used

Institutions and collections:

AMNH:	American Museum of Natural History, New York
BMNH:	British Museum of Natural History, London
CD:	Collection Dubois at the NNM
CVH:	Collection van Heekeren at the NNM
CV:	Collection Verhoeven (partly housed at the NNM)
GRDC:	Geological Research and Developemnt Center, Bandung, Indonesia.
IESU:	Institute of Earth Sciences, University of Utrecht, the Netherlands.
IIA:	Indonesian Institute of Archaeology, Jakarta, Indonesia.
MPC:	Museum of Prehistory at Calio, Soppeng District, South Sulawesi Province, Indonesia.
NNM:	National Museum of Natural History, Leiden, the Netherlands.
PMS:	Prehistory Museum at Sangiran, Central Java, Indonesia
VFUU:	Veterinary Faculty of the University of Utrecht.

Geomorphological and geological structures (see also Enclosures A and B):

BCF:	Bulu Cepo Fault

ESB:	East Sengkang Basin
EWF:	East Walanae Fault
LT:	Lakibong Triangle.
SA:	Sengkang Anticline
SB:	Soa Basin (Flores)
WFZ:	Walanae Fault Zone
WSB:	West Sengkang Basin
WWF:	West Walanae Fault

Other abbreviations and symbols:

AEY:	African elephant years
CV:	coefficient of variation
DWAC:	dental wear age class
EDJ:	enamel Dentine Junction
ESR:	electron Spin Resonance dating
FVL:	fossil vertebrate locality
HSB:	Hunther-Schreger Bands
IEL:	inner enamel layer
M:	mean value
MNI:	minimum number of individuals
n:	number of specimens
OEL:	outer enamel layer
PDS:	present day sea level
SD:	standard deviation

2. Additions to the fossil Elephantoidea from Java

Introduction

The Quaternary faunal succession of Java is relatively well studied and one of the best known in Asia. Since the early investigations of Dubois leading to the finding of his *Pithecanthropus erectus*, many researchers have shown their interest in the prehistory of this island. Though far from resolved in detail, the Javanese biostratigraphy as it is known today is well suited to serve as a basis for comparing the faunal successions of other areas in the southeast Asian region.

Proboscideans were amongst the first landmammals that reached Java. They constitute an important element of all successive fossil faunas of Java since its emergence above sea level. Identification of proboscidean remains enables to ascertain roughly the age of the layers in which they were found. In this chapter some additions to our knowledge of the fossil proboscideans from Java will be worked out. The Javanese succession will be used in the following chapters when discussing the taxonomic relationships amongst the proboscideans of the various Indonesian islands and the possible migration routes to and from those islands.

The faunal succession of Java

During the 1980s a new biostratigraphic scheme has been proposed for the Quaternary terrestrial deposits of Java (de Vos et al., 1982, Sondaar, 1984, de Vos, 1983, 1985), which replaced the widely used classical biozonation for Java by von Koenigswald (1933, 1934, 1935a, c, d). The latter was based on composite faunal assemblages and contained various inconsistencies (de Vos et al., 1982, Braches & Shutler, 1984a, Theunissen et al., 1990). The new biostratigraphic scheme for the Pleistocene of Java proposed by de Vos et al. (1982) and Sondaar (1984) is based on the faunal contents from single localities or composite faunas from localities that are closely superposed in thick stratigraphic sequences. This new mammalian biostratigraphy of Java runs from young to old:

Wajak Fauna
Punung Fauna
Ngandong Fauna
Kedung Brubus Fauna
Trinil H.K. Fauna (H.K.="Haupt-Knochenschicht")
Ci Saat Fauna
Satir Fauna

Ci Saat and Satir are the names of a small river and a village respectively, both located at close proximity northwest of Bumiayu. The location of Bumiayu and the other locality names are shown on Fig. 20. The contents of these faunas are given in Table 1.

The oldest, Early Pleistocene, Satir Fauna is characterized by only a few taxa. The fauna was obtained from five excavations (excavations 1-4 and 8) carried out by C. ter Haar and J. Zwierzycki of the Dutch East Indies Geological Survey. The excavations were carried out near Satir village at the base of the Kali Glagah Series near Bumiayu. The base of the Kali Glagah Formation of ter Haar (1934) is called "lower sandstone-conglomerate group" on the geological map presented by van der Maarel (1932), who described the fossils from these excavations. Sondaar (1984) based his Satir Fauna on the species that could be recognized amongst the fossils from these five excavations, notably *Mastodon bumiajuensis* van der Maarel, 1932. Saegusa (1995) noted recently that *bumiajuensis* possesses actually trilophodont molars and should be assigned to the genus *Sinomastodon* (see below). *S. bumiajuensis* is also known from the Sangiran area, although it is very rare there and no stratigraphic position is known for the *S. bumiajuensis* fossils originating from that area. By analyzing the fluorine content of a *S. bumiajuensis* mandible originating from the Sangiran area and comparing it with fluorine data from excavated fossils from several stratigraphic levels, as reported by Matsu'ura et al. (1985), Leinders et al. (1985) were able to show that it most likely originated from the so-called "black clays", also known as the Pucangan Formation (the "black clays" are called Sangiran Formation by Sudijono et al. (1995) instead of the old name Pucangan Formation, of which the type section is located several hundred kilometers east of Sangiran). Together with *Hexaprotodon simplex*, *S. bumiajuensis* is characteristic of the Satir fauna, which further contains cervids. Leinders et al. (1985) propose an age of 1.5 Ma for the Satir fauna based on fission track ages of volcanic ash layers (T5 and T6) in the Sangiran area as reported by Suzuki et al. (1985).

Palaeomagnetic evidence from the Kali Glagah Series in Bumiayu (Sémah, 1986) suggests that its base, including the level of excavation number 8 of van der Maarel

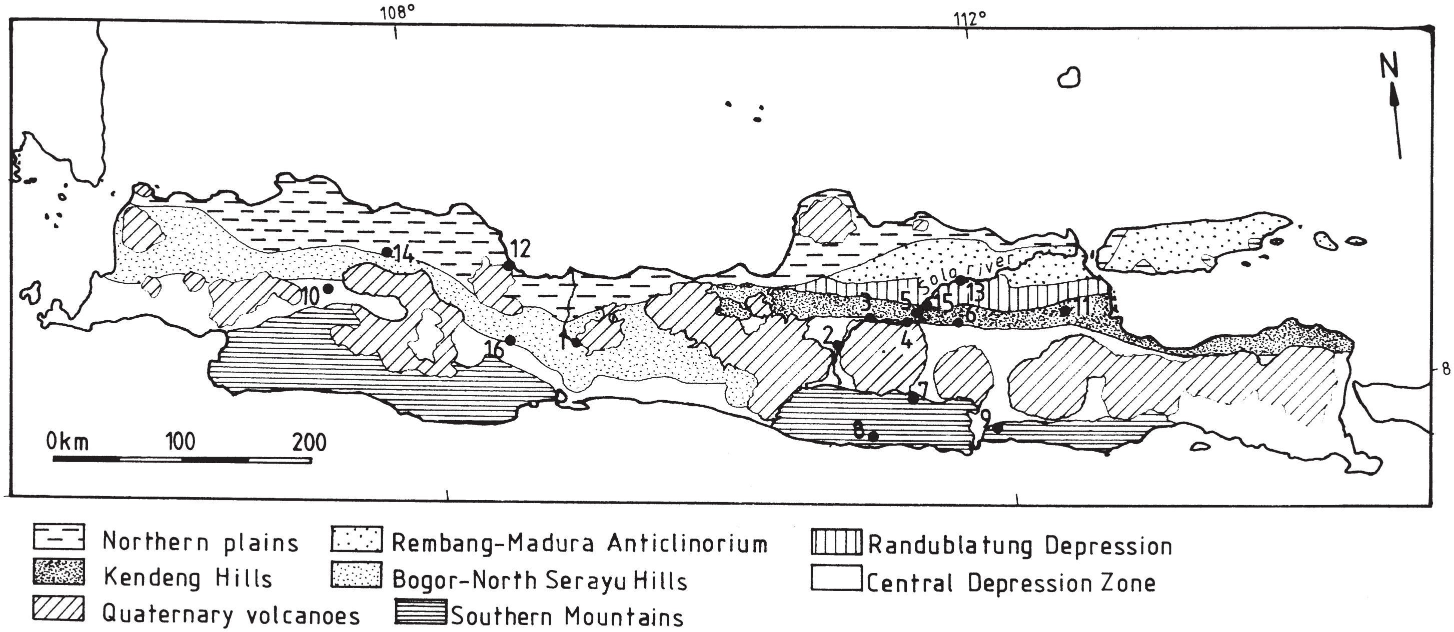


Fig. 20. Physiographic map of Java, including the location of the fossil vertebrate localities discussed in the text. Modified after van Bemmelen, 1949. 1 = Bumiayu; 2 = Sangiran; 3 = Sambungmacan; 4 = Trinil; 5 = Ngandong; 6 = Kedung Brubus; 7 = Sampung; 8 = Punung; 9 = Wajak; 10 = Cipeundeuy; 11 = Mojokerto; 12 = Cirebon; 13 = Grobogan; 14 = Subang; 15 = Tinggang; 16 = Cijulang.

(1932), antedates the Olduvai Event. Therefore the first occurrence of the Satir fauna might well be older than the 1.5 Ma originally proposed by Leinders et al. (1985). Thus, the first mammalian colonization of the western part of Java may have occurred as far back as about 2 Ma ago.

The Ci Saat Fauna is still poorly known and was originally proposed on hypothetical grounds by Sondaar (1984). It differs from the Satir Fauna by the replacement of *S. bumiajuensis* by *Stegodon*, and perhaps by the occurrence of the first felid.

Another important aspect to note is the occurrence of *Geochelone atlas* in the Sangiran area. The fluorine content of a fossil *Geochelone* fragment from the Sangiran area (exact locality unknown) was also compared with the fluorine data of Matsu'ura et al. (1985). Based on these comparisons it was concluded that it originated from the lower part of the Sangiran Formation and was thought to be equivalent in age with the Satir fauna from the localities near Bumiayu (Sondaar, 1984; Leinders et al., 1985). Giant tortoise remains have been found in situ in the Sangiran area, however. The excavation of trench I near Bukuran, 1.5 km ESE of Sangiran (Kadar et al., 1985), carried out by the Indonesian-Japanese team between 1977 and 1979, reportedly yielded remains of a turtle (Aimi & Aziz, 1985: 157). However, the fossils, which are erroneously indicated as turtle in their paper, actually represent the plastron fragments of a giant tortoise according to Dr Fachroel Aziz. The Bukuran excavation trenches are stratigraphically placed in the upper part of the Sangiran Formation just above tuff layer T9 and c. 10 m below tuff layer 10. The latter is well dated by means of fission-track dating (Suzuki et al., 1985) and has an age of 1.16 ± 0.24 Ma. This information suggests that *Geochelone* continues up to this age and might still be present in a fauna intermediate to the Satir and Ci Saat faunas of Sondaar (1984). The presence of a giant tortoise at around 1.2 Ma is considered an indirect indication that *Homo erectus* was not yet in Java at that time. Giant tortoises are an easy prey for hunter-gatherers and rapidly became extinct on islands where humans settled (Sondaar, 1981).

The successively younger Javanese faunas are characterized by an increasing exchange of faunal elements with the SE Asian continent (Table 1). An important shift from open woodland conditions to a tropical rainforest environment occurred between the late Middle or Late Pleistocene Ngandong Fauna and the Late Pleistocene Punung Fauna.

The dating of the mammalian faunal succession as originally proposed by de Vos et al. (1982) and Sondaar (1984) has increasingly improved during the last decades. The results of palaeomagnetic and fission-track analysis were used in combination with those of lithostratigraphic studies and with the observations made during the collecting of in situ vertebrate fossils in the Sangiran area and comparing the faunas from the Sangiran area with those of the fauna type localities elsewhere (Watanabe & Kadar, 1985; Aimi & Aziz, 1985; Leinders et al., 1985; Sémah, 1986; Hyodo et al., 1993). The palaeomagnetic results obtained by Hyodo et al. (1993) were successful in removing secondary magnetic overprints that hampered previous palaeomagnetic interpretations in the Sangiran area (Shimizu et al., 1985). As a result the Jaramillo normal event is now clearly shown to occur just below the "Grenzbank" in the Sangiran area. The fossil fauna from the "Grenzbank" can be correlated with the Trinil H.K. faunal stage (Leinders et al., 1985). This could mean that the Trinil H.K. fauna, which lacks the genera *Elephas*, *Tapirus* and *Hyaena*, has an age of c. 0.9 Ma, which is slightly younger than the 1 Ma originally proposed by Leinders et al. (1985).

Originally, Dubois (1908) considered the Trinil Fauna and the Kedung Brubus Fauna to be contemporaneous, explaining the relative poorness in species of the Trinil Fauna as due to palaeoenvironmental differences. Von Koenigswald (1934) basically followed this view and lumped the fossil assemblage from the locality Kedung Brubus with that from Trinil and considered this composite fauna as his Trinil Fauna. His Trinil Fauna is not to be confused with the Trinil H.K. Fauna *sensu* de Vos et al. (1982), which includes only those species originating from a single layer at Trinil, the so-called “Haupt-Knochenschicht”. According to these authors the difference in faunal composition between Trinil H.K. and Kedung Brubus is due to the higher age of the Trinil H.K. Fauna and the relatively isolated circumstances of Java at the time of its accumulation. Others have maintained that the Trinil mammalian assemblage is incomplete (e.g. Heaney, 1984), which is certainly true with respect to the small mammals. However, recent fossil finds in combination with palaeomagnetic results from the Kaliuter sections, 15 km N of the Sangiran Dome (Djubiantono, 1992) are in agreement with the hypothesis of de Vos et al. (1982), namely that a fauna corresponding in age with the Jaramillo Event and lacking *Elephas* but including *Stegodon*, is preceding a fauna correlating with the Brunhes Epoch, which includes *Elephas*. The fossil-bearing conglomerate at Kedung Cumpleng along the Kaliuter, which is correlated with the Jaramillo Event, includes *Stegodon* but has not yielded any *Elephas* remains. The fossil assemblage possibly corresponds to the Trinil H.K. fauna, while the younger excavation at Pancuran, correlated with the Brunhes Epoch, has yielded *Elephas*, and should either correlate with the Kedung Brubus or Ngandong faunal stage.

Palaeomagnetic analysis of a section at the type locality Kedung Brubus has been carried out as well (Mubroto et al., 1995). The results suggest that the Brunhes-Matuyama boundary corresponds with the lowermost part of the Kabuh Formation at Kedung Brubus, but are not unambiguous. This lowermost part also yielded the fossils collected by Dubois, which constitutes the assemblage on which the Kedung Brubus Fauna of de Vos et al. (1982) was originally based.

Recently, high ages for two hominid sites on Java have been published by Swisher et al. (1994). They claim that *Homo erectus* was already present on Java at 1.81 ± 0.04 Ma based on ^{40}Ar/^{39}Ar laser-incremental heating analysis on minerals from the supposed collecting locality of the Mojokerto child. They present another date of 1.66 ± 0.04 Ma for a site near Sangiran, where in the late 1970s two hominid specimens (S27 and S31) were recovered during the digging of an irrigation channel. Their ages contradict existing data on the detailed lithostratigraphy in combination with palaeomagnetic data and fission-track ages (Suzuki et al., 1985; Hyodo et al., 1993; de Vos & Sondaar, 1994). As suggested by de Vos & Sondaar (1994) the mineral samples dated by Swisher et al. (1994) might have been reworked from older strata, as they were obtained from fluvial deposits. There are also uncertainties about whether the dated samples correspond to the original layers from which the skull material originated or that they originate from different layers. On a detailed geological map of the central part of the Sangiran Dome (Itihara et al., 1985: fig. 6), the location of S27 is indicated with “H” (at the time of publication S27 had not yet been given an official code). This location is only 70 m northwest of a major fault and inside an area of a major landslide. A short section was measured within this landslide (section S61 in fig. 9 of Itihara et al., 1985), showing the position of S27 to correspond with the uppermost part of the Sangiran Formation just half a meter below a gravelly sandstone layer interpreted to represent the "Grenzbank". If a sample for dating had been taken only 25 m west of the hominid locality and outside the landslide zone, this would probably represent an older stratigraphic level of the Sangiran Formation. For the moment the absolute dates presented by Swisher et al. (1994) are not incorporated in the faunal succession presented below until other dates in combination with more detailed geological information are given. It is here assumed that the oldest presence of *Homo erectus* in Java was probably during the Ci Saat faunal stage and that its presence in Java was with certainty established during the Trinil Faunal stage.

Dating of the Ngandong Fauna presents some problems. The fauna is based on material excavated from the Solo River terrace at Ngandong by Oppenoorth during the 1930's. Bartstra et al. (1988) give a preliminary U-series age of 50-100 ka for fossil bone samples collected from an excavation in a terrace remnant at Ngandong. As they state, this age should be considered a minimum. The faunal composition of the Ngandong fauna is very similar to that of the Kedung Brubus Fauna but very different from the younger Punung Fauna. Many taxa in the Ngandong fauna, including *Homo erectus*, differ on subspecies level from those of the Kedung Brubus Fauna (de Vos et al., 1994), both faunas being characteristic of an open woodland environment. On the other hand, the Ngandong Fauna should be older than the Late Pleistocene Punung fauna (de Vos, 1983), which is characteristic of a tropical rainforest environment. The composition of the Punung Fauna is very similar to the fossil fauna excavated by Dubois from three caves in West Sumatra, Lida Ajer Cave, Djambu Cave and Sibrambang Cave (de Vos, 1983). Aspartic acid racemization analysis of fossils from Djambu and Lida Ajer caves gave ages of 60-70 ka and 80 ka, respectively (Skelton & de Vos, in prep.). Warm and humid conditions started on Java around 125 ka ago and lasted until c. 81 ka (van der Kaars & Dam, 1994). Therefore the age of the Punung Fauna has been inferred to correspond with this time interval (van den Bergh et al., 1996). The Ngandong Fauna should be older, and possibly corresponds with the glacial maximum at 135 ka. However, some very young ages for the deposit constituting the Ngandong terrace have been recently published, which are at odds with the inferred ages mentioned above. Swisher et al. (1996) carried out ESR and mass spectrometric U-series dating of bovid teeth collected from the hominid-bearing levels at Ngandong and Sambungmacan, giving mean ages of 53.3 ± 4 to 27 ± 2 ka. These very young ages are difficult to bring into line with the palaeontological data. Two bovid teeth dated by Swisher et al. (1996) were obtained from a layer at 220 cm depth in the Ngandong 20 m terrace. This layer was thought to correspond with layer 2 of Oppenoorth (1932). The latter author gave a simplified description of the terrace profile and distinguished 6 layers from bottom to top. He stated that the bone bed (layer 2) is a pebbly sandstone layer with hyperstene andesite components both as loose grains and small pebbles and unconformably overlying Tertiary marine tuffaceous marls (layer 1). Layer 2 yielded all Ngandong hominid calvaria besides a large number of vertebrate fossils. Of layers 3 and 4, consisting of tuffaceous sandstone, only layer 3 also reportedly contained vertebrate fossils. Layers 5 and 6 finally are gravely beds with abundant clasts of marine tuffaceous marl, but also volcanic pebbles (Oppenoorth, 1932). However, ter Haar (1934) provided a more detailed stratigraphy of the Ngandong terrace. He distinguished 2 complexes, A and B. Complex A covers the older layers, mainly consisting of andesitic sands and gravels, whereas complex B, the younger layers, cover complex A unconformably and consist of a mixture of loose sands with abundant rounded marl clasts. He also noted that the deposits belonging to complex A contained most fossils, including the Ngandong hominid calvaria, but that the deposits of complex B contained abundant reworked material from complex A, locally also vertebrate fossils. On the adjoining appendix ter Haar (1934: app. 3) showed a SW-NE profile through the Ngandong terrace. Significant is that the profile shows that complex A was eroded completely at some places, and that the layers of complex B filled in these erosional depressions or channels, locally resting directly on the Tertiary marine marls. Layers 2-4 and 5-6 of Oppenoorth (1932) presumably correspond with complex A and complex B of ter Haar (1934), respectively. Swisher et al. (1996) noted that the layer from which their bovid teeth were obtained also contained cobbles of marine marls. Their test pit therefore may have been located at a place where complex A had been eroded completely, so that they sampled in younger complex B layers.

As can be seen in Table 1, the Ngandong Fauna contains various archaic species whereas the Punung Fauna is largely modern. If the ages of Swisher et al. (1996) are correct, this would imply that the tropical rainforest fauna from Punung disappeared and was replaced by a more archaic fauna towards the end of the Late Pleistocene, to be replaced again by a modern Holocene fauna known from Wajak and some other Holocene caves on Java. Radiocarbon dates for some mammalian and human remains from the Wajak cave have recently become available, indicating an age between 6 ka and 10 ka for the Wajak Fauna (Storm, 1995; Shutler et al., 1996). For the time being, the age of the Ngandong Fauna will be considered here to be in excess of 125 ka.

Incorporating the data discussed above, the ages of the successive faunal units may be reconstructed as follows:

Wajak Fauna:	6-10 ka
Punung Fauna:	c. 60-125 ka
Ngandong Fauna:	Late Pleistocene
Kedung Brubus Fauna:	c. 0.7-0.8 Ma
Trinil H.K. Fauna:	c. 0.9 Ma
Ci Saat Fauna:	c. 1.0-1.2 Ma
Satir Fauna:	c. 1.5-2.0 Ma

There are still some considerable gaps in our knowledge of the faunal succession as it is shown above. Major gaps have to be filled in between the Kedung Brubus and the Ngandong faunal stages, while the Ci Saat faunal stage is still poorly known. The time range from 2 Ma until 1 Ma (Satir and Ci Saat faunal stages) is still poorly covered by the fossil record.

Elephantoidea of Java

Fossil Elephantoidea are important elements in each of the successive faunal units on Java. Their fossil remains are common in the vertebrate-bearing strata and they are good biostratigraphic indicators. Because of their great potential to colonize islands, fossil elephantoids are also frequently encountered on other islands in the region, which enhances their importance for biostratigraphic correlations of terrestrial deposits amongst the various islands. Below, first data on the elephantoid species recognized in the various faunal units of Java will be briefly summarized. Next, undescribed or poorly described elephantoid material from various localities in existing pre-war collections (GRDC, NNM) or recently discovered material will be treated. Their place in the biostratigraphic model given above will be discussed.

Gomphotheres

Van der Maarel (1932) described various mastodont cranial and dental elements as a new species, *Tetralophodon bumiajuensis*, placed by von Koenigswald (1933) in the genus *Mastodon*, based on the observation that intermediate molars were not tetralophodont but trilophodont. The fossils originated from excavations 1-4 and 8 carried out by the East Indies Geological Survey in the Bumiayu area. In the GRDC collection there is also fossil material attributable to *bumiajuensis*, which originated from the Sangiran area. Recently, Saegusa (1995) proposed that *bumiajuensis* should be placed in the genus *Sinomastodon*, erected by Tobien (1986). The combination of trilophodont intermediate molars and a brevirostrine mandible is only encountered in Chinese sinomastodonts and some New World mastodonts. Further there are similarities in skull and dental morphologies between *bumiajuensis* and the Chinese sinomastodonts. As reported by Saegusa (1995), the molar morphology of *S. bumiajuensis* is more derived compared to the Pliocene sinomastodonts from Japan and North China, but very similar to *Sinomastodon* remains from an Early Pleistocene cave faunas in South China.

Stegodonts

Stegodon fossils have been found in a great number of localities all over Java, but mainly in Central and East Java. The *Stegodon* from Java has been given various names and for a full list of synonyms of *S. trigonocephalus* the reader is referred to Hooijer (1955b). In 1884 Martin figured a molar of *Stegodon* sp. indet., and three years later he described a skull from the collection of Raden Saleh and named it *Stegodon trigonocephalus* Martin, after the triangular outline of the (juvenile) skull. This skull, and a lower M_2 described in the same paper as a second species, *Stegodon airawana*, were reportedly collected in the surroundings of Surakarta (Solo), which is not far from the famous hominid-bearing sites at Sangiran.

As expressed by the names *Stegodon javanoganesa* and *S. ganesa* var. *javanicus*, Dubois (1908) noted the close affinity between the *Stegodon* remains excavated by him at Trinil and *S. ganesa* from the Siwaliks. According to him there was a single species present on Java (Dubois, 1908). This conclusion was later also supported by Dietrich (1926), von Koenigswald (1933) and Hooijer (1955b). The latter author treated extensively the large collection of elephantoid fossils collected by Dubois at various localities on Java. With the exception of the lower dP_2, he described the full set of molars of *S. trigonocephalus*, besides various skulls and numerous postcranial elements (Hooijer, 1955b). Most fossils in the Dubois collection originate from the famous locality Trinil Haupt-Knochenschicht, type locality of *Homo erectus*. *Stegodon* fossils had also been collected at Trinil during the Selenka expedition. Janensch (1911) attributed them to *S. airawana*, which is generally considered to be a junior synonym of *S. trigonocephalus* (Hooijer, 1955b). From the localities Trinil H.K. and Kedung Brubus there are dozens of molars besides well preserved mandibles and skulls present in the Dubois Collection (DC) at the NNM. In addition, the DC contains numerous molar remains, various mandibles and skulls originating from a wealth of other fossil localities on Java. Janensch (1911) gave good descriptions of the well preserved material collected by the Selenka expedition at Trinil, but the collection was largely destroyed during World War II. Hooijer (1955b) lumped all this material into a single species: *S. trigonocephalus* Martin.

The only other stegodont on Java recognized by Hooijer (1954d, 1955b) was the small sized, subhypsodont *Stegodon hypsilophus* Hooijer, based on a pair of M^3 fragments from the surroundings of Jetis in East Java. He also attributed a molar fragment earlier described by von Koenigswald (1934) as *Elephas* sp. to this dwarf stegodont. Maglio (1973) considered *hypsilophus* a synonym for *Elephas celebensis* from South Sulawesi. This opinion was contested by van den Bergh et al. (1992), who argue that the unworn Jetis molars show clearly stegodont affinities, such as the thick, double-layered enamel consisting of two layers of approximately equal thickness and the absence of median pillars. The h/w indices of the ridges vary between 73-92, indices normally encountered in dwarfed insular stegodonts but never in large-sized stegodonts.

Though von Koenigswald (1933) distinguished only one *Stegodon* species on Java, he erected a subspecies, *S. trigonocephalus praecursor*, which was thought to be slightly more primitive as *S. trigonocephalus trigonocephalus* from Trinil. This primitive subspecies was based on a left mandible with complete M_3, reportedly originating from the lower layers of the Kali Glagah Formation at Bumiayu and served to indicate the older age of von Koenigswald's (1934, 1935b) Kali Glagah Fauna. The Kali Glagah subspecies was regarded as more primitive than *S. t. trigonocephalus* from Trinil because of its small size and because it had only 11 fully developed ridges in the lower M_3, whereas the Trinil variety had typically 13 ridges. Von Koenigswald (1935b) also included a lower jaw from Cipanaruban near Subang, West Java, in this subspecies. The idea of subspecific distinction was refuted by Hooijer (1955b), who considered that the number of ridges in the lower M_3 of *S. trigonocephalus* is variable between 11 and 13. As an example, he mentioned a lower M_3 from Lepen Alit near Tinggang, figured by van der Maarel (1932: pl. XII, fig.1), which also bears 11 ridges and which was regarded by von Koenigswald (1933: 104) as belonging to the typical Trinil subspecies *S. t. trigonocephalus*. With the lack of detailed stratigraphic data and age assessments of these isolated findings it is hard to decide whether the noted differences in the amount of ridges are due to intraspecific variability or due to differences in evolutionary stage.

The Ci Saat Fauna in the sense of Sondaar (1984) is based on the fossil taxa originating from the East Indies Geological Survey excavations 6, 9, 11 and 13 west of the Ci Saat River. These localities, which are indicated on the map presented by van der Maarel (1932), are stratigraphically situated in the Kali Glagah Formation of ter Haar (1934), between 150 and 350 m higher than excavation 8, which yielded *Sinomastodon bumiajuensis*. Though the exact faunal content from excavations 6, 9, 11 and 13 is not known, van der Maarel (1932), who only treated the elephantoids and hippos, does mention *Stegodon* molar remains from these localities. Thus, the Ci Saat Fauna, which has not more than an hypothetical status as also admitted by Sondaar (1984), is in fact based on the first occurrence of *Stegodon* in Java.

Due to the scattered nature and incompleteness of many isolated *Stegodon* molar findings, and of the uncertain stratigraphic position, it is hard to assess the variability ranges of the species or subspecies that lived on Java during successive periods. Hooijer (1955b) solved this problem by including all material in a single species, *S. trigonocephalus*. The bulk of the *Stegodon* and other vertebrate fossils from Java in the DC originate from the younger formations with a late Early or Middle Pleistocene age (e.g. from the Kabuh Formation at Trinil H.K. and Kedung Brubus). This would explain the reasonable uniformity of the dental material as presented by Hooijer (1955b), as most material in the Dubois Collection described by him originates from these two localities. However, some molars appear quite aberrant in their size and/or morphology. These are never from the well known localities Trinil H.K. and Kedung Brubus, from which relatively much material is available, but from unknown stratigraphic levels. For example, specimen CD-3818-3822 from Grobogan, a skull fragment with fragmentary dP^4's and both M^1's, is considered by Hooijer (1955b: 31) as *S. trigonocephalus*. The M^1's are considerably larger than the other 7 M^1's attributed to *S. trigonocephalus*, though its number of ridges is equal, x8x (Fig. 55). Likewise, there is an anomalous mandible with both fragmentary M_3's, that was allocated under *S. trigonocephalus* (Hooijer, 1955b: 45-46). This mandible is of unknown locality (CD-2296, dex. ramus and CD-2187, sin. ramus). Of the dextral M_3 there remain x10-ridges. I agree with the remark of Hooijer (1955b) that, judging from the posterior tapering, probably only one ridge is missing posteriorly, making a total of x11 ridges. The measurements of this molar are presented in Table 10, along with some other small-sized M_3's from Java. It is the smallest M_3 (W = 69 mm) amongst the 20 specimens listed by Hooijer (1955b: table 19; W varies between 76 and 98 mm in the remaining specimens; average W = 87.2 mm, n =19). Interestingly, the matrix of this small mandible consists of yellow limestone with marine molluscs. This suggests that it originates from Upper Pliocene or Lower Pleistocene shallow marine deposits which underlie the fossiliferous terrestrial sequences in the central and east Javanese sections (Sudijono et al., 1995). The relatively low number of ridges and the supposedly old age of this specimen bring new support to the original idea of von Koenigswald (1933) that successive stages in the number of molar ridges can be recognized in *S. trigonocephalus* trough time. There are various other elephantoid taxa in which succeeding evolutionary stages or subspecies are also recognized, such as *Elephas recki* and *Mammuthus meridionalis* (Maglio, 1970; Beden, 1979).

On Java the situation is expected to have been quite complicated due to periodic isolation of Java as a result of sea level fluctuations and subsequent new immigrations of mainland *Stegodon* populations. The multiple immigration model is supported by the findings of various dwarfed insular stegodonts on Java (Hooijer, 1954d; Aziz & van den Bergh, 1994), and by the recent finding of a primitive *Stegodon* mandible near Bukuran in the Sangiran area, which is clearly distinct from *S. trigonocephalus* and which is attributed to *S. elephantoides* in this thesis. This large mandible, presently stored in the Prehistory Museum at Sangiran (PMS Coll. no. 358), has an elongated symphysis and a very wide ramus, which clearly distinguishes it from *S. trigonocephalus*; it will be described below. In addition, the GRDC collection contains an undescribed *Stegodon* molar from West Java, which agrees better with specimen CD-2296-2187 than with the typical *S. t. trigonocephalus*. This specimen (GRDC no. K-391, a dextral M_3) originates from Jatisema near Ranji Kares, Cirebon District, according to the GRDC register. It will be treated in the descriptive section of this chapter. Other undescribed *Stegodon* material in the GRDC collection originates from the Ngandong excavations carried out by Oppenoorth during the 1930's. This material, mostly milkmolars, will also be described, as it is of interest to see if the molar remains are more advanced than those from the Trinil H.K. or Kedung Brubus Faunas.

Elephants

In the more recent revisions, four species of *Elephas* are recognized on Java. These are *Archidiskodon [Elephas] planifrons*, *E. celebensis*, *E. hysudrindicus*, and *E. maximus* (Hooijer, 1955b, 1974, 1982, Maglio, 1973). In contrast, van den Bergh et al. (1992) only accepted as proven the occurrence of three species: *E. maximus*, *E. hysudrindicus* and a species, which seems to be closely related to *"Elephas" celebensis* and referred to as *"E." indonesicus* (Kretzoi, 1950). Because of the uncertain generic status of the latter two species, they place the genus name between quotation marks. As discussed in van den Bergh et al. (1992), most of the molar material that has been attributed to *Archidiskodon [Elephas] planifrons* in the past (Hooijer, 1955b; von Koenigswald, 1934; van der Maarel, 1932; Maglio, 1973) in fact falls beyond the ranges of variation as given by Maglio (1973) for that species, and instead shows either stegodontine characteristics (like thick, double-layered enamel and stepwise wear) or can be attributed to *"E." indonesicus*, a dwarfed species. There remain only a few premolars from Java of unknown stratigraphic level (von Koenigswald, 1951, Braches & Shutler, 1984a) and some of them bought from the local inhabitants near Sangiran (Hooijer, 1982), which could belong to *Elephas planifrons*. However, these rare and poorly known elements make the presence of *E. planifrons* on Java far from certain and instead they could just as well represent dP2's of another primitive *Elephas* species or true premolars of *"E." indonesicus*. It has been pointed out previously (de Vos et al., 1982, Sondaar, 1984) that advanced elephants with hypsodont molars, represented by *E. hysudrindicus*, entered Java relatively late and are first recorded in the Kedung Brubus Fauna (*sensu* de Vos et al., 1982). *"E." indonesicus*, only based on a single molar from Ci Pangglosoran in the Bumiayu area and figured by van der Maarel (1932: pl. XVII, figs. 1-2) as *E. planifrons*, may be older, because the Ci Pangglosoran River only cuts trough the Kali Glagah Formation (van den Bergh et al., 1992).

Hooijer (1955b) doubted whether there existed proof that the Asian elephant, *Elephas maximus*, ever lived in Java during prehistoric times. Two partial molar plate fragments from the Sampung rock-shelter, of Holocene age, were recorded by Dammerman (1934: pl. II, fig.1), who stated that they match those of the recent Sumatran elephant exactly. Hooijer (1955b) suggested that these fragments equally well could represent a late survivor of the *E. hysudrindicus* stock. Actually, both fragments, currently housed in the GRDC collection (GRDC no.425), fit each other and together represent the basal portion of a single molar lamella. The width at the base is 74 mm and the minimum height as far as preserved is 77+ mm. The base of the lamella is straight, suggesting that it belonged to an upper molar. The flanks converge weakly in apical direction. The ET varies between 1.9 and 2.2 mm and the enamel is folded with 2-4 folds per cm and an amplitude between 1 and 2 mm. The enamel thins out near the base, suggesting that the lamella was not yet connected to the adjacent lamellae and that the molar to which it pertained was still under formation in the alveole. Indeed, this fragment forms no firm proof for the presence of *E. maximus* on Java. As noted by Hooijer (1955b), there is overlap in tooth morphology between *E. maximus* and *E. hysudrindicus*, and even when the total number of lamellae in combination with the hypsodonty index can be asserted, identification may remain problematic in some cases. One feature that might point in the direction of the recent Asian elephant is the weak apical convergence of the lamellar flanks observed in the Sampung specimen. In *E. hysudrindicus* the borders of opposite lamellar flanks are usually subparallel.

An other worn posterior M^3 fragment that has been attributed to *E. maximus* was described by Badoux (1959). It was amongst the fossil collection made by von Koenigswald at Punung. De Vos (1983) pointed out that the Punung fauna is characteristic for a tropical rainforest environment and suggests a Late Pleistocene age. Again, the elephant molar fragment is too small (-3x lamellae) to ascertain the identity of the species.

Some *Elephas* molar remains, which were discovered by Rien Dam in 1990 in a sand quarry 20 km west of Bandung near Cipeundeuy (Fig. 20), West Java, appeared more convincing in proving the former presence of *E. maximus* on Java. These fossils were briefly mentioned earlier (van den Bergh et al., 1992) but have not yet been described in detail, which is done below. The fluvial layer from which they originate is Late Pleistocene in age and contains some other faunal elements, all still extant on Java and/or Sumatra.

Stegodon elephantoides (Clift, 1828)

Stratigraphic position and age

A large mandible no. PMS-358 was found in 1993 in situ in the Sangiran Formation (sensu IJJST, 1991; 1995; = so-called 'Pucangan Formation' in the Sangiran Dome = 'black clays of Sangiran'). The collecting locality is located 1.5 km ESE of Sangiran (Central Java) and 50 m NW of trench I of the Bukuran excavation site. The latter excavation was carried out as part of the Indonesian-Japanese CTA-41 project between 1977 and 1979. A detailed map of the local situation is given in fig. 25 of Kadar et al. (1985). The finding spot of the mandible is on the east bank of the Pb stream indicated on this map. At the same spot a tusk of c. 3 m long was found during the CTA-41 project (Aziz, pers. comm.). Though it was practically impossible to trace the bedding plane in the weathered outcrops during the short fieldtrip that was made to the locality in 1994, it could be ascertained that the level of the mandible was situated just above the level with shells, which is indicated in fig. 25 of Kadar et al. (1985). This level occurs c. 10 m below the yellow tuff layer T9 exposed at the base of trench I, judging from the outcrop data presented in the same figure. Tuff layer T9 can be stratigraphically placed c. 12 m below tuff layer T10 (Yoshikawa & Suminto, 1985). The latter has yielded an age of 1.16 ± 0.24 Ma by means of fission-track dating

(Suzuki et al., 1985). Two layers T6 and T5, stratigraphically around 32 and 36 m below T9, have yielded ages of 1.49 ± 0.32 Ma and 1.51 ± 0.25 Ma, respectively (Suzuki et al., 1985). All these tuff layers correspond with an interval of reversed geomagnetic polarity (upper Matuyama), which in combination with the fission-track ages places the age of the present Bukuran mandible between 1.2 and 1.3 Ma. Mammalian fossils that have been found just above T9 in the excavations are listed by Aimi & Aziz (1985). These represent cervids, bovids and *Hippopotamus* sp. indet. As already mentioned before, the excavations yielded also various giant tortoise shell fragments, which were erroneously listed by Aimi & Aziz (1985: 157) as turtle shell fragments (Aziz, pers. comm.). The level may correspond with the poorly known and rather hypothetical Ci Saat faunal stage of Sondaar (1984), which was defined as recording the first occurrence of *Stegodon* on Java.

Description of the material

The Bukuran mandible (Pl. 1, figs. 1-4) is complete and includes both coronoid processes and condyles. Of the two largely worn M_3s the anterior portions are damaged. Measurements of the mandible are given in Table 13, those on the dextral, best preserved M_3 in Table 9. The dextral M_3 (Pl. 1, fig. 4) is almost an exact mirror image of the sinistral molar, which does not add extra information. Of ridge VII the buccal border is damaged, of ridge VIII both the buccal and lingual border are damaged and of ridge IX nothing more than the posterior part of the buccal half remains. It is not possible to ascertain the original total number of ridges. In front of both molars an alveole with blurred outlines and around 4 cm long can be discerned, which seems to have contained the anterior root. 1 or 2 ridges could be missing in front of the half preserved ridge IX, making a total of 10 or 11 ridges. The posterior ridges are all worn, showing completed enamel loops except for the posterior halfridge in both molars. The enamel loops or enamel wear patterns are somewhat expanded along the median axis. These single median expansions do not show any constriction in the middle, and no traces of a median sulcus can be observed in the halfworn ridges. If a median sulcus was originally developed in the unworn molar, it must have been rather shallow or only developed in the most anterior ridges. The scalloped enamel is rather thick (Table 9) and shows ‘Stufenbildung’ at the occlusal surface. These characteristics, and the minimum number of 9 ridges, exclude the possibility that we are dealing with *Stegolophodon*. They clearly point to *Stegodon*. Other characters conform *Stegodon* are the development of cementum between the ridges and the inclination of the ridges in anterior direction with the anterior face oriented at right angles with the crownbase and the posterior face sloping backward. The W of 85 mm occurs at ridge VI. It falls within the range of variation of the W in the M_3s of *S. trigonocephalus* (only including referred specimens from the localities Trinil H.K. and Kedung Brubus: 71e - 98 mm). The LF of 3.9 falls just below the range in *S. trigonocephalus* (Trinil H.K. and Kedung Brubus specimens combined: LF M_3 between 4.0 and 5.0), but this difference seems not significant. If the molar remnant from the Bukuran mandible had been found isolated, it could be referred to *S. trigonocephalus*, although with rather thick enamel (compare Tables 9 and 31). If the plate number could be ascertained at 9 or 10, then this attribution would be invalid.

However, the adjoining mandible differs widely from *S. trigonocephalus*. The most remarkable aspect of the mandible is the elongated symphysis (Pl. 1, figs. 1-3). Though in the generally descriptive terms used in elephantoid terminology the mandible should be called brevirostrine, lacking lower incisors, the deflected symphysal rostrum of PMS-358 is far less reduced than in any known *Stegodon* species. The symphysis is 28.5 cm long and 11.5 cm thick. A narrow gutter is bordered by two thick, parallel interalveolar crests, which terminate abruptly in distal direction with a downward nod. The gutter ends distally in a small protruding lip. The mandible is further characterized by low, laterally expanded, bulging rami horizontales, a characteristic often encountered in brevirostrine mastodonts and which is expressed by the relatively low values of the ratios M25/M18, M6/M18 and M5/M18 (Table 13). The lowness and thickness of the rami horizontales also can be seen in the log-ratio diagram of Fig. 21 (see also the section 'study methods' in chapter 1 for an explanation of the log-ratio diagrams), where the logarithm of the ratio between measurements taken on several *S. trigonocephalus* mandibles in various ontogenetic stages, and the same measurements on mandible PMS-358, are plotted. In all *S. trigonocephalus* mandibles on which sufficient measurements could be taken, the heights of the rami horizontales (measurements M5 and M6) are relatively smaller compared to the widths (M18), to the total lengths (M1), and to the total heights (M2), then in the Bukuran mandible. Also the relatively long symphysis (measurement M21) of the Bukuran mandible shows well in Fig. 21 The large size of the mandible compared to other *Stegodon* mandibles from Java is also shown in Fig. 74.

Discussion

From these morphological differences it is clear that the Bukuran mandible cannot be ascribed to *S. trigonocephalus*. Its M_3s show much resemblance with the lectotype of *S. elephantoides*, as figured by Osborn (1943: fig. 738; measurements of the lectotype are given in Table 9). The *S. elephantoides* M_3 has thick enamel and a lower LF than *S. trigonocephalus* homologues (Table 31). The Bukuran M_3s also agree well with specimens referred to *S. bombifrons*, but this species is characterized by a short mandibular symphysis (Osborn, 1943). The same holds true for mandibles referred to *S. ganesa* or to *S. insignis*, which besides have a higher plate formula. The symphysal region of *S. elephantoides* is not known, but the lectotype molar occurs in a portion of a sinistral mandibular ramus, on which measurements M5 and M6 could be taken and measurement M18 could be estimated fairly well. It appears that there is a considerable conformity between both specimens, both in absolute size of the molars and horizontal ramus, as well as in relative proportions of the dentition and mandible. Based on these similarities mandible PMS-358 is here attributed to *S. elephantoides*. This species has been only reported from Burma. The lectotype originates from '250 miles below Ava' near Yenangyaung, from the upper levels of the Irrawadi beds, Early Pleistocene in age according to Colbert (1938), but possibly covering a much wider timespan. The Upper Irrawadi beds have yielded *E. hysudricus*, which has its first occurrence in the Upper Siwaliks at around 2.7 Ma and continues until at least 2.1 Ma (Hussain et al., 1992). Another element of the Upper Irrawadies is the anthracothere *Merycopotamus dissimilis*. This rare species is recorded from the Upper Siwaliks until at least 2.5 Ma (Steensma & Hussain, 1992) and is also known from Cijulang in west Java (von Koenigswald, 1933), though of uncertain stratigraphic level and age (Braches & Shut-

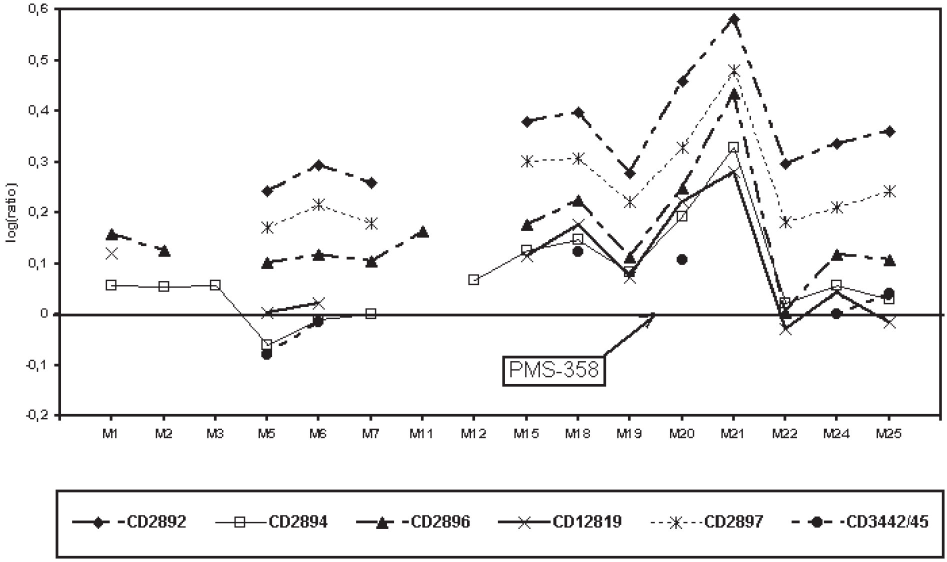


Fig. 21. Comparative log-ratio diagram of measurements taken on *Stegodon* mandibles (based on the method of Simpson, 1945). Size parameters are plotted on the x-axis for each mandible. On the y-axis the logarithm of the ratio between measurements in the mandible considered and the same measurements taken on the reference mandible are plotted. In this way marked size differences in proportions between the reference mandible and the other specimens can be visualized. For example, supposing that if the proportions in a certain mandible would be exactly the same as in the reference mandible, though its absolute size would be larger, its connected log ratio values would show negative values on a horizontal line parallel to the horizontal x-axis of the reference specimen. For further explanation, see chapter 1.
Indicated are the log-ratio values of *Stegodon elephantoides* mandible PMS 358 from Bukuran, Sangiran (= reference specimen) and on several *S. trigonocephalus* mandibles in various ontogenetic stages. The dental wear stages of the various mandibles are: *S. elephantoides* = all ridges M_3 worn; CD-2892 = 5 ridges dP_4 worn; CD-2894 = 3 ridges of M_3 worn; CD-2896 = 2 ridges of M_3 worn; CD-12819 = all ridges of M_3 worn; CD-2897 = 3 ridges of M_1 worn; CD-3442-3445 = 4 ridges of M_3 worn.

ler, 1984; Sondaar, 1984; Leinders et al., 1985). *M. dissimilis* may have migrated to Java during the Early Pleistocene together with the archaic *S. elephantoides*.

Small-sized *Stegodon* molars

Description of the material

In the GRDC Collection from Java a *Stegodon* molar was encountered, which could not be allocated to *Stegodon trigonocephalus*. The molar was found broken into various fragments, which could be fitted together. This lower dextral molar bears two numbers: K-391 and 61.L. According to the register K-391 was found near Ranji Kares (Randji Kares), Cirebon Residency, in eastern West Java. Measurements of this molar are presented in Table 10. Apart from some damage on the buccal side of ridges 2-4, the 218 mm long molar is intact. The anterior 4 ridges are slightly worn but in none of the ridges enamel loops have completely formed yet. It is a lower molar and carries x8x or x9 ridges (w measurements given in Table 10). The shape with the marked posterior tapering indicates that we are dealing with an M_3, and obviously a small one, with relatively few ridges. The h/w indices of ridges 5 and 6 amount 61 and 60, respectively. The molar ridges are widely spaced as expressed by the relatively low LF value of 4.2, despite its small size. Even though the molar falls below the size range observed in *S. trigonocephalus*, its LF is within the size range of the latter, due to the relatively low plate formula. Another plesiomorphic character is the limited number of digitations, 4-7, with 4 digitations clearly larger than the remaining ones. The enamel shows 'Stufenbildung' and is 4-5 mm thick. Cement is deposited between the ridges only. The ridges are inclined forward, with the posterior faces sloping and slightly convex and the anterior faces vertical and slightly concave. A median expansion on the anterior and posterior ridge faces is developed only in ridge 1.

Another lower M_3 from Java of unknown stratigraphic level bears GRDC collection number 93.L. It is of the left side, carries x11x ridges and is 238 mm long. Its measurements are also presented in Table 10. It is very similar to the already mentioned specimen CD-2296-2187, and, apart from being relatively narrower, to von Koenigswald's (1933) type specimen of *S. trigonocephalus praecursor*.

Discussion

Though the above described M_3s are all characterized by a relatively small size and most bear a lower number of ridges than in *S. t. trigonocephalus* from Trinil H.K. and Kedung Brubus (compare Tables 10 and 31), only specimen K-391 from Cirebon, with its combination of small size and a very low number of widely spaced ridges, seems to be distinct on species level from *S. trigonocephalus*. Apart from the low number of ridges, the Cirebon specimen shows an additional primitive aspect in bearing a relatively low number of apical digitations per ridge. It may represent a diminutive insular form of one of the earliest *Stegodon* invaders of Java and may have descended from *S. elephantoides*. At present it can only be speculated that the Cirebon area (Fig. 20) may have constituted a separate palaeo-island during the early part of the Pleistocene. Another palaeo-island inhabited by a pygmy *Stegodon* species was inferred to have existed north of Sambungmacan (Aziz & van den Bergh, 1995). Additional fossil remains from the Cirebon area would be required to test this hypothesis.

The small-sized Trinil specimen (CD-2896, Table 10) is attributed to a small, female individual of *S. t. trigonocephalus*. Unlike the other small M_3s listed in the same table, the Trinil specimen is the only specimen that carries 13 ridges, the same number as in other, larger M_3's from the same locality. Also its relatively large L/W index and high number of apical digitations correspond with the other Trinil homologues (Table 31).

The remaining specimens listed in Table 10 possibly represent populations of a *S. trigonocephalus* subspecies that inhabited Java relatively early (they all show a low number of ridges), and may still be closer to the first invading population of *S. ganesa*, the presumed ancestor of *S. t.* Insular conditions or deteriorating environmental conditions may have caused some degree of dwarfing. Amongst these specimens is GRDC/K-133, which was originally referred to as *S. t. praecursor* by von Koenigswald (1933). It is deemed desirable to retain this subspecies name, to express the more primitive dental stage as encountered in the Trinil and later fossil assemblages. Due to the limited stratigraphic and paleontological data this designation must be considered as tentative. Hypothetically, the periodic isolation of Java from the SE Asian mainland due to eustatic sea level fluctuations, and even isolation of parts of Java that are now connected with the main island, would be expected to have caused repeatedly the genetic separation of *Stegodon* populations from the main(land) stock. The genetic isolation during periods of high sea level could have led to the evolution of distinct subspecies and even speciation various times.

Stegodon trigonocephalus ngandongensis subsp. nov.

Stratigraphic position

An enormous collection of fossil vertebrates was excavated by the Dutch East Indies Geological Survey from the Solo River terrace near Ngandong and from other localities during the early 1930's. Near Ngandong the deposits constituting the terrace are unconformably overlying Pliocene marine deposits along the slopes of the Solo River transverse valley, which cuts through the Kendeng Mountains (Figs. 20, 22). The terrace occurs 20 m above the present day Solo river (Oppenoorth, 1932). Apart from the *Homo erectus* calvaria, for which the locality is now well known, over 20000 vertebrate fossils were excavated (Ter Haar, unpublished report, 1934). Nowadays, there remains only one drawer with fossils from Ngandong in the Collection of the GRDC, mostly representing specimens figured by von Koenigswald (1933), but also including some fossils left undescribed. Amongst the latter mentioned are 4 milkmolars and an M^1 of *Stegodon*, with their original labels attached to them, providing data on the collecting circumstances. In addition there is a dozen of *Stegodon* molar remains in the GRDC collection with original labels, indicating that they were obtained from the excavations near Watualang (Watoealang) and the Grenjengan (Grendjengan) river (Fig. 22). It is generally thought that the fossil assemblage from Ngandong is younger than that from Trinil and Kedung Brubus; many species, including *Homo erectus*, differ on a subspecies level from their close allies in the older faunas (de Vos et al., 1994). Von Koenigswald (1934) considered the fauna from Watualang as equivalent with that of Ngandong, both Late Pleistocene in age, but he did not refer to the faunal remains from the Grenjengan excavation.

Because of the supposed younger age of the Ngandong remains it is worthwhile to see whether the *Stegodon* from Ngandong and the other terrace sites is more advanced than that from Trinil and Kedung Brubus. Unfortunately, there are no M3s in the Ngandong collection. Von Koenigswald (1933) merely noted that the *Stegodon* remains from the Ngandong excavation resemble those described by Soergel (1912), Janensch (1911) and van der Maarel (1932), and he attributed the Ngandong material to *S. trigonocephalus*. The GRDC specimens from Ngandong are mostly milkmolars. Fortunately there are a reasonable number of milkmolars from the Trinil H.K. and Kedung Brubus localities to allow a comparison with the Ngandong specimens. Below only those dental elements from the GRDC Collection will be treated, which according to their attached labels originate from the Ngandong excavation with certainty. The collection numbers written on the labels correspond to the numbers in the original Ngandong fossil register kept up to date during the excavation, and differ from the GRDC registration numbers, which were written on the molars subsequently. The labels mention the finding date, the excavation number and the layer and

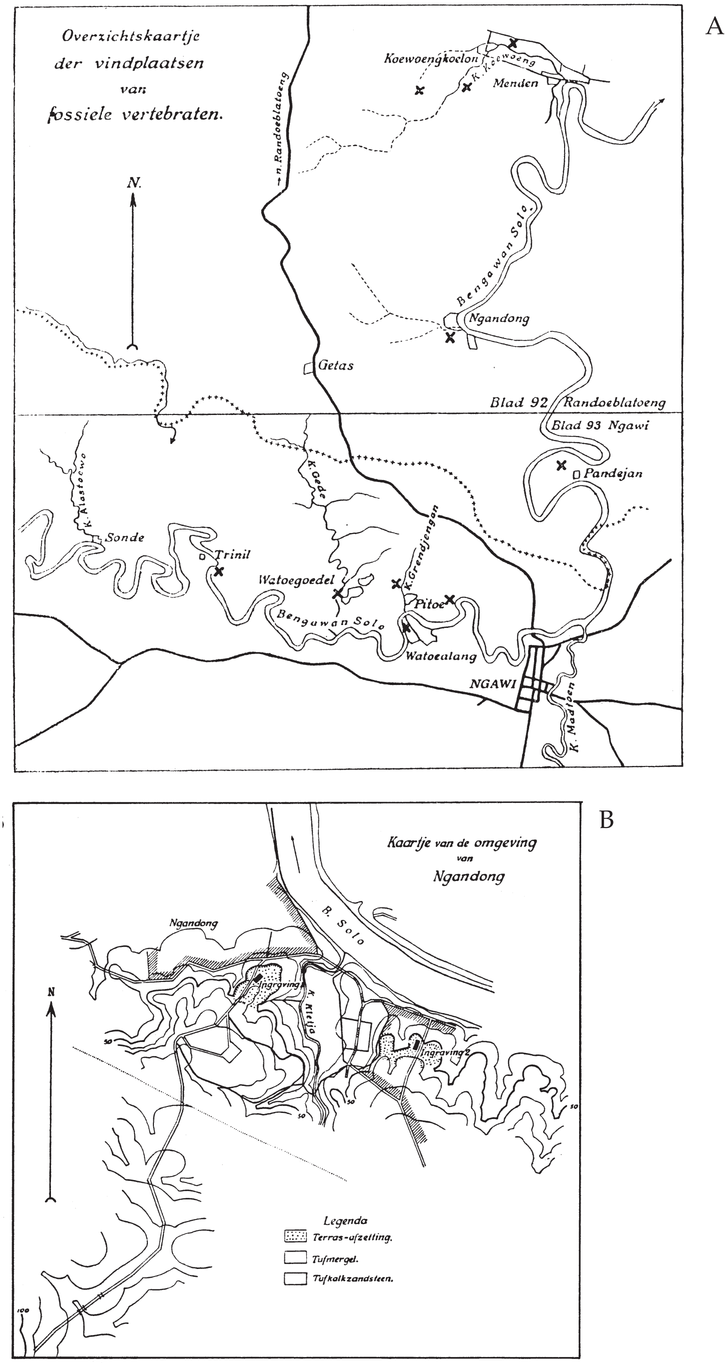


Fig. 22. Map of the Solo River transverse valley (A) and detailed map of the excavation sites in the Ngandong terrace (B) (after Oppenoorth, 1932).

quadrant from which the fossil was recovered. The excavation numbers on the labels do not correspond with the excavation numbers 1 and 2 of Oppenoorth, which are also shown in Fig. 22B. On the excavation plan of ter Haar (1934, app. 3) the main excavation 1 of Oppenoorth (1932) is subdivided into various areas some of which are indicated with an excavation number. Shown on the plan are excavation numbers 1b, 1c, 1D and VIII, which thus represent subdivisions of the excavation. It seems that the excavation (= 'ingraving') numbers on the labels correspond to the numbers of this subdivision. The layer (= 'laag') numbers written on the labels were not always consistently used according to ter Haar (1934), and may deviate from the layering division given by Oppenoorth (1932).

The measurements of the Ngandong milkmolars are given in Table 11.

Description of the material

Specimen GRDC/K-363 is an isolated dextral upper molar. Its label in Dutch language reads as follows: '11309, Ingr.I^B: blok F, Ngandong, laag IV, 22-9-32'. The first number represents the original registration number of the specimen. 'Ingr.(aving)' = excavation, 'blok' = quadrant, 'laag' = layer and the last numbers refer to the collecting date. Of this specimen the 6 anterior ridges are worn, the anterior 3 showing completed enamel loops. The latter are broken on the lingual side. Ridge 1 is more heavily damaged, but shows on the anterior surface of the buccal portion a small portion of the anterior contact facet with the foregoing molar. This proves that this ridge indeed represents the most anterior one. In front of the lingual half of the anterior ridge a small halfridge may have been present. The plate formula can thus be reconstructed as (x)8x. Its length lies around 160e mm and the maximum width of 77e mm is at ridge 4. Additional measurements are given in Table 11. The enamel loop of the second ridge shows a weak double median expansion with a constriction in the middle, reminiscent of a median sulcus, which, however, is not developed on the posterior, unworn portion of the molar. The enamel is crenulated and double-layered with stepwise wear at the occlusal surface. Cement is abundantly present between the ridges and on their flanks.

Specimen GRDC/K-351 is a dextral mandibular fragment with worn dP_3 and unworn anterior dP_4 fragment. Its label reads as follows: '13322, Ingr: IB blok g, Ngandong, laag III, 14-12-32'. This dP_3 is 63 mm long and carries 7 ridges, 6 of which are worn. The lingual borders of the anterior three ridges are damaged, but on the buccal side the constriction characteristic for lower dP_3's can be noticed behind ridge 1. Measurements are given in Table 11. Of the dP_4 behind it only x5- ridges remain. All 5 ridges have a strongly developed median sulcus.

A well pronounced median sulcus is also developed in the next specimen, GRDC/K-330B (Pl. 2,fig. 1). It is an isolated, unworn, dextral dP_3 with a label that reads: 'Nʃ 20862, Bl.XIV, Ngandong'. The milkmolar carries x7x ridges and is constricted between ridges 1 and 2. Only the buccal half of ridge 1 is touched by abrasion. The number of digitations varies between 9 and 15.

The label of an anterior portion of a lower, sinistral dP_4, specimen GRDC/K-320, reads: '9875, Ingr.I.B. bl. E, Ngandong, laag 3'. It has x$6^1/_2$- ridges preserved, all unworn. Again this milkmolar is characterized by a strongly developed median sulcus.

Discussion

The only true molar amongst the Ngandong specimens (GRDC/K-363) is larger than the M^1s of *S. trigonocephalus* from the localities Trinil H.K. and Kedung Brubus but smaller than the M^2's from the latter mentioned localities (compare L and W in Table 31A-B with Table 11A). Its plate formula ((x)8x) is also intermediate between that of the M^1 and M^2 of *S. trigonocephalus* from Trinil and Kedung Brubus (x7x and x9x, respectively). Thus we can choose to interpret the Ngandong molar as a rather large, advanced M^1 with a relatively high plate formula, or a rather small M^2 with a relatively low plate formula. The first interpretation is more likely, because the milkmolars from Ngandong, of which the serial position is more easy to determine, indicate a relatively large size in combination with an advanced plate formula.

When comparing the Ngandong milkmolars with those of *S. trigonocephalus* from the localities Trinil and Kedung Brubus (Table 31A-B), it follows that the Ngandong lower dP_3s have one ridge more. The h/w indices of the dP3s in general are less suitable for comparison, because the anterior constriction leads to a high range of h/w indices within a single element, as is the case in the unworn Ngandong dP_3 (GRDC/K-330). In any case, the h/w indices of both unworn Ngandong dP_4s and the dP_3 fall within the range of homologue elements from Trinil. Other size parameters measured on the Ngandong milkmolars tend to show overlap with homologue elements from Trinil H.K. and Kedung Brubus (compare L, W, L/W, H, ET in Tables 11A and 31A-B). There is one qualitative character in which the Ngandong milkmolars tend to differ from their Trinil homologues, namely in the development of the median sulcus. The median sulcus is generally more pronounced and deeper in the Ngandong specimens than in the Trinil specimens.

The more advanced plate formula of the Ngandong molar remains are in accordance with the presumed younger age relative to the material from Trinil H.K. and Kedung Brubus. Unfortunately, the material is limited, but there are some additional molar remains from the excavations at Watualang and Grenjengan, which support the differentiation between the molar material from the Solo terraces on the one hand and Trinil H.K. and Kedung Brubus on the other. The Watualang and Grenjengan material corresponds well in their more advanced morphology with the Ngandong remains and will be treated next.

Description of the material from Grenjengan and Watualang

A dP_3 from the excavations at Watualang (GRDC/K330A) carries a label that reads: 'Watoealang, Ing.I laag II, 6-11-30'. The unworn dextral milkmolar (Pl. 2, fig. 2) carries 7x ridges and measures 66.5 x 37 mm, with a LF of 9.8. Its h/w indices vary between 44 and 64, it has a very marked median sulcus and is very similar to the Ngandong dP_3s.

There is also an anterior M_3 fragment from the same locality (GRDC/K387), with a label that reads: '2205, Ingraving 1.N., laag II, 13-10-31, Watoealang'. Only x$2^1/_2$-halfworn ridges remain, all showing the presence of a marked median sulcus. The width of ridge 1 is 95 mm, which was probably not the maximum width. The W range of the Trinil M_3's varies between 71 and 98 mm, which again indicates a rather large size, comparable to the Ngandong molar elements.

A complete, only slightly worn sinistral dP_4 (GRDC/K337) originates from Grenjengan. Its label reads: 'Ingr. VIII, Grindjingan, P1 tot laag II, Bl. Congl., 6-8-31'. It carries x9x ridges, of which the anterior 2 are worn. It is 124 mm long, which is just above the range of homologue elements from Trinil, which besides have only x8x ridges (n = 5). The maximum width of 50 mm occurs at ridge 7. The LF amounts 7.8, and the ET lies around 2 mm, with stepwise wear and delicate wrinkles. A median sulcus is strongly developed in the anterior two ridges, but shallows in posterior direction. Cement is only deposited in the valleys between the ridges but leaves the digitations and flanks free.

A second incomplete dextral dP_4 from the same locality (GRDC/K404) bears a label with the inscription: 'Ingr.VIII, 248, vol laag, Grindjingan, Bl. Cong., 10-8-31'. It is half worn and broken just in front of the posterior rootmass. There are -8x ridges as far as the specimen is preserved. If only one ridge is missing, which would be on top of the broken anterior hook of the root, the plate formula would be (x1)8x. The length as far as preserved is 108+ mm. The maximum width of 50 mm occurs at ridge III. The LF amounts 7.8, and overall, this dP_4 is of much the same proportions as the foregoing specimen, though its wear is in a more advanced stage, only ridge I not being touched by abrasion. The enamel wear patterns of the less worn ridges II-V clearly show the presence of a median sulcus.

An anterior fragment of a dextral M_1 (GRDC/K376) from the same locality and carrying 9- ridges has a label on which some information has been blurred. However, the name "Grindjingan" can still be distinguished. Only the anterior two ridges are slightly worn. Ridge 3 is irregular, i.e. it is developed only on the buccal half of the crown (this incomplete ridge is included in the plate formula of 9-). Judging from the broken posterior outline at least one ridge is missing. Ridge 9 is the widest, with a width of 65 mm, just within the upper limits of M_1's from Trinil. Again, the molar is characterized by a well developed median sulcus.

There is in addition a posterior fragment of a sinistral dP_4 still embedded in a portion of the mandibular ramus (GRDC/K371). The attached label reads: '1223, Ingraving VIII.P., K.Grendjengan, laag VI, 24-7-32'. There remain -7x ridges, all worn except for the posterior halfridge, which consists of a single conule. The most anterior preserved ones are worn down to the crownbase. The anterior portion of the molar is missing, but the anterior hook of the root is still visible in the alveole in front of the molar remnant. Judging from this alveole, the total length would have been around 120e mm. The maximum width of 51 mm occurs at ridge II. The LF is 8.1 and the ET lies between 2 and 2.5 mm. The enamel loops of ridges II-IV are constricted in the middle, marking the median sulcus.

A second mandible fragment, of the dextral side, bears the posterior portion of a dP_3 (GRDC/K402). Its label reads: '1228, Ingraving VIII.P., K.Grendjengan, Laag VI, 27-7-32'. There remain -3x worn ridges of the dP_3. The ramus is broken through the alveole of the dP_4 behind it, which is empty. The largest width of the dP_3 occurs at ridge I and is 35 mm. Again, the enamel wear pattern of the half worn ridge II consists of a lingual and buccal part, separated by the median sulcus.

Discussion

The *Stegodon* molar material from Ngandong, Grenjengan and Watualang appears to be uniform and can be clearly distinguished from homologue elements from Trinil

H.K. and Kedung Brubus. The Solo terrace molars have one ridge more per homologue element, and their dimensions are slightly larger or within the upper size ranges compared to the Trinil/Kedung Brubus homologues. Furthermore, they are characterized by a more pronounced median sulcus, which especially in the true molars is usually lacking in the Trinil and Kedung Brubus specimens except for the anterior two ridges. These differences justify the erection of a distinct subspecies of the common Java stegodont, *Stegodon trigonocephalus*. Von Koenigswald (1934) distinguished two subspecies: the older *S. t. praecursor* from the Kali Glagah Formation, and the more advanced *S. t. trigonocephalus* from Trinil, Kedung Brubus, but also from Ngandong and Watualang. However, he never presented sound molar descriptions of the latter subspecies. As it has been shown above that the *Stegodon* from Ngandong (and also from Watualang and Grenjengan) has molars which can be distinguished from homologues from Trinil and Kedung Brubus, it is here proposed to separate them on subspecies level. The material from Ngandong is here designated as *S. t. ngandongensis* subsp. nov. The measurements of the dental elements of this new subspecies are summarized in Table 11B, including all the above mentioned excavated material from Ngandong, Watualang and Grenjengan. The more advanced plate formula of *S. t. ngandongensis* as compared to *S. t. trigonocephalus* is in accordance with its younger age.

In conclusion, it can be stated that apart from the more archaic *Stegodon elephantoides*, also three successive subspecies of *S. trigonocephalus* can now be recognized on Java. *S. trigonocephalus* is closely related to *S. ganesa*. The three subspecies of *S. trigonocephalus* are considered to portray three successive evolutionary stages, which can be tied to the faunal succession in the following way: The Early Pleistocene, poorly known, *S. t. praecursor* predates the Trinil Fauna. *S. t. trigonocephalus* occurs in the Late Early Pleistocene Trinil and Kedung Brubus Faunas. The Late Pleistocene *S. t. ngandongensis* subsp. nov. occurs in the Ngandong Fauna. The latter shows the most advanced ridge formula of its intermediate molars. The ridge formula of the three successive subspecies can be given as follows (excluding anterior and posterior half-ridges):

	dP2	dP3	dP4	M1	M2	M3
S. t. praecursor:	—	—	—	—	—	—
	—	—	—	—	—	11
S. t. trigonocephalus:	—	6	7-8	7	9	11
	—	6	8	8-9	10	13
S. t. ngandongensis:	—	—	—	8	—	—
	—	7	9	9+	—	—

In addition, various dwarfed stegodonts have been living on Java, probably in isolated subregions. Most likely, they evolved during times of separation from the SE Asian mainland. To date, dwarf stegodonts are known from Cirebon (this thesis) and

Sambungmacan (Aziz & van den Bergh, 1994), both probably of Late Pliocene or Early Pleistocene age, and from the surroundings of Djetis. The latter has been named *Stegodon hypsilophus* Hooijer, 1954d. The stegodont succession is schematically shown in Fig. 24.

Elephas maximus Linnaeus, 1758

Stratigraphic position and age

The *Elephas* remains from Cipeundeuy originate from a sand quarry near Padalarang, 20 km W of Bandung, West Java. Their Late Pleistocene age is reasonably well ascertained by means of radiocarbon dating of two samples from below and above the fossil-bearing fluvial layer at Cipeundeuy (Fig. 23). The radiocarbon ages of these samples (Dam, 1994) are 35.500 +4600/-2900 (sample GrN.16208, a wood fragment from the underlying lahar deposit) and 29.600 +450/-420 (sample GrN.16209, organic material from overlying lacustrine clay).

Description of the material

The *Elephas* remains from Cipeundeuy comprise one proximal metatarsus-IV and five molar remains, of which the measurements are presented in Table 12.

There is a large anterior portion of a lower sinistral molar broken behind lamella 12 (Pl. 2, figs. 3-4; no. GRDC/CPD90-1). The length, as far as preserved and measured perpendicularly to the average lamellar plane (method C of Maglio, 1973: 11), is 181+ mm. When viewed from aside with the occlusal surface in a horizontal position, the lamellae appear to be folded in a sinusoidal way, a feature common in high-crowned lower *Elephas* molars (Pl. 2, fig. 4). Another character identifying the present molar as a lower one, is the slight convergence of the lamellae in apical direction. This is expressed by the difference between the LF (according to the definition used here taken as the average of the lingual and buccal lamellar frequencies at the crown-root transition), which is 5.9, and the lamellar frequency on the occlusal surface, which is 6.5. In M_3s of *E. maximus* the apical convergence of the lamellae is more pronounced, indicating that the present molar most likely represents an M_2. The largest width of 71 mm occurs at lamella 9, which would be too large for an M_1 of either *E. maximus*, *E. hysudrindicus* or *E. namadicus*. (Hooijer, 1955b, Maglio, 1973, Roth, 1988). The largest width of individual lamellae is not near the roots, but approximately halfway the height. Above this point the lamellar flanks converge slightly in apical direction and terminate in a rounded apical profile, the digitations covered with cementum. The anterior 8 ridges are worn, together forming a longitudinally concave occlusal surface of 130 mm long, which makes an angle of c. 70° with the orientation of the lamellae. The enamel wear patterns of lamellae 4-7, which are abraded up to about 25% of the total lamellar height, are tripartite, typical for *Elephas*. Of lamella 8 only the four central digitations are worn open. The anterior three lamellae show single enamel loops. Of these enamel loops a posterior median dilatation is developed in the anterior two lamellae, consisting of multiple enamel folds. The posterior enamel face of the most posteriorly preserved lamella, does not show any median pillar or expansion that would give rise to a dilatation in the wear pattern upon abrasion. The enamel is thin and heavily folded, with 4-5 folds per cm and amplitudes mostly exceed-

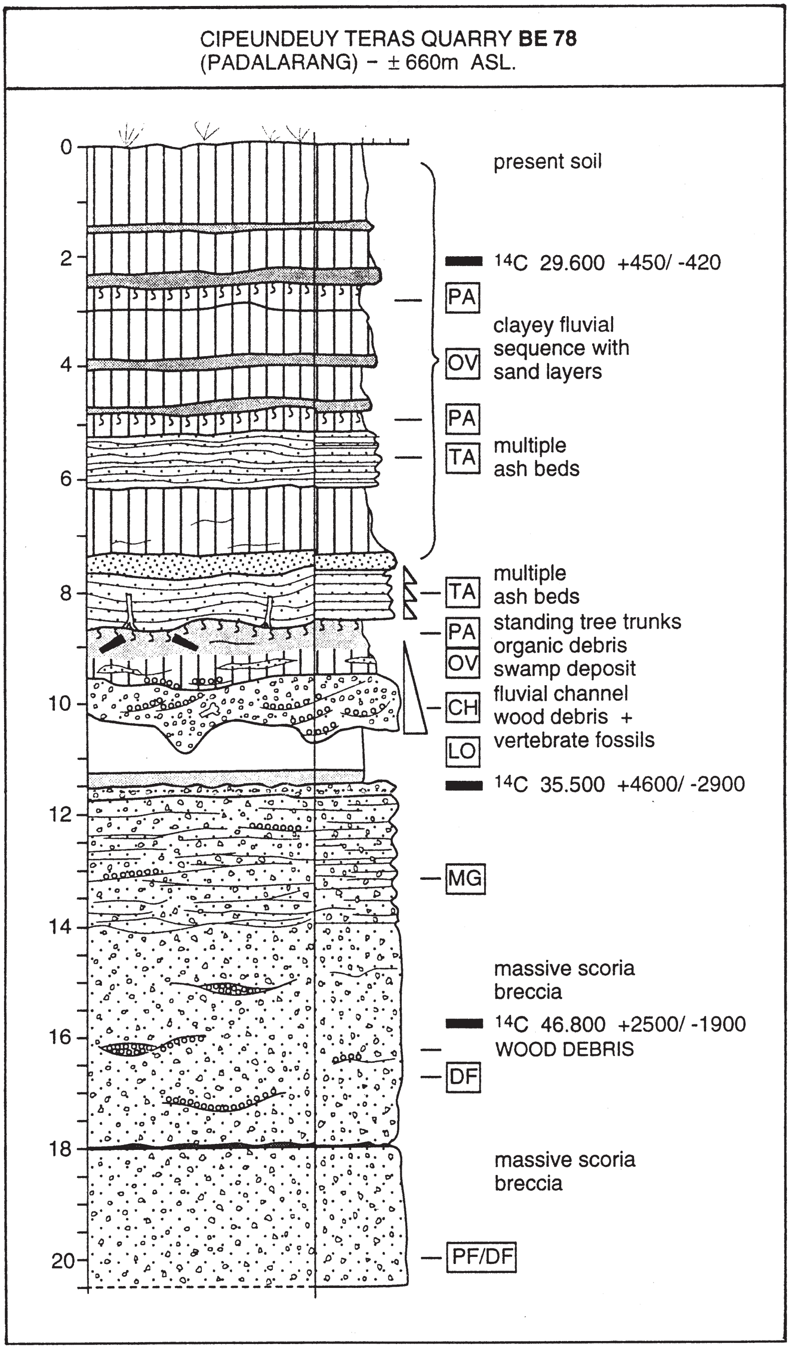


Fig. 23. Stratigraphic profile of the sand quarry near Cipeundeuy, West Java, showing the fluvial layer which yielded *Elephas maximus* molars and remains of various other vertebrate species and the radiocarbon dated levels. The figure is taken from Dam (1994).

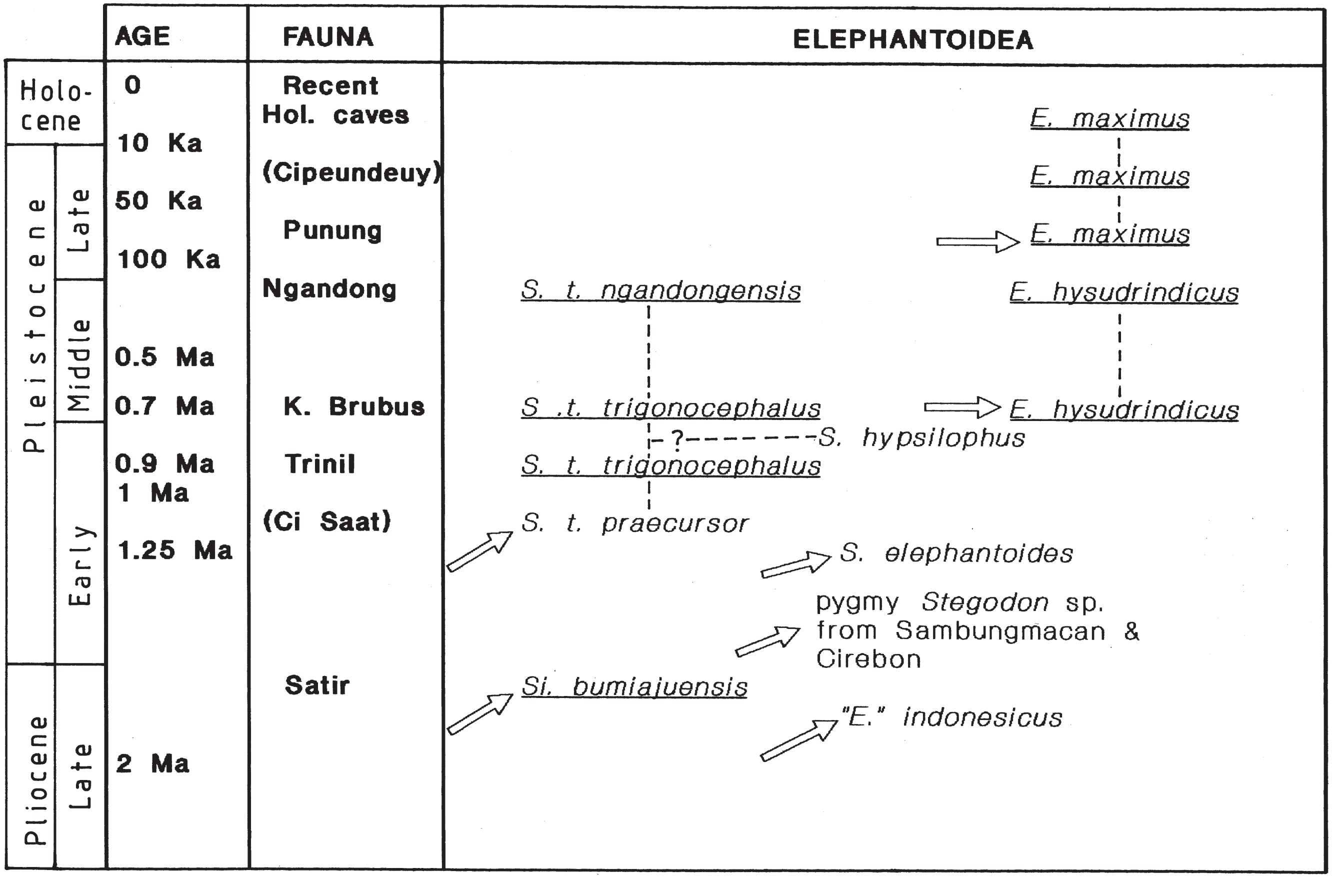


Fig. 24. Ranges of Elephantoidea species from Java relative to time. Species present in the type faunas of the faunal stages have been underlined. Lineages which are thought to be continuous are connected with dashed lines. Immigration events are indicated by arrows.

ing the thickness of the enamel. The h/w indices vary between 178 and 184 in the four unworn posterior lamellae. It is not possible to give the exact number of lamellae that are missing at the back of the present M_2. However, the heights and widths of the successive lamellae are rapidly decreasing towards the back, suggesting that at most 2-5 lamellae are missing.

A second lower molar of larger dimensions is represented by GRDC/CPD90-36. It is an anterior fragment of a sinistral molar, comprising x3- worn lamellae. Lamellae 2 and 3 are broken buccally from occlusal surface to the root. Like in the foregoing specimen, the lamellae are folded vertically and the occlusal surface makes an angle of 70° with the apical portion of the lamellae, showing this molar to be a lower one. The small preserved portion of the grinding surface is plane in antero-posterior direction. The width of lamella 2 can be estimated to have been at least 82+ mm, assuming that it was wider buccally than lamella 1. The maximum width of the molar must have been even larger than that. Also the enamel is thicker than in the M_2 CPD90-1 (Table 12), allowing to determine this fragment safely as an M_3. The incomplete wear patterns of lamellae 2 and 3 show two enamel islands; a third one must be missing on the broken buccal portion. Lamella 1 shows a single enamel loop, which is expanded posteriorly along the median axis of the crown. The enamel is irregularly folded to a similar degree as in the M_2. The worn height of lamella 3 is 129+ mm.

An upper molar fragment consisting of -6- lamellae is represented by specimen GRDC/CPD90-3. The lamellae are not folded vertically, and the longitudinal profile over the unworn lamellar apices is slightly convex, making an angle of c. 60° with the lamellae. Therefore, this fragment represents an upper molar. Only the most anteriorly preserved lamella is slightly worn, the central digitations showing rounded dentine islands. The maximum width of 66 mm occurs at the second preserved ridge at the back, which suggests that the fragment is of an M^1. The maximum width of individual lamellae is reached at about one third of the total height away from the crown-root boundary. The h/w indices of individual ridges vary between 191e and 208. The anterior face of the most anterior lamella is flat without a median pillar or expansion visible.

There is an anterior fragment of an upper molar with a slightly convex occlusal surface (GRDC/CPD90-2). The wear surface makes an angle of 63° with the lamellae. There are x5- lamellae preserved, all worn. The three most posterior lamellae have trifold, the anterior two ones single enamel wear patterns, all lacking median dilatations. The thin enamel (ET between 1.5 and 1.8 mm) is irregularly folded with an amplitude exceeding the ET. The LF is 7.9, whereas the lamellar frequency along the median axis of the occlusal surface is 6.9. The latter is smaller as usual in upper molars where the lamellae diverge in apical direction. The maximum width (W = 69 mm) occurs at lamella 3. The W falls within the upper range of variation observed in the M^1 of *E. maximus* or corresponding with the lowermost limit of the width in the M^2 of the Recent Asian elephant, as given by Roth (1988). The worn height of the least worn, most posterior lamella is 133+ mm, giving an h/w index of at least 196+.

The last dental specimen to be described is a complete lower molar (GRDC/CPD-114). It carries x16x lamellae and has a total length of 290 mm. The maximum width of 76 mm occurs at lamella 7. Lamellae 1-11 are worn, of which the anterior two almost down to the crownbase. The unworn height of lamella 12 is 147 mm, while the height of individual lamellae decreases further backward. The h/w indices of the unworn posterior lamellae varies between 188-210+, while the H/W index comes probably close to 200e. Unworn lamellae show 6 digitations. Two longitudinal grooves divide the enamel loops of slightly worn lamellae into a trifold pattern. The LF is 5.4, while the ET lies between 2.0 and 2.3 mm. The frequency of the enamel folding is 3-4 folds per cm, with the enamel amplitude varying between 1 and 3 mm. Like in specimen CDP90-1, the lamellae have an S-shaped curvature in lateral view, and have their maximum width about halfway their height. The dimensions of CPD-114 are very close to those of specimen CPD90-1, both representing M_2s.

Specimen GRDC/CPD-61 is a damaged proximal fragment of a metatarsus IV. The only measurements that can be given are the transverse diameter of the proximal articulation surface measured anteriorly (95e mm) and the minimum antero-posterior diameter of the shaft (46 mm). The shaft is slenderly built and the proximal epiphysis protrudes widely beyond the shaft posteriorly.

Discussion

The widths and heights of the fragmentary Cipeundeuy molars fall within the range of variation of molar samples of extant *E. maximus* as given by Roth (1988). But as indicated by various authors (van der Maarel, 1932; Hooijer, 1955b; Maglio, 1973), there is a considerable overlap in size and morphology between molars of the Recent Asian elephant and the fossil species *E. namadicus* and *E. hysudrindicus*.

Molars of the three *Elephas* species mentioned above show a considerable overlap in their h/w indices. The molar height is generally 50-100 % higher than the width in *E. hysudrindicus*, and 50-150 % higher in *E. namadicus* and *E. maximus* (Maglio, 1973). The h/w indices of unworn lamellae in the Cipeundeuy molars vary between 178 and 210, which is just within the upper limits of variation known to occur in *E. hysudrindicus* (Hooijer, 1955b), but more closely to the values in *E. maximus* and *E. namadicus*.

There is one aspect that points to the recent elephant. That is the number of x16x lamellae in the complete lower M_2 (GRDC/CPD-114). In *E. namadicus* the plate number of the M_2 varies between 9 and 14 (Maglio, 1973), whereas in *E. maximus* it varies between 16 and 21 (Roth, 1988). The plate number of the M_2 of *E. hysudrindicus* is not known, but its M_3 has 18-21 plates, which is lower than the range observed in *E. maximus* (21-29 plates: Roth, 1988). It can therefore be assumed that the plate number in the M_2 of *E. hysudrindicus* may also have been lower on average than in the homologue molar of the Indian elephant. A plate number of 16 for the M_2 thus favours a designation of the Cipeundeuy material to *E. maximus*.

Further characteristics pleading in favour to attribute the Cipeundeuy molars to *E. maximus*, are the general lack of median dilatations or expansions in the enamel loops of worn plates. However, it should be noted that the lack of median dilatations is not strictly restricted to molars of *E. maximus* and there are some molars that have been attributed to *E. namadicus* which lack such expansions as well (Hooijer, 1955b). On the other hand median expansions do occur occasionally in *E. maximus* molars (e.g. in the M_3 fragment from Sibrambang Cave, Sumatra, attributed to *E. maximus*: Hooijer, 1955b: pl. XVII, fig. 3).

A character that tends to exclude the assignment of the Cipeundeuy molars to *E. hysudrindicus* can be found in the lamellae of upper molars of this fossil species. In *E.*

hysudrindicus upper molars the lamellae tend to have their opposite buccal and lingual flanks running parallel over most of their height. The lamellae of upper molar fragments from Cipeundeuy in contrast, have their flanks diverging from the crown-base in apical direction to about one third the distance of the total height, and then steadily converging again in apical direction close to the apex.

Summarizing, it is concluded that the combination of the various morphological features of the Cipeundeuy molars allows their attribution to *Elephas maximus*.

A preliminary examination of the accompanying fossil assemblage from the same fluvial layer, comprising around 140 fossils of mostly postcranial elements, revealed the presence of the following taxa: *Elephas maximus* (sin. M_2 fragm., sin. M_2, anterior M_3 fragm., dex. M^1 fragm., dex. M^1 or M^2 fragm.), *Rhinoceros sondaicus* (M^2, I_1), *Muntiacus* sp. (mandible with P_2-M_3, M^2, distal tibia fragm.), medium-sized cervid (*Axis* sp.; mandible with P_4-M_3, 3 proximal metatarsus fragments, 2 distal humerus fragments), large cervid (various antler fragments), *Bubalus* sp. (horncore fragm.), bovid (metatars prox., M^2, horncore fragm. with rounded keel), *Hystrix* sp. (gnaw marks on fossil bone).

The Cipeundeuy Fauna, radiocarbon dated at 30 ka, is younger than the West Sumatran Cave Faunas, which include *E. maximus* and which are characterized by the dominance of *Pongo* teeth. Hooijer (1955b) assumed a Holocene age for this fauna, but recent aspartic acid racemization datings on fossils from Jambu and Lida Ajer Caves, place them between 60 and 80 ka (Skelton & de Vos, in prep.). Based on faunal similarity the Punung Fauna from Java was assumed to be of similar age as the Sumatran Cave Faunas, corresponding with the last interglacial. The poorly known Cipeundeuy Fauna only contains recent elements, as far as determinations permit to asses, and is younger than the Punung Fauna. It is older than the Holocene Cave Faunas from Java (Wadjak, Sampung). Though the Punung Fauna perhaps records the oldest known remains of *E. maximus* on Java and the fauna from Sampung the latest occurrence of the Asian elephant, the very fragmentary remains from these sites do not allow any determination at species level with certainty. The Cipeundeuy remains constitute the first unambiguous evidence for *E. maximus* on Java.

Elephantoids, sea level fluctuations and climate

Based on the present data the Quaternary succession of Elephantoidea on Java can be schematically shown as in Fig. 24. The successive faunal stages and their estimated ages are indicated to the left. The various Elephantoidea taxa from Java that have been recognized are indicated to the right. Species that are recorded from the type faunas of the successive faunal stages are underlined. At least 6 immigration events can be recognized (indicated by arrows in Fig. 24). Local evolutionary lineages are indicated by dotted lines.

So far there is no proof for the presence of mammals on Java at 2.4 Ma, when the first marked glacio-eustatic sea level lowerings are thought to have occurred (van den Bergh et al., 1996). The Satir fauna is the oldest recognizable faunal unit on Java, of which the chronostratigraphic position is known. It has an age of between 2 and 1.5 Ma and is characteristic for island conditions. *Sinomastodon bumiajuensis* is the only elephantoid known from this fauna.

Java gradually emerged due to tectonic and volcanic processes during the Late Pliocene. Hominids are still lacking at this stage. Fairly isolated conditions of Java seem to have continued until c. 0.8 Ma, as suggested by the still unbalanced character of the Trinil Fauna, with endemics such as *Duboisia santeng*. The Trinil Fauna has an age of c. 0.9 Ma. From the Upper Pliocene and Lower Pleistocene deposits several isolated findings of dwarfed elephantoids are known, of which the stratigraphic position and age can only be roughly estimated. These are the archaic and small-sized *Elephas indonesicus* from Ci Pangglosoran near Bumiayu (van den Bergh et al., 1992), and the pygmy stegodonts from Sambungmacan (Aziz & van den Bergh, 1994) and Cirebon (this thesis), the latter probably derived from the rare *Stegodon elephantoides*. A single specimen of the archaic *S. elephantoides* from Bukuran is dated at between 1.3 and 1.2 Ma (this thesis).

During this early period of mammalian colonization of Java, between 2.4 and 0.8 Ma, the eustatic sea level as deduced from ice volume estimations based on isotopic ratios in foraminifera tests, is thought to have shown moderate fluctuations, with a mean of around 70 m below present day level (PDL) and lowest sea levels at around 100 m below PDL (Vrba, 1990). This fluctuation mode appears to have remained constant until around 0.8 Ma (Fig. 25A).

A major faunal immigration event to Java, leading to a maximum number of medium to large-sized mammalian species, as recorded in the 0.7-0.8 Ma old Kedung Brubus Fauna (Table 1), corresponds well with the onset of a distinct mode of eustatic sea level fluctuations as compared to the foregoing period (van den Bergh et al., 1996). At 0.8 Ma the mode of sea level fluctuation changed drastically to high amplitude fluctuations with minimum sea levels down to 170 m below PDL and an average sea level of around 90 m below PDL. This fluctuation mode continued up to Recent times (Vrba, 1990). This change at 0.8 Ma has also been detected using the seismostratigraphic method (Vail et al., 1977; Haq, 1991). Though this method is not able to detect short-term sea level fluctuations, a worldwide low sea level stand can be recognized, which started at 0.8 Ma. From this time onward low sea levels apparently lasted for sufficiently prolonged periods and were of sufficient amplitude to mark their presence in a large number of seismic profiles worldwide.

In Java relatively open and dry conditions prevailed at this stage as deduced from the composition of the Kedung Brubus Fauna (de Vos et al., 1982; Sondaar, 1984) and pollen analysis of sections in the Sangiran area (Sémah, 1984). These palynological results show that the pollen spectra from levels corresponding with the upper part of the ‘black clays’ (= Sangiran Formation) just below the Grenzbank (South Cemoro section) and the lower part of the ‘Kabuh Formation’ (= Bapang Formation) just above the Grenzbank (Jengglong section) are poor in tree pollen and spores and dominated by pollen of herbaceous plants, indicating an open vegetation. There is some discrepancy with another one meter thick section situated one meter above the Grenzbank (Bapang section), where there is a rapid increase in spores and *Podocarpus* trees, suggesting increasing humidity. This discrepancy might be due to local circumstances or horizontal facies changes (Sémah, 1984) or to long distance transport of *Podocarpus* pollen.

It is during this period that *E. hysudrindicus* has its first recording on Java in the

Kedung Brubus Fauna. The composition of the younger Ngandong Fauna appears basically similar to the Kedung Brubus Fauna, though various species, including *Homo erectus* and *Stegodon trigonocephalus* can be distinguished on a subspecies level.

A second major faunal turnover event is recorded in the Late Pleistocene Punung fauna, which shows the first recordings of *Homo sapiens* and *Elephas maximus* on Java. When comparing the Kedung Brubus Fauna with the Punung Fauna (Table 1), it follows that 17 taxa present in the first mentioned fauna are absent in the Punung Fauna. On the other hand, there are 10 new recordings in the Punung fauna. The Punung fauna contains large numbers of primates such as *Pongo* and *Hylobates*, for the first time indicating humid forest conditions on Java (de Vos, 1983). This is in sharp contrast with the previous faunas, which represent an open woodland habitat (Trinil, Kedung Brubus and Ngandong Faunas). As will be argued below, it is likely that most replacements recorded in the Punung fauna took place during a time interval when the sea level was some 40 to 65 m below PDL prior to 70 ka, but after the glacial maximum at 135 ka, as deduced from the sea level fluctuation curve (Fig. 25B) based on dated raised coral terraces from the Huon Peninsula in Papua New Guinea (Chappell & Shackleton, 1986). During the glacial maximum at 135 ka dry climatic conditions presumably prevailed in the exposed Sunda shelf region. At least for west Java there is now strong evidence for such drier conditions during the penultimate glaciation. In a drill core from the Bandung Basin (Dam, 1994), the occurrence of pedogenic carbonate concretions (kankar nodules) at a depth of 50-58 m points to a substantial evaporation surplus and a considerably longer dry season than occurs at present. This kankar interval has been dated with the U/Th disequilibrium method at approximately 135 ka (equivalent with oxygen isotopic stage 6, Martinson et al., 1987). The entrance on Java of the orang utang, *Pongo pygmaeus*, first recorded in the Punung fauna, certainly required a continuous forest canopy. It is therefore unlikely that it coincided with the dry period during the glacial maximum. The Punung Fauna also includes *Homo sapiens*, which must have entered Java after the penultimate glaciation. Therefore, the major faunal event leading to the establishment of the Punung Fauna on Java probably took place after the period of high sea level at 125 ka, when climatic conditions started to become more humid as evidenced by palynological data from the Bandung Basin core mentioned above (van der Kaars & Dam, 1994). Though these humid climatic conditions were potentially suitable for a rainforest fauna to enter the island, Java was probably isolated from the mainland by a sea barrier at that time, as follows from the sea level curve of Chappell & Shackleton (1986). A sea-barrier would have been insurmountable for the orang utang. More likely, the immigration of the typical forest elements of the Punung fauna took place during the later part of oxygen isotopic stage 5, roughly between 110 ka and 70 ka. Palynological evidence (van der Kaars & Dam, 1994) indicates that the climate remained warm and humid until c. 81 ka, while sea level during this stage was fluctuating around 50 m below PDL (Chappel & Shackleton, 1986). With a sea level of 50 m below PDL, Java would have been largely surrounded by sea, providing relative humid conditions. At the same time a land corridor in the west would have permitted overland migration to Java (Fig. 1). Thus a sea level lowstand of around 50 m below PDL, in combination with relatively humid conditions, probably permitted the rainforest elements such as *Pongo* and *Hylobates* to enter Java. These rainforest taxa had supposedly been driven

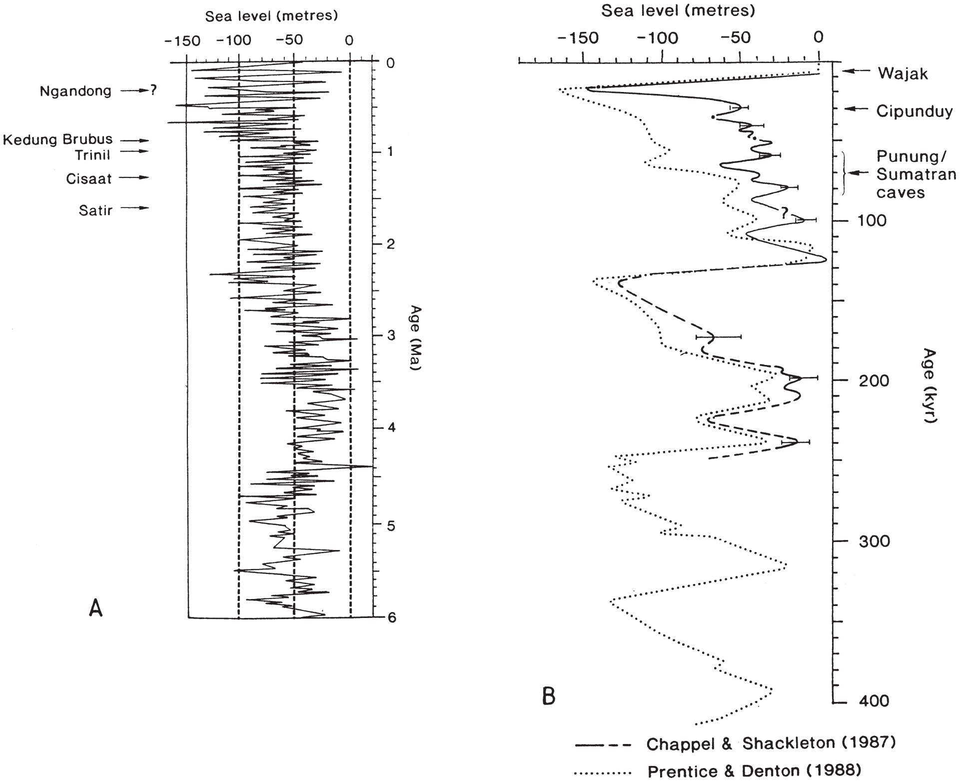


Fig. 25. A: Glacio-eustatic sea level fluctuations chart for the last 6 million years as calculated from the oxygen isotope composite derived from tropical shallow water planktonic foraminifera (after Prentice & Denton, 1988). Also indicated are the major faunal stages that can be recognized on Java (after van den Bergh et al., 1996).
B: Sea level chart for the Late Pleistocene-Holocene based on dated raised coral reefs in the Huon Peninsula, Papua New Guinea (after Chappel & Shackleton, 1986). The sea level chart of Prentice & Denton (1988) is shown for comparison. Late Pleistocene and Holocene faunas from Java and Sumatra are also indicated. The Sumatran cave faunas refer to the Lida Ayer and Sibrambang caves.

south by the preceding glacial maximum at 135 ka via the so-called Sino-Malayan route (de Vos et al., in press). They probably survived during the penultimate glacial maximum in isolated mountainous and humid environments on the Sunda Shelf, to spread further south into Java between 110 ka and 70 ka.

The presumed age of the Punung fauna is 80-60 ka. This age is rather speculative and not based on direct age determinations, but on faunal similarities between the Punung assemblage and the Sumatran cave faunas. As an age of 80-60 ka would be in accordance with the arguments concerning sea level fluctuations outlined above, it is taken as a reasonable estimate.

During the last glaciation, again a major faunal event took place. *Pongo* is not recorded from the Holocene composite cave fauna (including faunal elements from the caves Wajak, Sampung, Hoekgrot, and Goa Jimbe) of Table 1. It probably disappeared from Java during the last glacial maximum, when drier conditions and increased seasonality again disrupted the rain-forests in that region (Morley & Flenley, 1985). These climatic changes are evidenced by an increase in grass pollen and a decrease in fern spores at this time in deep-sea cores from the region (van der Kaars, 1991). Small mountainous areas with rainforest could have served as refuges for some of the typical forest dwellers during this stage, but apparently *Pongo* was not able to cope with these changes and disappeared from Java. Comparing the Late Pleistocene Punung Fauna and the Holocene composite Fauna (Table 1), it follows that not only *Pongo* disappeared from Java, but also a large number of extinctions occurred, while replacement by new immigrations during the last glacial maximum appears to have been limited. Also *E. maximus*, still recorded from the Sampung Cave, eventually did not survive on Java either, probably due to a shrinking land area following the Holocene sea level rise in combination with increased pressures from human populations on the fertile grounds of Java.

3. Sulawesi: the stratigraphy and faunal succession of terrestrial vertebrates

Introduction

Before the descriptions and systematics of the elephantoid fossils from Sulawesi will be treated in detail in the next chapter, it is necessary to give an account on the local geology and stratigraphy of the fossil-bearing deposits. The vertebrate faunal succession of Sulawesi as it appears now, is more complicated than it once seemed. The reconstruction of the fauna evolution, though still with considerable gaps in our knowledge, has been only possible by detailed stratigraphic studies of the fossil-bearing sequences.

Apart from an important random component, the dispersal of terrestrial biota has been influenced to a large extent by the complex tectonic movements that have taken place in the region, which need to be analyzed in order to understand the terrestrial fauna succession.

In this chapter the aspects of the geology and stratigraphy of Sulawesi will be discussed first, followed by an account of the local stratigraphy of the area where vertebrate fossils are common: the southwestern peninsula of Sulawesi island, administratively designated as South Sulawesi. Sedimentological descriptions of the most important fossil sections and localities will be given and the sequential order of the various fossil localities will be discussed. An excursion will be made to the taphonomy of the fossil sites in South Sulawesi, mainly focussing on the most abundantly encountered species, *Celebochoerus heekereni*. With the results of the taphonomical study it can be concluded that the collected fossil assemblages give a good impression of the ancient faunal structure and composition. Based on the stratigraphical data the successive faunas that can be recognized will be discussed next. After that, chapter 4 will deal with the description of the elephantoid fossils in existing and newly made collections, together with their systematics.

South Sulawesi

Physiography

The location of the study area in South Sulawesi is indicated in Fig. 2. It is located south of the town Sengkang on both sides of the Walanae River. The course of the Walanae River is determined by a geological structure called the Walanae Depression (Fig. 26). This depression is a north-south trending fault bounded graben-like structure, which is developed over the entire length of the South Sulawesi peninsula. The Walanae depression is flanked at both sides by roughly N-S trending mountain chains: the Western Divide Range in the west and the Bone Mountains in the east.

The Neogene sedimentary rocks deposited in the Walanae Depression have been gently folded and faulted in the south. Subsequent erosion has shaped this area into a hilly terrain. The meandering Walanae River has cut deeply into the Neogene bedrock in this area.

Towards the north, the Walanae River valley widens into an alluvial plain. Here, the meandering river has built up a slightly elevated levee complex. Alluvial fans prograde into this alluvial plain from the west, where deeply incised valleys from the Western Divide Range supply large quantities of sediment. To the east the alluvial plain is bounded by a marked hilly ridge, the Sengkang Anticline (Fig. 26). Sediment supply from this ridge by small brooks is less pronounced, and no alluvial fans have been formed. The westward flowing drainage system from the Sengkang Anticline consists of a dendritic pattern of small brooks, most of which are dry during the dry season.

Further north, the Walanae Alluvial Plain merges into swampy lowlands around Lake Tempe (Fig. 2). This flat area, the Lake Tempe Depression, merges into the coastal plain to the northwest of Lake Tempe and is bounded in the east by the Sengkang Anticline. West of the town of Sengkang the Walanae River turns to the east and has broken through the Sengkang Anticline. It flows eastward through slightly undulous terrain of gently folded Neogene deposits, before it debauches into the Gulf of Bone. At the bending point west of Sengkang the outlet of the Tempe Lake, which is fed by various smaller rivers from the west and north, enters the Walanae River. During the rainy season however, part of the Walanae River discharge flows into the Tempe Lake, where various distributaries of the Walanae River feed a shallow deltaic complex.

Geodynamic setting

Sulawesi lies near the junction of three major converging plates: the Eurasian Plate in the northwest, the northwards moving Indo-Australian Plate in the south and the westward moving Pacific Plate in the east (Fig. 27). In the area where these three plates converge several minor plates can be distinguished, which are remnants of once larger plates or which have been formed by relatively small spreading centers or marginal fragmentation of the major plates. Most notable is the Philippine Sea Plate. The smaller Moluccas Sea Plate probably formed part of the latter during the Oligocene but became separated from it through the formation of a subduction zone during the Middle Miocene, some 15 Ma ago (Hall, 1996).

The Eurasian Plate consists largely of continental crust, but along the eastern mar-

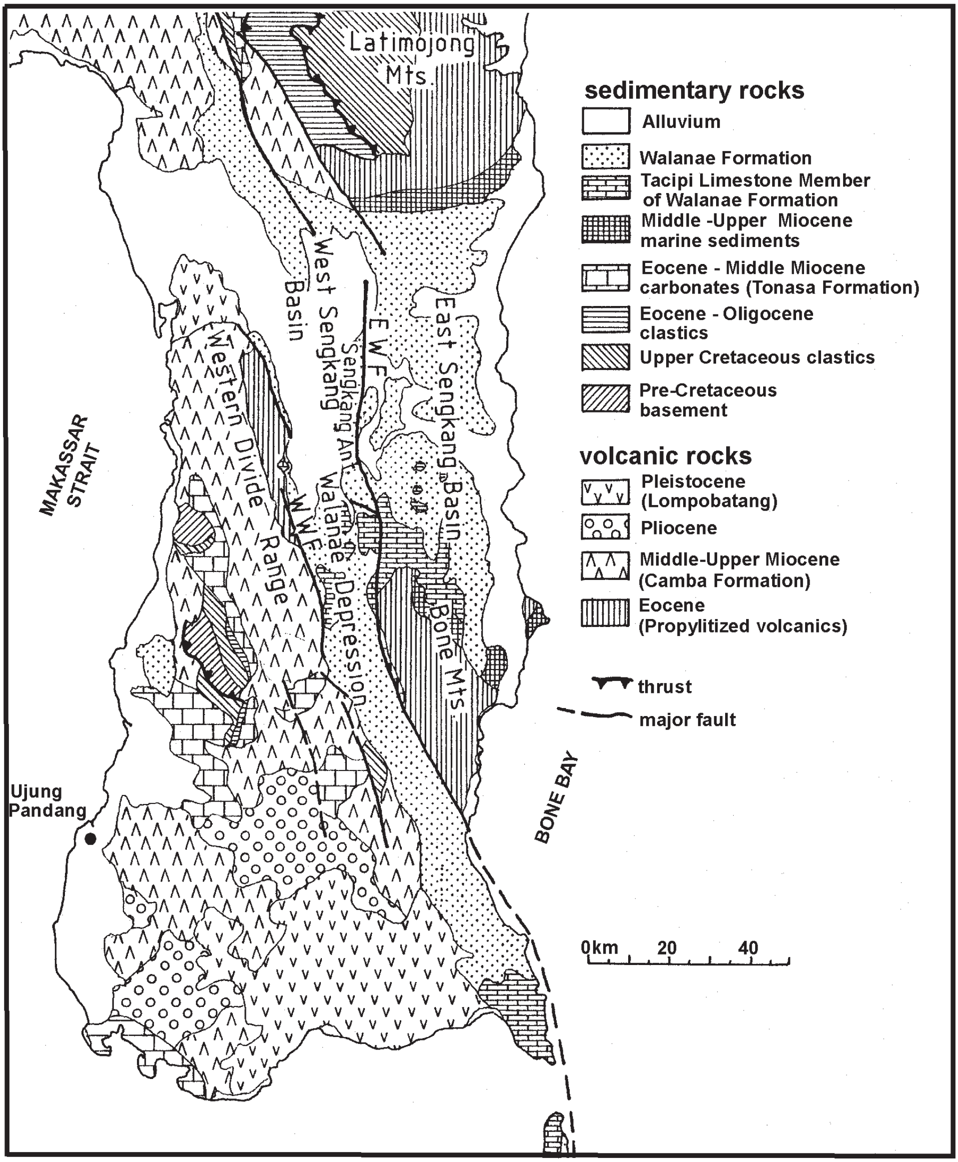


Fig. 26. Geological map of South Sulawesi (Modified after Sukamto, 1975, and van Leeuwen, 1981).

gin of the Sunda shelf rifting has led to the formation of small oceanic basins during the Tertiary, viz. the South China Sea, the Sulu Sea, the Celebes Sea and the Makassar Strait (Figs. 27-28). Also the greater Australian Continent, including the Sahul and Arafura Shelves and the southern part of New Guinea, is underlain by continental crust. West of Australia the Indian-Australian Plate consists of oceanic crust, which is being subducted underneath Java and Sumatra. The continental crust of northern Australia has been partly subducted below the Banda Arc, but because of the low

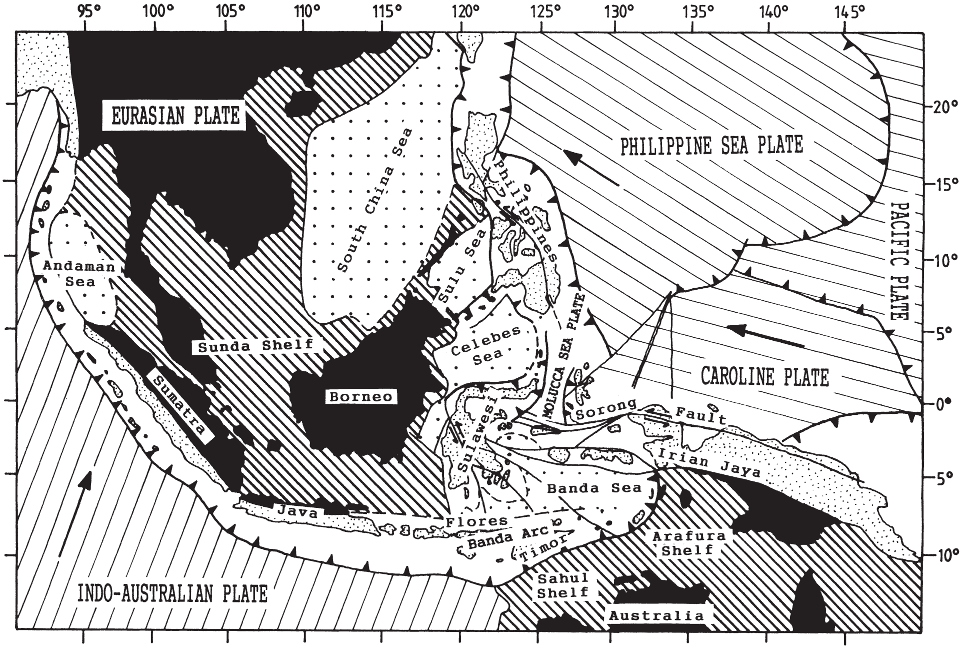


Fig. 27. Tectonic setting of the Indonesian region (modified after Simandjuntak & Barber, 1996). Black = emerged parts of continent; heavy hatching = submerged parts of continent; thick dotting = marginal seas; thin hatching = oceanic plates; thin dotting = transitional complexes. Arrows indicate relative movements of oceanic plates.

density of continental crust subduction has stopped at the most northward protruding part of the Australian continental crust south of Timor (Fig. 27). The island of Timor is presently being bulldozed northwards.

The northern part of New Guinea has been formed by accretion of smaller continental fragments and/or island arcs. The northern margin of New Guinea is cut by a major east-west oriented zone of left lateral strike slip movement, the Sorong Fault System, which merges westward into various transcurrent faults in the Molucca Sea. Several small continental fragments that can be recognized east of Sulawesi have been detached from the Australian Continent during the Tertiary and were subsequently transported westwards along the Sorong Fault System along with the moving Philippine Sea Plate (Hall, 1996).

Geologic setting of Sulawesi

The island Sulawesi can be divided into four tectonic units or belts (Hall, 1996; Simandjuntak & Barber, 1996). These units are (Fig. 28):

1) The western volcano-plutonic arc, which runs from Selayer island in the south all the way north to Minahasa, the tip of the northern Sulawesi peninsula. The igneous rocks and associated volcanoclastics are of Tertiary and Quaternary age. Largely contemporaneous with these igneous rocks are limestones and clastic sediments. In the south the Tertiary deposits cover a sequence of Cretaceous-Paleogene

flysch-type sediments, which in turn overlies a metamorphic and ultrabasic Mesozoic basement complex.

2) The central Sulawesi metamorphic belt, consisting of rocks of both continental and oceanic origin.

3) The East Sulawesi ophiolite belt, consisting of obducted ocean floor rocks.

4) Several small fragments underlain by continental crust, which have collided with eastern Sulawesi: Banggai-Sula, Tukang Besi and Buton.

Towards the west the up to 2500 m deep Makassar Basin separates Sulawesi from Borneo (Fig. 29). It is thought that this deep-water through was formed by Tertiary rifting resulting from NW-SE extension along the Makassar Strait (e.g. Audley-Charles, 1977, Katili, 1978, Hamilton, 1979, Burolet & Salle, 1981, Hall, 1996). Collision of East Sulawesi with the West Sulawesi Arc along a subduction zone resulted in metamorphism in Central Sulawesi and emplacement of ophiolitic rocks over these metamorphics. Subsequently, collision of the micro-continental fragments Banggai-Sula and Buton-Tukang Besi from the east has caused additional compressional deformation in this area. The leading edges of the continental fragments were thrust beneath the ophiolite complex, which resulted in the uplift of the ophiolite complex and its pelagic cover. In addition, as a result of this collision, the metamorphic belt was thrust westwards over the western volcano-plutonic arc. The arrival of the Banggai-Sula and Buton continental fragments is thought to have taken place during the Late Miocene-Early Pliocene and Early-Middle Miocene, respectively (Garrard et al., 1988; Fortuin et al., 1990; Smith & Silver, 1991; Parkinson, 1991; Davidson, 1991). The Tukang Besi continental fragment collided with Buton during the late Pliocene (Ali et al., 1996). Recently, it has become clear that compression in west Sulawesi continues at present, and Tertiary sediments are being detached from the basement in a series of eastward dipping thrusts in the Majene Fold Belt (Fig. 29), also affecting Recent sediments in the Makassar Strait (Coffield et al., 1993; Bergman et al., 1996). A major NNW-SSE trending sinistral transcurrent fault, the Palu Fault (Figs. 28-29), displaces the eastern part of Sulawesi northwards with respect to the western part. This fault is thought to have developed during, or shortly after the collision with the continental fragments (Simandjuntak & Barber, 1996).

An active volcanic arc and associated subduction zone extends from the north-eastern tip of North Sulawesi northwards (Fig. 28). Oceanic crust of the Molucca Sea is being thrusted beneath the Sangihe Volcanic Arc in a westward dipping subduction zone. Seismic data have shown that the west dipping subducting slab can be identified to a depth of c. 600 km beneath the Celebes Sea. East of this subduction zone another westward dipping subduction zone is present, with its corresponding arc, the Halmahera Volcanic Arc. The strongly deformed ophiolites and melanges exposed in the islands Talaud and Tifore have been interpreted as fragments of the almost subducted Molucca Sea floor in between the two colliding island arcs (Silver & Moore, 1981), but the Talaud-Tifore Ridge has also been interpreted as a backstop within the Sangihe Forearc (Rangin et al., 1996). The ridge, is locally covered by uplifted Quaternary reef limestones (Simandjuntak, 1992).

Geology of South Sulawesi

The basement beneath South Sulawesi probably consists of old continental crust

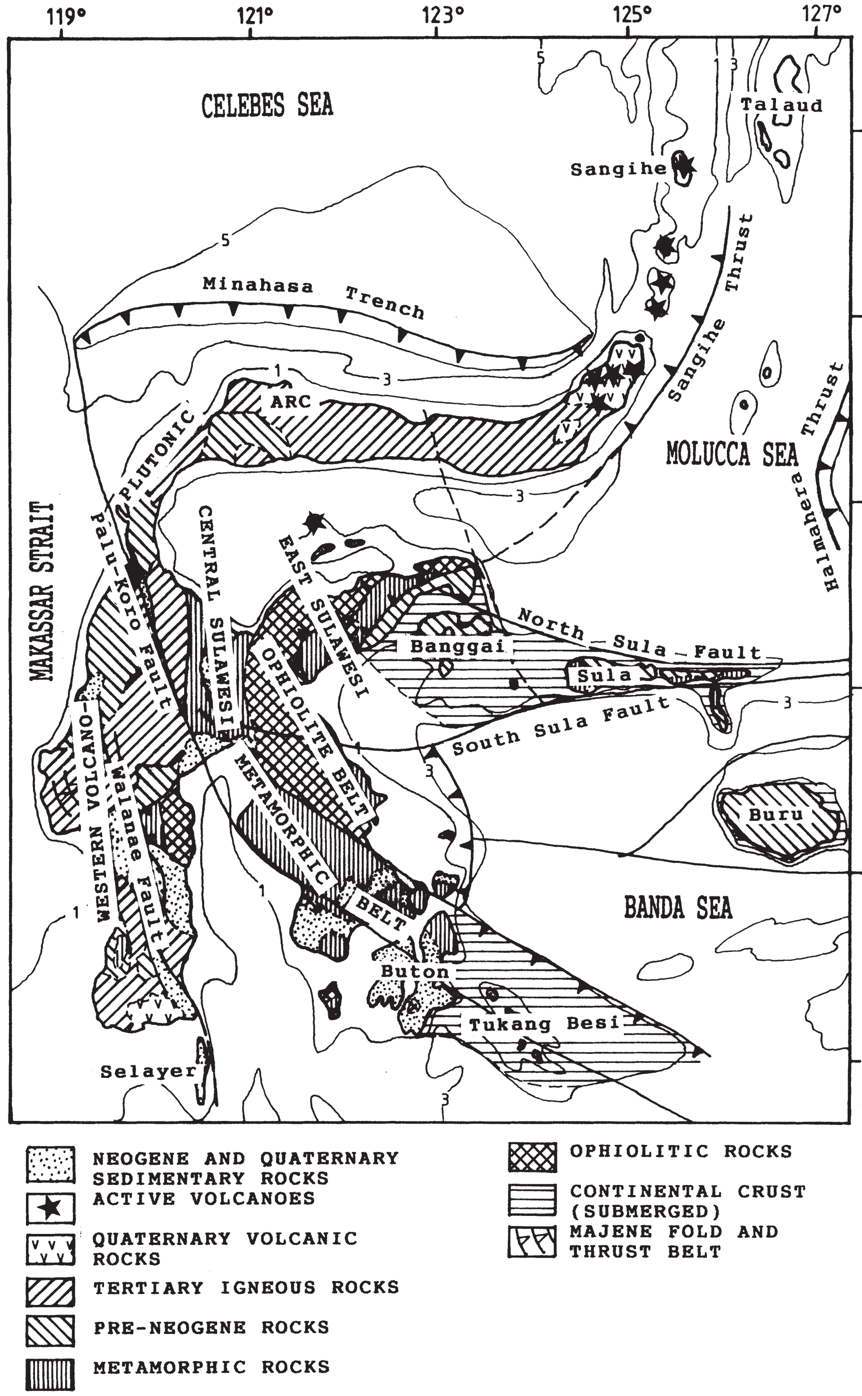


Fig. 28. Map of Sulawesi showing its division into four tectonic belts or units (modified after Simandjuntak & Barber, 1996).

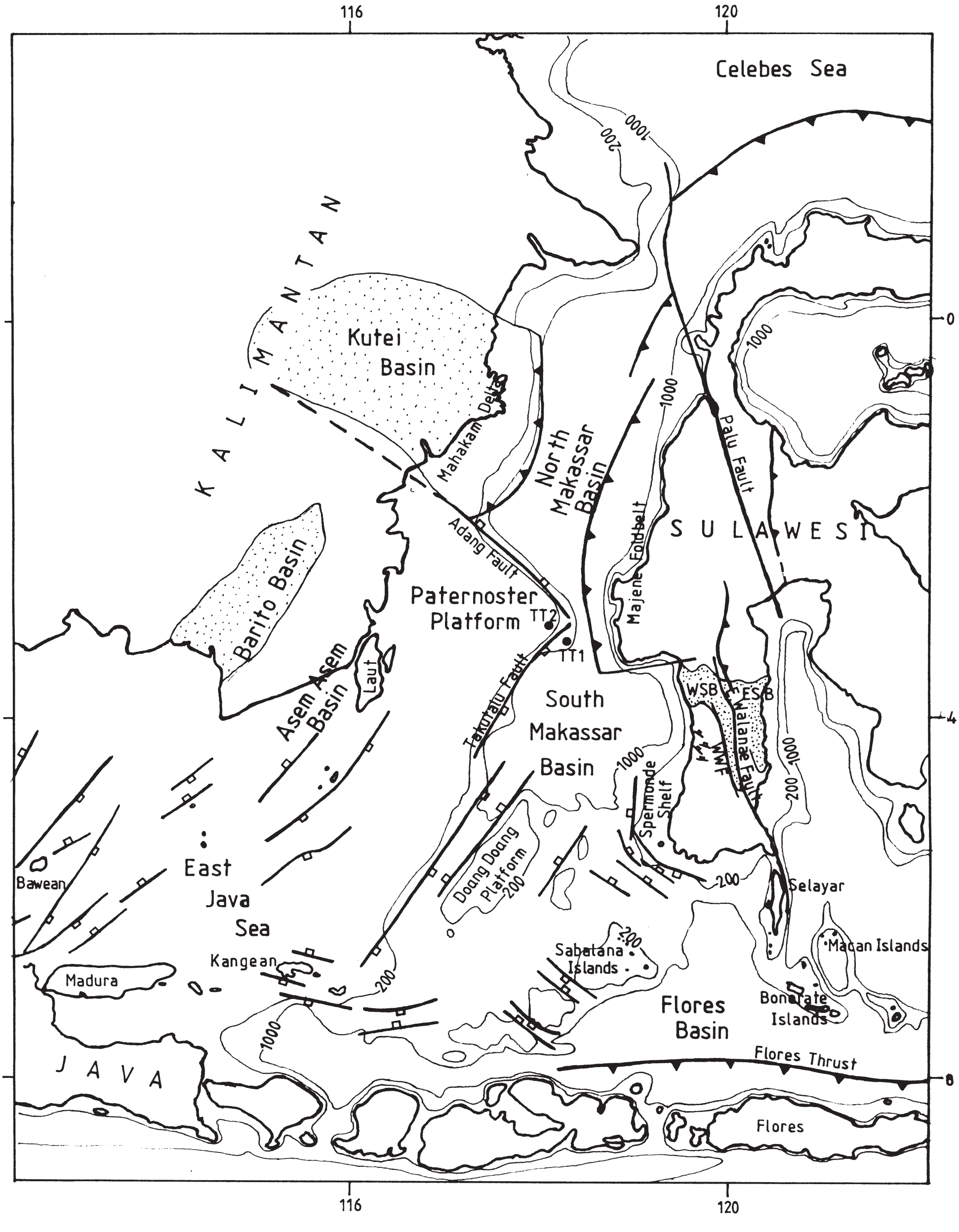


Fig. 29. Map of the Makassar Strait and surrounding areas showing the present bathymetry (200-m and 1000-m depth contours) and the main tectonic features discussed in the text (modified after van de Weerd & Armin, 1992; Bransden & Matthews, 1992).

presumably of Australian origin (Coffield et al., 1993; Priadi et al., 1993; Bergman et al., 1996). This continental crust is thought to have become accreted to Sundaland before the Early Cretaceous. The accreted eastern margin of Sundaland was unconformably covered by cherts and deep marine clastics of Middle and Late Cretaceous age (Wakita et al., 1996). The basement rocks have become tectonically sliced into an imbricated complex.

The pre-Upper Cretaceous basement complex is unconformably overlain by Paleocene volcanics, which locally crop out in the western Divide Range. Marginal marine coal-bearing deposits of the Malawa Formation were formed during the Early and Middle Eocene in the area now located west of the Walanae depression (Sukamto, 1982). Volcanism continued at least until the end of the Late Oligocene, but became increasingly concentrated towards the east, where Paleogene volcanic rocks constitute the core of the Bone Mountains (Fig. 26). In the west volcanic activity must have largely ceased at the beginning of the Middle Eocene, so that an extensive carbonate platform could develop here. These marine carbonates, named the Tonasa Formation, were initially deposited on a shallow marine platform (Sukamto, 1982; Wilson & Bosence, 1996). The base of the Tonasa Formation interfingers with the upper part of the coal-bearing Malawa Formation. During the Oligocene the Tonasa carbonate platform underwent blockfaulting, as did other contemporaneous carbonate platforms located in the East Java Sea and basins in the southeastern part of Kalimantan (Fig. 29) (Situmorang, 1987; van de Weerd et al., 1987; Kusuma & Darin, 1989; Bransden & Matthews, 1992). This tectonism is recorded in the lateral deposition of reworked carbonate facies deposited in the downfaulted blocks. The formation of the Tonasa Limestones continued until the end of the Early Miocene (Wilson & Bosence, 1996).

During the Middle Miocene volcanic activity affected the entire southwestern Sulawesi peninsula again (Camba Formation). The volcanic products of the Camba Formation cover most older deposits in the Western Divide Range. The volcanism, related to the formation of a north-south trending arc system (Sukamto, 1982), brought an abrupt end to the limestone deposition (Wilson & Bosence, 1996).

Towards the beginning of the Late Miocene small carbonate reefs fringed the northern outliers of what are now the Bone Mountains. These shallow marine reef limestones are overlain, and perhaps partly interfinger with, deep marine clastics, which accumulated in the downfaulted Walanae depression and north of the Bone Mountains (Grange & Davies, 1983). These limestones and marine clays constitute the base of the Walanae Formation.

The Walanae Fault Zone, a major NNW-SSE trending fault system that separates the western part of South Sulawesi from the eastern part, influenced deposition during Late Miocene to Recent times (Sukamto, 1975; van Leeuwen, 1981; Grange & Davies, 1983). The Walanae Fault Zone comprises two major faults that bound the Walanae Depression to the west and to the east (Fig. 26). Following van Leeuwen (1981) the main western fault is here designated as the West Walanae Fault (WWF) and the main eastern fault as the East Walanae Fault (EWF). The Neogene basins on both sides of the EWF have been divided by Grainge & Davies (1983) into the West Sengkang Basin (WSB), which corresponds with the Walanae and Lake Tempe Depressions, and the East Sengkang Basin (ESB) located east of the EWF and north of the Bone Mountains (Fig. 26).

The basin infill, the Walanae Formation, shows a gradual shallowing upwards and is capped by fluviatile sandstones and conglomerates. These fluviatile deposits contain the vertebrate fossils that form the main topic of this study.

At the southern tip of South Sulawesi the Neogene deposits are covered by a now extinct Quaternary volcano and its deposits, Mount Lompobatang (Figs. 2, 26).

Cenozoic History of Sulawesi and adjacent areas

The information on the geology of Sulawesi and the surrounding areas is far from complete. Several questions remain unresolved, for example the structural setting of the Gulf of Bone, the deep basin east of South Sulawesi, which is possibly underlain by oceanic crust. Various plate tectonic reconstructions have been proposed.

According to one of the earliest reconstructions (Katili, 1978) the Makassar Strait between Borneo and Sulawesi closed at the end of the Pliocene, and reopened again during the Pleistocene, leading to the present-day configuration. At the end of the seventies there were very limited data from the Makassar Strait. Since then, seismic profiles and data from deep wells have become available, and the earlier model has now been abandoned.

Paleocene-Eocene — It is certain now that west Sulawesi formed part of Sundaland since Late Cretaceous times. Palaeomagnetic evidence suggests that west Sulawesi has remained close to its present latitude throughout the Tertiary (Haile, 1981; Sasajima et al., 1981). During the Early-Middle Eocene regional processes of basin formation affected the southeastern margin of the Eurasian Continent, including South Sulawesi, the Makassar Strait, east Kalimantan and the East Java Sea. This episode of basin formation was perhaps triggered by the collision of India with Eurasia, which resulted in a widespread plate reorganization (van de Weerd & Armin, 1992; Daly et al., 1987, 1991). The northwest directed motion of the Pacific Plate also shifted to a more westerly direction around this time (Kenneth, 1982; Daly et al., 1987; Hall, 1996). The oldest crust of the Celebes Sea (Figs. 28-29) is also of Middle to Late Eocene age (Weissel, 1980), and its opening may be attributed to this phase of plate reorganization.

The Eocene phase of basin-formation is documented in the Western Divide Mountains by the unconformable contact between the coal-bearing clastics of the Malawa Formation and the Cretaceous basement rocks. Eocene terrestrial clastics and marginal marine clastics unconformably overlying basement rocks have also been found in western Sulawesi (Bergman et al., 1996), in the Makassar Strait (Situmorang, 1987), in SE Kalimantan (van de Weerd & Armin, 1992), and in the East Java Sea (Bishop, 1980). The development of the North and South Makassar Basins (Fig. 29) has been related to extensional back-arc spreading by some workers (Hamilton, 1979; Daly et al., 1987, 1991 a.o.). According to this model the Eocene-Oligocene volcanics of south Sulawesi are thought to be related to subduction in the east and to mark the eastern margin of the Eurasian Plate at that time. An alternative possibility brought forward by Hutchison (1988) is that the Makassar Strait is a failed arm of the sea floor spreading in the Celebes Sea. Although fitting of the bathymetric contours on the west and east side of the Makassar Strait has been obliterated by the thick Neogene sediments of the Mahakam Delta and Neogene deformation in west Sulawesi (Bergman et al., 1996), it can be achieved using a rotation pole NE of the north end of the Makassar Strait at 6°N and 128°E requiring a rotation of 6° (Hall, 1996).

Sedimentation has been far less than the total amount of subsidence in the North and South Makassar Basins, resulting in the present deep basins. The geometry of major faults and the timing of motion along these faults as deduced from seismic and outcrop data, suggest that regional extension started during the Early Eocene, and was widespread by Late Eocene times (van de Weerd et al., 1987; Letouzey et al., 1990; Bransden & Matthews, 1992). The widespread development of upper Eocene shallow-water carbonate platforms and deep marine deposits is also characteristic of extensional block faulting (Wilson & Bosence, 1996).

Oligocene-Early Miocene — East Sulawesi, which originates from a southern position at a latitude of 17° ± 4°, as indicated by palaeomagnetic data (Mubroto et al., 1994), is thought to have collided with the western volcano-plutonic arc sometime between the end of the Eocene and the Middle Miocene (Hamilton, 1979; Audley-Charles, 1981, 1987; Sukamto & Simandjuntak, 1983; Hall, 1996). The collision suture between both domains is located in Central Sulawesi, but disappears southwards into the Gulf of Bone. A mid-Oligocene unconformity has been reported from many offshore and onshore areas in the region (van Leeuwen, 1981; Kusuma & Darin, 1989; Bransden & Matthews, 1992; van de Weerd & Armin, 1992). Some have related this unconformity with an eustatic sea level low-stand Bransden & Matthews, 1992), but others have inferred tectonic activity (van de Weerd et al., 1987; van de Weerd & Armin, 1992; Saller et al., 1992; Wilson & Bosence, 1996). On both sides of the Makassar Basin and in the East Java Sea Oligocene extensional faulting is recorded by redeposited carbonate facies derived from shallow water carbonate shelves (Situmorang, 1987; van de Weerd & Armin, 1992; Bransden & Matthews, 1992; Wilson & Bosence, 1996). Sea floor spreading began in the South China Sea during the Oligocene (Holloway, 1982; Ru & Pigott, 1986) and the East Sulawesi ophiolite complex was obducted (Parkinson, 1991).

During Early to Middle Miocene times the Makassar Strait had obtained a depth of c. 1000 m. Information from boreholes in Makassar Strait revealed that marine sedimentation continued into the Pliocene and Quaternary (Situmorang, 1987; Nishimura & Suparka, 1990). Based on seismic profiles from the East Java Sea and Makassar Strait it has been inferred that syntectonic graben fills developed during Oligocene and early Miocene times (Bishop, 1980; Cater, 1981; Letouzey et al., 1990). Illustrative are the seismic and borehole data from two wells located on both sides of the NE-SW trending Takutalu Fault (Situmorang, 1987) (Wells TT-1 and TT-2; Fig. 29). These data revealed that during the Eocene to Early Miocene subsidence rates were much higher in the South Makassar Basin than in the adjacent Paternoster Platform (Situmorang, 1987). Active downfaulting of the South Makassar Basin is evidenced by a thickened hanging wall sequence of redeposited carbonate clastics in well TT-1. These clastic carbonates were derived from the relatively stable Paternoster Platform, where shallow water carbonate sedimentation continued during the same period.

Another major fault bounding the Paternoster Platform to the north, is the NW-SE trending Adang Fault (Fig. 29), which is thought to extend in western direction to form the southern margin of the Kutei Basin (Bransden & Matthews, 1992; van de Weerd & Armin, 1992). During the Eocene to Early Miocene normal movements along the Adang Fault have been inferred with downthrowing of the northern side (Biantoro et al., 1992). Deep marine sedimentation occurred in the Kutei Basin (Fig. 29) during this period, whereas the Paternoster Platform and Barito Basins were the sites of shallow-water carbonate accumulation at the same time (van de Weerd et al., 1987; Wain & Berod, 1989). In South Sulawesi NW-SE trending normal faults were also active from the Late Eocene to Early and Middle Miocene, with downthrowing towards the north (Wilson & Bosence, 1996). A period of tectonic quiescence and continued foundering of the crust along the SE margin of the Eurasian Continent seems to have prevailed during the Oligocene. Oligocene volcanics in the region have been only reported from Java and the upper Kutei Basin (van de Weerd & Armin, 1992).

Middle-Late Miocene — A compressive tectonic regime resulting in inversion of many of the earlier generated normal faults has been recognized to start during the Middle Miocene at various places in the region (Situmorang, 1987; Letouzey et al., 1990; Bransden & Matthews, 1992; Bergman et al., 1996). In the Makassar Basin the Takutalu Fault underwent an inversion from normal to reversed faulting during the Middle to Late Miocene. The compression was accompanied by subsidence, resulting in the deposition of deep marine clays on both sides of the Takutalu Fault (Situmorang, 1987). Compression in the Majene Fold and Thrust Belt in western Sulawesi (Fig. 29) was initiated during the Middle Miocene (Bergman et al., 1996). Thrust loading in western Sulawesi in combination with sediment loading associated with the Mahakam Delta in eastern Kalimantan resulted in strong subsidence of the Makassar Basin. In East Kalimantan, the East Java Sea and South Sulawesi the Miocene rock sequence typically show regressive trends (van de Weerd & Armin, 1992). It is widely believed that the compressive regime, which locally persisted until the present day, must be attributed to the collision of various microcontinental blocks from the east with western Sulawesi. In the East Java Sea compressive features were largely oriented parallel to the Java Trench Subduction Zone (Letouzey et al., 1990).

During the Middle to Late Miocene also strong calcalkaline volcanism started in the southwestern and western parts of Sulawesi (Camba Formation), indicating the presence of a subduction zone to the east (Sukamto, 1975; Coffield et al., 1993; Bergman et al., 1996). Based on geochemical analysis of the volcanic and intrusive rocks Bergman et al. (1996) concluded that continental lithosphere was involved in the subduction beneath the continental lithosphere of west Sulawesi.

The oldest fission-track dated volcanic rocks on Flores are of late Early and Middle Miocene age (Nishimura et al., 1981). At this stage subduction of the Indo-Australian Plate below the Sunda continental region seems to have occurred along a continuous zone running from Java eastward, passing south of Flores and bending northwards east of the western volcanoplutonic arc and the accreted central and eastern parts of Sulawesi.

The Walanae Fault Zone is thought to have been initiated during the Middle Miocene (Grange & Davies, 1983; van Leeuwen, 1981), perhaps in response to oblique subduction. Alternatively, the deformation along this fault zone may have been induced by the buoyancy of subducted continental lithosphere. Van Leeuwen (1981) concluded that important vertical movements must have taken place along the WWF during the early Middle Miocene, with a relative uplift of the eastern block. Rapid subsidence of the West Sengkang Basin as a deep marine trough is thought to have taken place through normal faulting along the EWF during the early Late Miocene, as inferred from seismic data (Grange & Davies, 1983). Shallow water carbonate accumulation took place in the East Sengkang Basin at that time (Tacipi Member of the Walanae Formation). During the Late Miocene to Early Pliocene this carbonate platform drowned with only local pinnacle reefs keeping pace with the subsidence here, whereas the West Sengkang Basin was gradually filled in with marine clastics.

A SW-NE oriented seismic profile from the Flores Sea located halfway between the Doang Doang Platform and the Sabalana Islands (Fig. 29) and with well control from the surrounding area, indicates the presence of a Middle and Upper Miocene shallow-water carbonate shelf in the NE, which has laterally prograded over deep-water basinal deposits towards the SW (Tyrrell & Davies, 1989). The carbonate shelf prograded southwards over a distance of c. 9 km over deep water basinal deposits during the Miocene and possibly Early Pliocene.

Pliocene-Recent — The West Sengkang Basin was rapidly filled in during the Pliocene. Terrestrial and lacustrine deposition continues up to the present day in the central part of the WSB, where the Walanae River enters Lake Tempe. The depocenter of the WSB is located northeast of Lake Tempe, with an Upper Neogene basinfill of up to 3500 m thick (Grange & Davies, 1983). Seismic data N-S across the Sengkang Basin reveal normal block-faulting with downthrowing towards the depocenter of the basin (A. Ngakan pers. comm. in Wilson & Bosence, 1996). The Sengkang Basin thus appears to separate South Sulawesi structurally from the rest of the western arc of Sulawesi.

The inversion from normal to reverse faulting along the EWF is thought to have started during the Pliocene (Grange & Davies, 1983). This is later than the beginning of inversion of major faults in the Makassar Basin and East Java Sea. The present-day configuration of the Sengkang Anticline as the surface expression of the westward dipping EWF (Fig. 26) is also the result of this latest compressional phase. The compressional faulting was accompanied by a general uplift of the area. In the ESB and along the southern margin of the WSB an unconformity marks uplift and erosion during this compressive phase. Sukamto (1975) postulated a left-lateral movement along the EWF, which is in accordance with seismic data (Grainge & Davies, 1983). Activity along the WWF appears to have been less marked during the Late Pliocene-Early Pleistocene (van Leeuwen, 1981). Volcanism continued during the Late Miocene and Pliocene as is evidenced by tuffaceous intervals in the Walanae Formation. The Late Neogene volcanic activity seems to have been concentrated in the southwest, as the amount of volcanic components in the Walanae Formation increases in this direction (Grange & Davies, 1983; own observations). In the southern part of the Walanae Depression (Biru Area) also volcanic breccias and lava flow deposits alternate with marine sediments of the Walanae Formation (van Leeuwen, 1981).

The shallow-water carbonate shelf located SW of the southwestern peninsula underwent rapid subsidence during the Pliocene. This caused the drowning of the shelfmargin, after which the shelfedge slope was onlapped by deep-water sediments (Tyrell & Davis, 1989). In other fault-bounded blocks in the Flores Sea more to the southwest, notably the Doang Doang Platform and the Sabalana Islands (Fig. 29), carbonate accumulation could apparently cope with the subsidence and continues up to present times. The subsidence may be related to the formation of the Flores Thrust (Fig. 29) during the Pliocene.

The Spermonde Shelf west of Ujung Pandang (Fig. 29), which is also underlain by Miocene shallow-water carbonates, has been affected by Pleistocene sea level fluctuations, as indicated by the presence of a submarine dendritic pattern of drowned river valleys (de Klerk, 1983). Folding has been inactive since the Pliocene in this area. The end of the compressive deformation here has been explained by the northward movement of northeastern Sulawesi along the Palu Fault Zone in response to E-W shortening and the formation of free boundary conditions along the north Minahasa Trench (Letouzey et al., 1990).

Tertiary land-connections between west Sulawesi and Sundaland

For palaeozoogeographic reconstructions, it is of importance to consider whether regional geological and seismic data can provide evidence concerning the former presence or absence of land connections between Sulawesi and the adjacent Sunda Shelf. The widespread Eocene rifting phase presumably effectively separated western Sulawesi from East Kalimantan and from the continental crust underlying the East Java Sea. During the Early Eocene, when the coal-bearing Malawa Formation accumulated, there must have been land areas exposed in South Sulawesi. There are also indications that land areas were (periodically?) exposed in South Sulawesi during the Late Eocene to Early Miocene, as the reworked facies of the Tonasa Limestone Formation contains clasts showing carstic features (Wilson & Bosence, 1996). Data from wells in the Makassar Strait reveal the presence of terrestrial clastics of Eocene age, but since the Eocene marine deposition has continued here (Situmorang, 1987). Land connections between west Sulawesi and Kalimantan may have come into existence during the mid-Oligocene, corresponding with the unconformities recognized in various basins of the region. In the East Java Sea terrestrial clastics and marginal marine clastics accumulated locally from the mid-Oligocene until the beginning of the Miocene, indicating the existence of emerged areas in that region (Bishop, 1980; Cater, 1981; Bransden & Matthews, 1992), which could have served as stepping stones for terrestrial mammals on a migration to Sulawesi.

During the Early Miocene marine shales and marls were deposited in the Makassar Strait and on the Paternoster Platform, in South Sulawesi, the East Java Sea and the basins in southeastern Kalimantan, while locally accumulation of shallow marine carbonates continued (Wilson & Bosence, 1996). Towards the end of the Middle Miocene the carbonate formation came to an end all over the area, and deposition of shallow marine clastics started. This new depositional mode corresponds with the onset of the compressive regime related to the collision of the various microcontinental fragments with Sulawesi from the east. In west Sulawesi strong volcanism started during the late Middle Miocene and culminated during the Late Miocene. This must have contributed to the emergence of a chain of islands at this position.

The geological outline which has been presented in the sections above allow to draw the following conclusions concerning possible former land connections:

1) West Sulawesi was connected to the Sunda Shelf by widely exposed land surfaces from the Late Cretaceous until the Middle Eocene. Since stretching of the

Makassar Strait and East Java Sea started during the Middle and Late Eocene, these land areas became largely or completely flooded.

2) Exposed land areas in the region must have existed during the mid-Oligocene, as deduced from the unconformities recognized throughout the area, but it is not certain whether these resulted in continuous land connections to southern and western Sulawesi or not.

3) A next possible land connection, in any case of limited extent, may have occurred during the Middle Miocene, when the regional extensional tectonic regime changed into a compressive regime related to the collision of East Sulawesi. However, a complete land connection is unlikely, as shallow marine deposition is widespread throughout the area, including in South Sulawesi itself. The Middle Miocene Camba Volcanics cover most of the Western Divide Range and are intercalated with marine clastics. However, the local presence of ignimbritic rocks in the southern part of South Sulawesi (van Leeuwen, 1981) indicate that parts of the Western Divide Range were above sea level at that time. The presence of one or more islands aligned in a N-S trending volcanic arc during the Middle Miocene is thus plausible. This situation likely continued during the Late Miocene.

4) Full emergence of South Sulawesi above sea level must have taken place during the Pliocene and Early Pleistocene, as recorded in the Walanae Formation. However, the Makassar Strait was fully established as a deep marine basin during the Pliocene, thus creating an effective marine barrier between Sulawesi and Kalimantan.

5) Discontinuous land extensions may have existed from south Sulawesi in southwestern direction over the Doang Doang and Sabalena Platforms until the Early Pliocene. However, a full land connection with Java is unlikely because shallow marine deposition along the northern part of Java did not end until the Late Pliocene. Major parts of the shallow shelf extending into the Flores Sea adjacent to the SW arm of Sulawesi, rapidly subsided during the Pliocene, increasing the extend of the marine barriers there as well.

6) South Sulawesi was separated from Central Sulawesi as a separate palaeo-island during the Late Miocene and Early Pliocene, and probably throughout the Early Pleistocene as well.

Other land connections that have been postulated in order to explain land-vertebrate migrations to Sulawesi pass over Taiwan and the Philippines via the Sangihe Arc to North Sulawesi (see chapter 7 of this thesis, for a more complete overview of postulated land connections and vertebrate migration routes to Sulawesi). Recently, stegodont fossils have been found on the small volcanic island of Sangihe (Fig. 28) between the northern peninsula of Sulawesi and the southern Philippine island of Mindanao (Aziz, 1990; Samodra & Satria, 1991). As was stated earlier, the presence of elephantoids on an island is no proof for the former existence of a land connection between that island and the mainland, as elephantoids may have reached islands across the sea.

The volcanoes of the Sangihe Arc are mostly submarine or occur as small isolated volcanic islands with steep slopes. Some Neogene volcanics and granites occur in the southern part of the Sangihe Volcanic Arc (Simandjuntak, 1992). It is thought that subduction and formation of the Sangihe Arc began c. 25 Ma ago, when there was a change in motion of the Philippine Sea Plate (Hall, 1996). Several deep-sea gaps of over 1000 m depth nowadays separate Sangihe from North Sulawesi and Mindanao (Mammerickx et al., 1976; Aziz, 1990). If one assumes the existence of former land connections between Mindanao and Sulawesi, this would imply that strong subsidence should have occurred along the Sangihe Arc during Recent times. As Tjia (1993) notes, strong vertical movements of the order of 1-2 mm per year do occur in Eastern Indonesia nowadays, which implies that palaeogeographic reconstructions based on the present-day bathymetry should be handled with care. Most of these calculated vertical movement rates are based on strongly uplifted and exposed areas. Subsidence is more difficult to detect unless deep-sea drilling data are available.

Extensive seismic and gravity studies in combination with swath mapping have been carried out recently in the northern Molucca Sea (Rangin et al., 1996). Preliminary interpretation of these data revealed the presence of an almost complete Sangihe Arc and Forearc. According to this interpretation the Talaud ridge is part of the Sangihe Forearc, and the ophiolites exposed in Talaud could represent its basement, uplifted along the outer arc ridge. East of the ridge very contrasting terranes are separated by a major NW-SE crustal discontinuity interpreted as a left-lateral strike-slip fault. Subduction of the buoyant Snellius Ridge below the Sangihe Forearc terrane has induced incipient subduction along a new plate boundary more eastward, the Philippine Trench. The situation appears to be more complex because an incipient subduction zone is being formed along the northwestern part of the Sangihe Arc, with Celebes Sea Floor being thrusted below the northern part of the Sangihe Arc and SW Mindanao (Fig. 27). Despite the various uncertainties it is clear that the Talud-Tifore Ridge east of the Sangihe Volcanic Arc has been recently uplifted, as evidenced by the raised coral limestones reported by Simandjuntak (1992). It is thought unlikely that a continuous land connection between Sulawesi and Mindanao existed in the nearby past, but this assumption is based on recent faunal distribution patterns (Groves, 1976) rather than on geological evidence.

Stratigraphy of the Sengkang Basin

Previous studies

The Late Neogene sedimentary basin fills of South and West Sulawesi correspond roughly with the Celebes Molasse of Sarasin & Sarasin (1901), a name which was also used by van Bemmelen (1949). The name Walanae Formation for these synorogenetic molasse deposits in South Sulawesi was first used by 't Hoen & Ziegler (1917) for a series of clastic deposits outcropping along the eastern flank of the Walanae Depression in South Sulawesi (Fig. 26). Sartono (1979) divided the Late Neogene sediments into two formations: the name Walanae Formation became restricted to the Late Miocene to Early Pliocene marine muds, whereas the overlying sandy interval was given the name Beru Formation. This subdivision has not been followed by most subsequent workers, and indeed there are no indications for a marked boundary between the lower and upper parts of the sequence. The name Walanae Formation is used here for the Upper Miocene to Holocene clastic sequence developed in the Walanae Depression and its northern extension, the Sengkang Basin (Fig. 26). The basal contact of the Walanae Formation is usually not exposed. Exposed contacts with older formations are mostly fault-bounded. High gamma ray peaks in wells from the central part of the Sengkang Basin suggest that there the Walanae Formation rests unconformable on the Camba Formation, the latter of Middle to Late Miocene age (Grange & Davies, 1983). These authors mentioned that an angular unconformable contact at the base of the Walanae Formation shows up in seismic profiles from the basin margins. Seismic profiles also reveal that in the central part of the West Sengkang Basin the Walanae Formation comprises a continuous sequence up to the modern floodplain and lake deposits around lake Tempe.

The study area is included in the 1:250 000 geological map of the Pangkajene and western part of Watampone quadrangles, Sulawesi, prepared by Sukamto (1982). The Late Neogene Basin has been subdivided by Grange & Davies (1983) into the West Sengkang Basin (WSB) and East Sengkang Basin (ESB) (Figs. 26, 29). The Sengkang Anticline is the surface expression of a west dipping thrust fault, the East Walanae Fault, which delineates the eastern margin of the West Sengkang Basin. Seismic profiles (Grange & Davies, 1983; see also Fig. 35) reveal that the WSB is asymmetrical in EW transverse cross-section, having steeper dipping layers along its eastern flank. The thickness of the WSB-fill increases to at least 3500 m NE of Lake Tempe (Grange & Davies, 1983). Towards the south the thickness of the WSB-fill decreases gradually (Grange & Davies, 1983), and 50 km south of Sengkang along the Bengo River the sequence (excluding the basal Tacipi Limestones) of the Walanae Formation is only 600 m thick (Suminto, 1991). The basal Tacipi Limestones are included in the Walanae Formation by Sukamto (1982) but treated as a separate formation by Grange & Davies (1983). Because reef talus of the Tacipi Limestones is said to interfinger at places with the lower mudstones of the Walanae Formation by the latter authors, it is preferred here to include these limestones in the Walanae Formation.

Geological map of the Sengkang Anticline Area

A geological map of the study area has been prepared as part of this study, on a scale of 1:125 000 (Encl. A). A more detailed geological map on a scale of 1:34 500 (Encl. B) depicts the southern part of that map in more detail, i.e. the Lakibong Triangle (LT; see below). Most of the fossil localities mentioned in the text are concentrated in the LT and are indicated on Encl. B. Fossil localities outside the LT are indicated on Encl. A. On the geological map of Sukamto (1982) the Walanae Formation has not been subdivided, apart from the Tacipi Limestone Member. Except for Holocene alluvium, no older fan and terrace systems are indicated on this map either. The present map attempts to fill these gaps, in order to clarify the stratigraphic position of the fossil vertebrate remains that have been reported in previous studies without detailed stratigraphical information.

The map of Encl. A is centered around the N-S trending Sengkang Anticline, which forms the dominant structure in the area. An E-W profile through the Sengkang Anticline and the Lakibong Triangle is shown in Fig. 30.

The Sengkang Anticline is bounded in the east by a westward dipping reverse fault, the EWF. In the south, the Sengkang Anticline is cut off by a WNW-ESE trending fault, which joins with the EWF to the east. The Puncakoro Block, with a core of reef limestones of the Tacipi Member, has been uplifted along this fault (not downfaulted as indicated on the map of Sukamto (1982)). Aerial photographs and field studies have revealed that this fault has a more EW course than indicated on the geo-

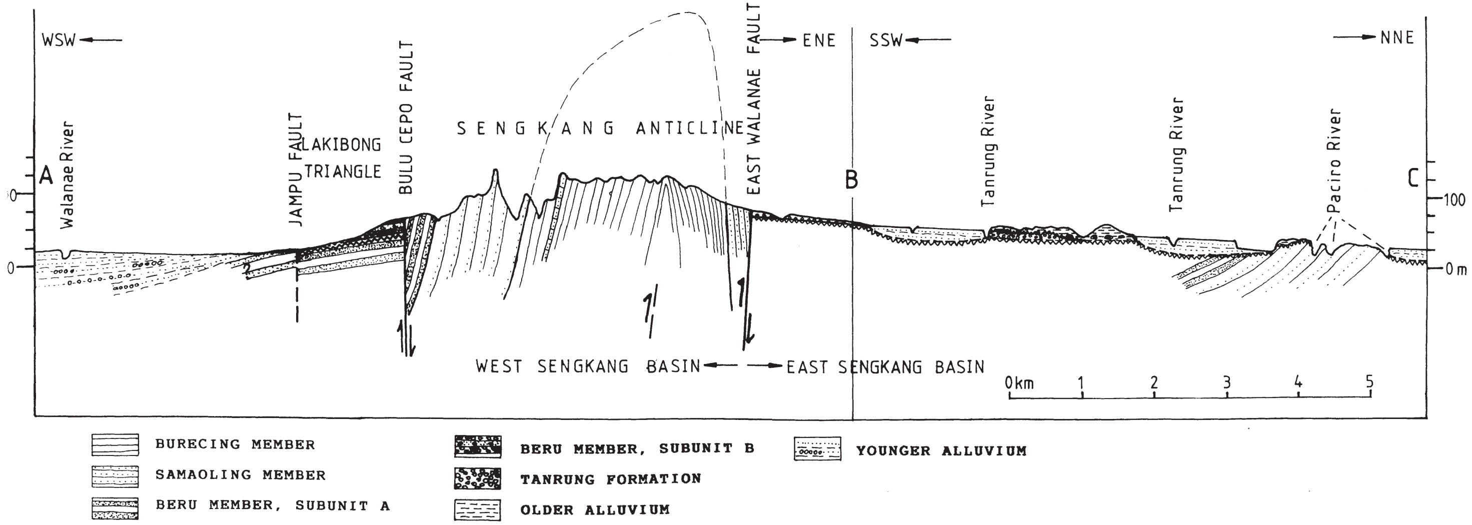


Fig. 30. E-W Cross-section through the study area, including the Lakibong Triangle, the Sengkang Anticline and the southwestern part of the East Sengkang Basin, based on outcrop data and fieldmeasurements. Note the vertical exaggeration. Line of cross section indicated on Encl. A. Saw-toothed lines indicate major unconformities or depositional hiatuses.

logical map of Sukamto (1982). The local structure is determined by the massive Puncakoro Block, with its core of Tacipi Limestones. During the latest, Quaternary EW compressional phase, a triangular area north of the western part of the Puncakoro Block has remained relatively free of deformation and folding (Encl. A). This triangular area, in which the bedding plane is horizontal to subhorizontal, is of particular interest, because many fossil and archaeological sites can be found here. This area is referred to as the Lakibong Triangle (LT), named after the Lakibong River, which dissects this small structural unit (Encl. B). The eastern boundary of the LT is determined by a fault, the Bulu Cepo Fault (BCF; named after Bulu Cepo Hill), which is exposed at several places in the field and clearly visible on the aerial photographs. East of the BCF the Walanae Formation is dipping 40-60°W, whereas west of this fault the bedding is subhorizontal. The western boundary of the LT seems to be determined by another fault, which also forms the western boundary of the Puncakoro Block, but which disappears below the deposits of the modern Walanae alluvial plain northwards (Encl. A) and has not been observed in the field north of Jampu. As will be shown later, the earlier confusion concerning the various fluvial terraces recognized in the surroundings of Beru by van Heekeren (1958, 1972), Sartono (1979), Bartstra (1977) and Bartstra et al. (1991, 1994), is likely due to the fact that this particular structural setting had not been recognized.

A NW-SE trending fault cuts the Sengkang Anticlinal axis east of Sompe (Encl. A). The offset along this subsidiary fault of the EWF is in accordance with left-lateral movements along the EWF, as was assumed to have taken place by Sukamto (1982). The western flank of the Sengkang Anticline is dipping less steep (20 to 30 WNW) near this area.

In the ESB, east of the EWF, the Walanae Formation is gently folded, with dips of less than 10°W in the area covered by this study (Encl. A). The axis of a second NS trending anticline is located just outside the map of Encl. A. The ESB has been levelled into a very weakly undulous terrain. The inclined beds of the Walanae Formation are locally covered unconformably by horizontally bedded younger deposits (Encl. A, Fig. 30), named here the Tanrung Formation. The Tanrung Formation is of limited thickness (10 m thick at most) and consists entirely of conglomeratic fluviatile facies of presumably Middle Pleistocene age. The Tanrung Formation in turn has been eroded, and both the Walanae and Tanrung Formations are unconformably overlain by younger Alluvium in the ESB.

Lithostratigraphy of the Sengkang Basin

The locations of the measured sections are indicated in Encl. A and B. The various units defined below, are indicated on the maps of Encl. A and B and illustrated in the schematic lithostratigraphic division shown in Fig. 31. The location of the various sections which have been logged during this study are indicated on Encl. A. The stratigraphic columns are shown in Encl. C and Fig. 40.

Walanae Formation — The oldest rocks outcropping in the study area are the Upper Miocene limestones of the Tacipi Member, which constitute the base of the Walanae Formation (Fig. 31). The limestones of the Tacipi Member are widely exposed along the southern margin of the ESB, but seismic profiles have shown that

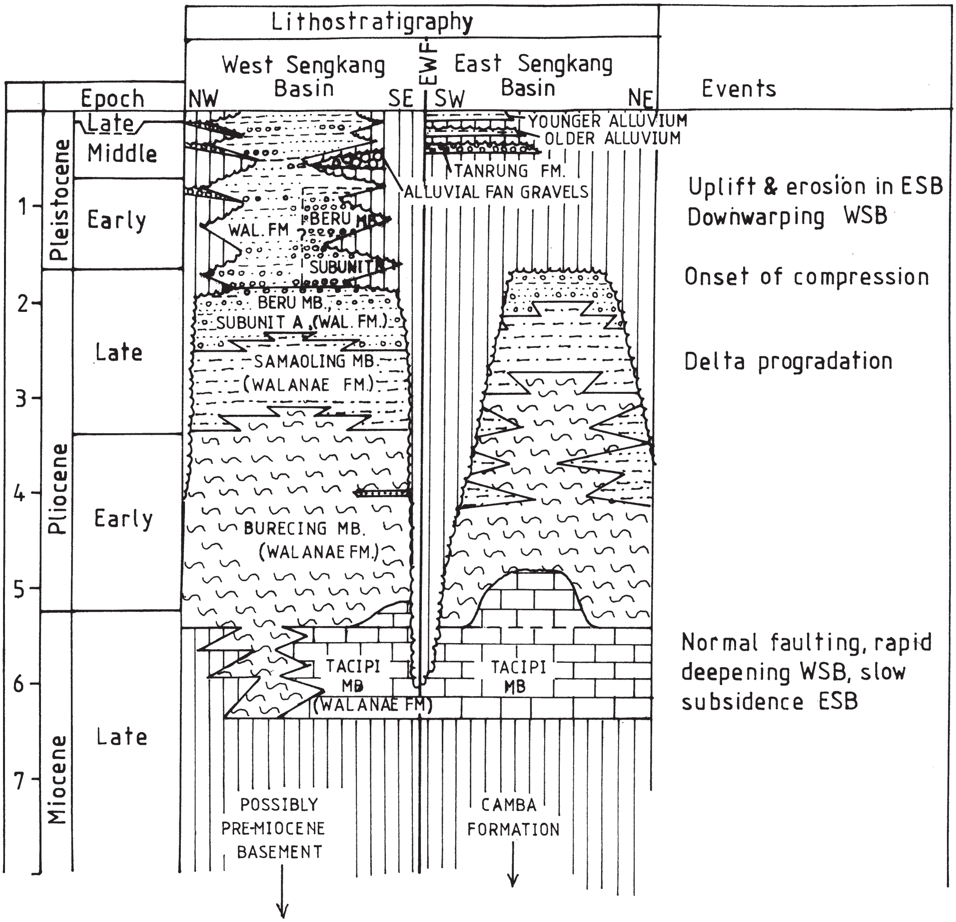


Fig. 31. Schematic lithostratigraphic subdivision of the Sengkang Basin, based on the present study and on Grange & Davies (1983).

they occur also in the subsurface towards the north (Grainge & Davies, 1983). In the WSB the Tacipi Member crops out south and southeast of the Sengkang Anticline in the uplifted Puncakoro Block, but it is not evidenced on seismic profiles throughout the northern part of the WSB nor in the subsurface of the Sengkang Anticline.

In the Sengkang Anticline, east of the town of Cabenge and further north, only clastic deposits pertaining to the Walanae Formation are exposed (Encl. A, Fig. 30). The Upper Miocene to Upper Pliocene, folded sequence is 1800 m thick, as follows from the measured sections presented in this thesis. Tacipi Limestones are not outcropping in the Sengkang Anticline. Northeast of the Tempe Lake the thickness increases to at least 3500 m (Grange & Davies, 1983). The sequence exposed in the Sengkang Anticline south of the town of Sengkang is here subdivided into three clastic members. From old to young these are: the Burecing Member (marine marls), the Samaoling Member (shallow marine sandstones and siltstones) and the Beru Member (fluvio-estuarine sandstones, lagoonal claystones and fluvial conglomerates) (Fig. 31). These three members can still be recognized in the more condensed, 600 m thick sections located 40 km S of the study area as reported by Suminto (1991).

In the depocentral axis of the WSB, the three above mentioned clastic members of the Walanae Formation are conformably overlain by a sequence of younger deposits (Fig. 35B), as follows from seismic profiles (Grainge & Davies, 1983). At least the upper 100 m of this sequence consist of fluviatile and lacustrine sediments, which have been encountered in various boreholes (Kusbini & Najamuddin, 1991). This upper sequence may be included in the Walanae Formation, but remains unnamed here as it has not been studied in detail.

In the ESB, the thickness of the gently folded Walanae Formation has not been measured, but seismic profiles reveal a sequence of up to 1800 m (Grange & Davies, 1983), which is of similar magnitude as the sequence exposed in the Sengkang Anticline. No attempt has been made here to subdivide the Walanae Formation in the ESB, but deep wells show a similar sequence as that exposed in the Sengkang Anticline, with marine muds in the lower part (Burecing Member) and more sandy marine deposits in the upper part (Samaoling Member). Fluvio-estuarine facies characteristic of the Beru Member, which constitute the upper 100-150 m of the sequence in the Sengkang Anticline, appear to have been largely eroded in the ESB. However, that the Beru Member was developed at least locally in the ESB, is indicated by an outcrop north of Bulu Barere (FVL-28 in Encl. A). At this place fluvio-estuarine facies was found, which contain terrestrial faunal elements characteristic of the Beru Member. The occurrence of terrestrial vertebrate remains encrusted with shallow marine invertebrata (*Balanus* and *Ostrea*), suggest that the transitional zone between the Samaoling Member and Beru Member is represented here. Fluvial clastics were also reported to occur in the northern part of the East Sengkang Basin (Grainge & Davies, 1983).

Old Alluvial Fan Gravels — In the WSB the Walanae Formation is locally, northwest of the Puncakoro Block, unconformably overlain by alluvial fan gravels. Their development is probably related to the Pleistocene uplift of this structural block, and they are mostly restricted to the western side of the Walanae River except for a few places on the east bank of the river at altitudes of at most 7 m above the low water level of the river. Contrary to the opinion of earlier workers, no fluvial terraces could be ascertained on the higher reaches west of the Walanae River. Only poorly sorted and unconsolidated colluvium, consisting of the erosion products derived from the Walanae Formation, have locally accumulated in small pockets along the mainly E-W trending valleys cutting through the Sengkang Anticline.

Tanrung Formation — Locally in the ESB, sub-horizontally bedded conglomeratic fluvial deposits unconformably overlie the slightly folded marine part of the Walanae Formation along the Tanrung River (Encl. A). These well cemented conglomerates, which are named here the Tanrung Formation, contain a different and younger vertebrate fauna than the Beru Member of the Walanae Formation. The Tanrung Formation has been eroded partly in turn, and is unconformably overlain by horizontally bedded black clays and unconsolidated sandy deposits, designated as the Older Alluvium.

Alluvium — Two geomorphologically distinct alluvial units could be distinguished in the ESB, designated as Older Alluvium and Youngest Alluvium. The Older Alluvium covers the Tanrung Formation with an erosional contact. It consists dominantly of black clays, but also sandy deposits are intercalated. The facies suggests deposition in coastal swamps and small rivulets. The inferred age is Late Pleistocene. Subsequent erosion in the ESB has shaped the Older Alluvium into a dissected terrace.

The youngest deposits in the ESB consist of Holocene gray to black silty clays and sands, very similar to the facies of the Older Alluvium. The Youngest Alluvium has filled in valleys eroded in the older deposits (Walanae Formation, Tanrung Formation, and Older Alluvium). These valleys were probably formed during the last glacial maximum, and their sediment infill presumably occurred following the Holocene sea level rise. The top of the Youngest Alluvium forms flat lowlands, which merge into the Walanae River floodplain to the north. The elevation of the flat top surface of these Holocene alluvial deposits is at an elevation several meters below the dissected top surface of the older deposits of the Tanrung Formation and overlying Older Alluvium (Fig. 37).

In the WSB a continuous sequence of clastic deposits was deposited along the depocentral basin axis, as indicated by seismic profiles (Grange & Davies, 1983) and borehole data (Kusbini & Najamuddin (1991). Here the Walanae Formation grades upward into the modern alluvial plain deposits of the Walanae River (Fig. 31).

Description and interpretation of the lithologic units studied

West Sengkang Basin

Burecing Member — The lower 900 m of the Walanae Formation, exposed in the Sengkang Anticline, consist of deep marine calcareous gray clays (yellow when weathered). These clays contain foraminifera, nannoplankton and marine molluscs. This clay unit is designated here as the Burecing Member of the Walanae Formation, named after the village Burecing along the Cabenge-Pampanua road (Encl. B). South of the Sengkang Anticline coralline limestones of the Tacipi Member underlie and probably partly interfinger with the basal part of the Burecing Member. However, the contact between the marine clays of the Burecing Member as exposed in the Sengkang Anticline and the Tacipi Member exposed in the Puncakoro Block is a fault contact (Encl. A). In the Cabenge-Pampanua road section (section III), stratigraphically 375 m above the lowermost exposed level, a 10 m thick massive, poorly sorted sandstone with abundant reworked calcareous marine organisms is the only coarse-grained layer encountered in the Burecing Member (Fig. 40). This marker bed was also observed in section I. It possibly consists of reworked clastic material, which could have been mass-transported from the shallower shelf of the ESB east of the EWF into the deeper WSB, or the material may originate from a carbonate reef in the same area or on the Puncakoro Block to the south.

Foraminifera in the Burecing Member suggest an open marine, outer sublittoral to upper bathyal depositional environment (Sudijono, pers. comm., 1994).

Samaoling Member — The marine clays of the Burecing Member are overlain by a

850 m thick interval of alternating siltstones, claystones and sandstones. This sandy interval has a marine lower part and a fluvio-deltaic upper part and has been named Beru Formation by Sartono (1979). Here, it is preferred to designate only the upper terrestrial part of this sandstone interval as the Beru Member of the Walanae Formation (Fig. 31). For the lower, marine part of the sandy interval the new name Samaoling Member of the Walanae Formation is proposed. The member is named after the village Samaoling located along the Cabenge-Pampanua road (Encl. B). The Samaoling Member is fairly well exposed along this transect. It is characterized by an alternation of shallow marine siltstones and fine to medium grained well sorted sandstones. These siliciclastic deposits contain an increasing amount of volcanic components towards the top. The presence of minor amounts of biotite is characteristic. Locally, plant remains are included, indicating shallow marine conditions. Calcareous fossils have been mostly leached out from the sandstones remaining as casts, but can be found at a few places in the finer grained layers.

Near Samaoling village (section III), an interval of c. 100 m of the lower part of the Samaoling Member is well exposed. A detailed representation of this lower interval is shown in Fig. 32. This interval is characterized by an alternation of gray siltstone layers with very fine to medium grained sandstone layers, individual layers varying between 1 and 35 cm in thickness. The thicker sandstone layers are the coarsest and often show a scouring base. The sands are well sorted and massive, only rarely exhibiting foresets. Such foresets can only be recognized due to alignments of silty intraclasts, which have been eroded from intercalated siltstones. The thinner, fine-grained sandstone layers on the other hand, show abundant wave-ripple cross-laminations. Ripple crest heights vary between 1 and 2 cm and the wavelengths between 7 and 17 cm. The highest ripples have the greatest wavelengths. Both straight-crested, symmetrical ripples as well as asymmetrical ripples can be observed in distinct layers. Larger wave ripples with a crest height of 4 cm and a wavelength of 30 to 50 cm are recognizable on top of one of the medium grained sandstone layers.

The interbedded siltstones in the same interval are parallel-laminated and frequently include poorly preserved plant debris. Horizontally continuous siltstone layers sometimes grade upwards into wavy laminated flaser structures.

This lower sandy interval of the Samaoling Member is not developed in section I towards the south. Here the base of this member is characterized by bioturbated siltstones and minor amounts of thin fine-grained sandstone layers (Fig. 40).

In the Cabenge-Pampanua road section (section III) the amount of sandstone decreases gradually upwards, and the deposits become more homogeneous due to bioturbation. The middle interval of the Samaoling Member is poorly exposed here, but seems to be dominated by siltstones and claystones. Calcareous concretionary layers of 5-20 cm thick and silty layers with molluscs occur in this interval. Shallow marine molluscs such as *Placuna placenta* and *Arca* sp. can occasionally be found in live position in the fine-grained sandy layers. Near the top of the Samaoling Member the amount of sandstone increases in both sections I and III, but siltstones and claystones still constitute the major component (Encl. C). The colour of the upper sandstones of the Samaoling Member is yellowish brown and differs from the gray sandstones near the base of the same member. The brown colour is due to weathering of siderite, which constitutes the main cement of the upper sandstones. In this upper

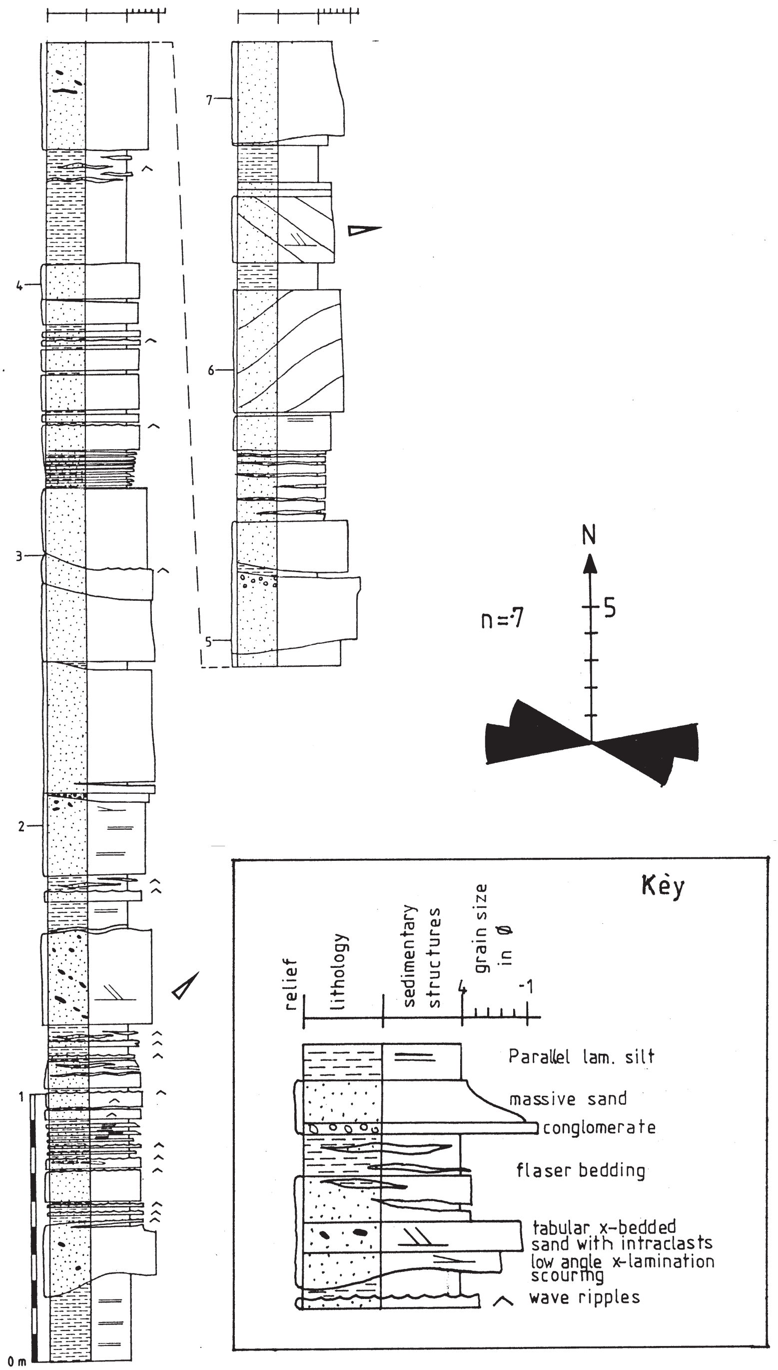


Fig. 32. Detailed section logged near the base of the Samaoling Member (Walanae Formation) along the road Cabenge-Pampanoa (section III). Arrows indicate palaeocurrent directions. Rosediagram shows the orientations measured perpendicular to wave-ripple crests.

interval the frequent occurrence of sand/mud couplets reveals the influence of tidal currents. This interval, deposited under tidal influence, can be recognized in sections I, III and XI and in other outcrops along the Sengkang Anticline. The sand-dominated intervals in this upper part of the Samaoling Member exhibit different sedimentary structures as compared to the sandstones and siltstones near the base of the Samaoling Member in section III. Wave-ripple structures and flaser bedding were not encountered in the uppermost part of the member. Instead, this is characterized by tabular and trough-cross bedded structures with foresets of up to 0.5 m high, in which sandy foresets alternate with mud drapes. Marine fossils and signs of bioturbation are absent in these fine- to medium-grained sandstones. Mostly, the mud drapes are irregularly spaced and interrupted by erosional surfaces. In one case in section I cosets of cross-bedded strata with double mud drapes alternating with sandy tabular foresets could be distinguished. Such structures have been designated as bundle sequences, and are diagnostic for a subtidal channel environment (Visser, 1980; de Boer et al., 1989). The outcrop under consideration, located near the village of Lepangeng, consists of a freshly excavated vertical surface (Fig. 33). Two superimposed bundle sequences could be distinguished. The lower, most complete one, consists of 45 bundles, i.e. unidirectional cross-bedded strata with foresets up to 0.5 m high. Sandy, large-scale ripple foresets (1 in Fig. 33), generated by the predominant tidal current, alternate with thin couplets of mud (2 and 3 in Fig. 33), in some cases separated by thin sand laminae. The mud drapes were deposited from suspension at high and low slack water during a single ebb/flood cycle, when the current velocity decreased to near zero. The thin sandy laminae between two mud drapes were deposited during the subordinate tidal current (which can have been either the ebb or the flood current). Ideally, an individual bundle should consist of a thick sandy foreset, a mud drape, a thin sandy foreset and a second mud drape. However, due to random events caused by e.g. wind-generated currents, or due to (partial) erosion of the mud drapes by the dominant or subordinate tidal currents, complete bundles are not developed in many cases. Some bundles lacking double mud drapes at their boundaries can be recognized due to grainsize variations. Each bundle, whether completely developed or not, is thought to represent one ebb/flood cycle, with a dominant current event (either the ebb or the flood current at any particular place), a water standstill event (during either high or low slackwater), a subordinate current event and a second slackwater event (Visser, 1980). The special hydraulic conditions, under which such tidal bundle sequences can be preserved, include a subtidal environment, probably in a laterally migrating tidal channel, with relatively weak but strongly asymmetrical tidal currents. The predominant tidal current should be able to transport sand and the subordinate current only very little, so that there is little erosion of the crossstrata formed by the dominant current. Furthermore, the environment should also be rich in suspended mud, either flocculated or in organically pelleted form, and also sand should be available in sufficiently large amounts (Middleton, 1990). The formation of stable megaripples or sandwaves in a zone predominated by one of the tidal currents, usually occurs in the channelized inshore parts of estuaries or tidal embayments, under mesotidal regimes.

The bundle sequence from Lepangen in section I appears incompletely preserved, as follows from the rare preservation of continuous mud drapes. This means that cau-

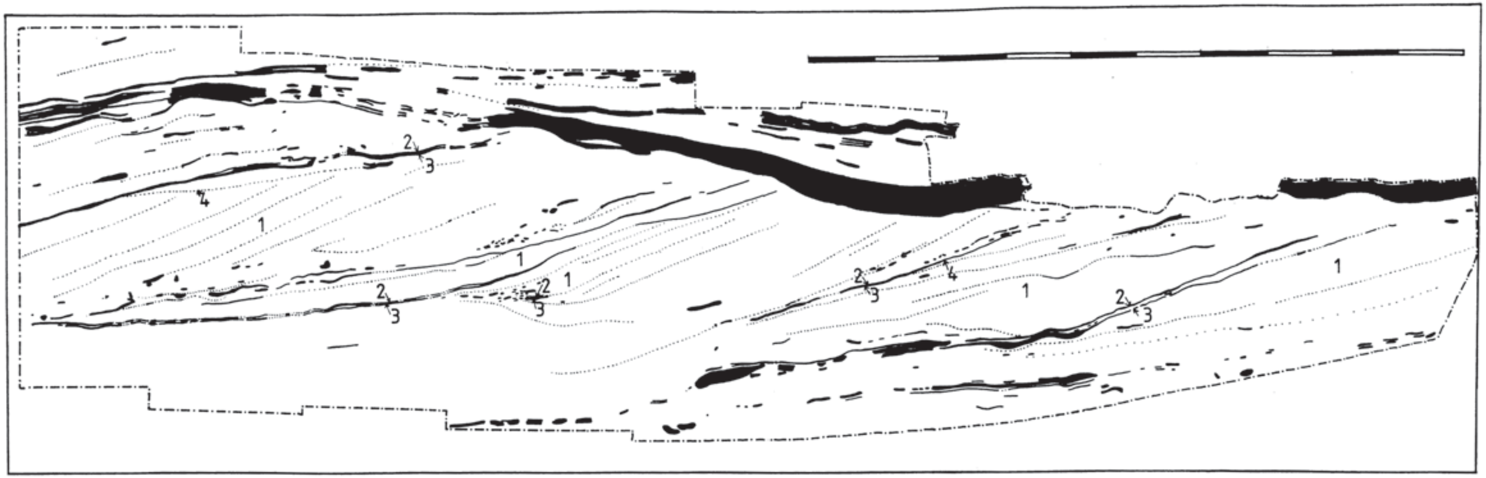


Fig. 33. Part of a tidal bundle sequence exposed in the upper part of the Samaoling Member (Walanae Formation, section I). 1 = sandy megaripple foresets deposited by the dominant tidal current; 2-3 = double mud drapes separated by thin sandy laminae; 4 = internal erosional contact. For further explanation see text.

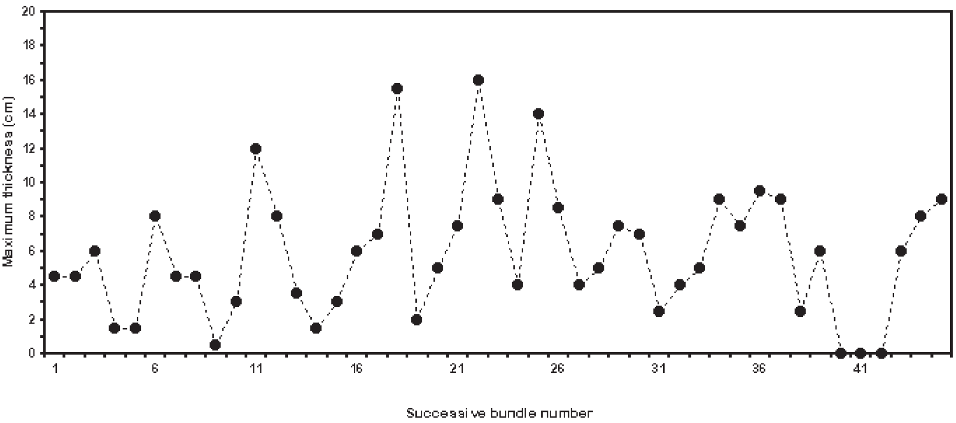


Fig. 34. Maximum thicknesses of successive bundles as measured in the field for the bundle sequence partly shown in Fig. 33. A cyclic pattern of gradually increasing and decreasing bundle thicknesses can be distinguished, each cycle comprising between 4-5 bundles on average.

tion should be taken in interpreting the tidal regime from measurements of the thicknesses of successive bundles, as has been done with other recent and fossil examples of tidal bundle sequences (Visser, 1980; Allen & Homewood, 1984; Yang & Nio, 1985). In the bundle sequence from section I the maximum preserved thicknesses of individual bundles were measured; the results are plotted in Fig. 34. In total 45 bundles were recognized, with thicknesses varying between 0 and 16 cm, measured perpendicularly to the cross-bedding plane. A thickness of 0 cm was measured in bundles 40 to 42, of which only the muddrapes in the toesets have been preserved. The diagram of Fig. 34 reveals that the thicknesses of successive bundles exhibit a cyclicity of 4-5 bundles per cycle, each cycle showing an increase and again decrease in the bundle thicknesses. Such cycles have also been observed in other recent and fossil bundle sequences, and are induced by cyclic variations in the dominant tidal current velocities during the neap/spring/neap cycles (Visser, 1980). In the Lepangen bundle sequence the average preserved neap/spring/neap cycle comprises 4 to 5 dominant current events (each one represented by single bundles within one cycle). In total 10 of such cycles can be recognized in the series of 45 bundles that could be measured.

In a pure diurnal tidal system the number of dominant current events corresponding with one neap/spring tidal cycle should be 14. In mixed or semi-diurnal tidal systems the number of dominant current events can increase to an average of 28 dominant current events per neap/spring cycle.

Characteristic for the Lepangen bundle thickness sequence is the general lack of thin-thick alternations. The successive bundles show steadily increasing and than again decreasing thicknesses. In bundle sequences formed under the influence of a semi-diurnal tidal regime, trends of thin-thick alternations are superimposed upon lower frequency neap/spring cycles (de Boer et al., 1989). The lack of such thin-thick alternations in the Lepangen sequence constitutes a strong argument in favour of a diurnal tidal regime. This means that in the Lepangen sequence on average only during 4 to 5 dominant current events within one neap/spring/neap tidal cycle currents were strong enough to propagate megaripple migration so that a thick sandy foreset could be formed. Around neap-tide the dominant current velocities within individual ebb/flood cycles were seemingly not strong enough for bedform migration, and a period of standstill without dune migration and even with erosion of earlier deposited bundles occurred (e.g. the erosional reactivation surface marked with 4 in Fig. 34). If the tidal regime under which the Lepangen sequence was formed was indeed diurnal, then on average 9 to 10 dominant current events, representing a timespan of a same number of days, are not recorded between two successive bundle thickness cycles.

In the most northerly measured section near Sengkang (section XI, Encl. C) only a 267 m thick interval, forming part of the middle and upper part of the Samaoling Member, is exposed along the road to Sengkang (Encl.A). Here, the Samaoling Member appears to be more sandy than in sections I and III. Trough-cross bedded subtidal deposits with mud drapes occur 40 m below the top of section XI, but the alternation of sand and mud is rather irregular.

Beru Member — As stated above, the name Beru Member used here refers only to the upper, terrestrial part of Sartono’s (1979) sandstone-dominated Beru Formation, a name which was rather unluckily chosen, because no continuous outcrops occur along the road at Beru. In addition, the strata at Beru, located in the fault-bounded Lakibong Triangle, can not be tied directly to the long sections (sections I, II and III) measured on the west flank of the Sengkang Anticline. Besides, some gravels associated with stone artefacts, which occur south and directly east of Beru, have been interpreted by some authors (e.g. van Heekeren, 1958; Bartstra, 1977; Sartono, 1979b) as remnants of Late Pleistocene fluvial deposits, which were subsequently shaped in to terraces. It is to these gravels to which the name Beru is mainly associated. For the sake of continuity, we will retain the name Beru Member to designate the upper, terrestrial part of the Walanae Formation as it is developed in the Sengkang Anticline and adjacent areas. Good outcrops of the Beru Member exist along the road passing Beru, not near Beru, however, but more to the east, near the village of Ciangkange where the strata of the Beru Member dip westward in the west flank of the Sengkang Anticline. Also along section I, near Lepangeng, and near Sompe (FVL-25, Encl. A), good outcrops exist.

Intercalation of fluvial layers with lagoonal/estuarine layers near the transition of the Beru and Samaoling Members has been observed at several places, for example at FVL-25 near Sompe (former spelling Sompo or Sompoh; section IV) and near Leppangen (section I). The lowermost coarse-grained, poorly sorted fluvial sandstone is taken as the boundary between the two members (Encl. C). In most cases, this lower fluvial sandstone is also the lowermost layer containing terrestrial vertebrate fossils.

The Beru Member as exposed along the western flank of the Sengkang Anticline comprises the upper 100-150 m of the Walanae Formation. The member is there characterized by lagoonal/estuarine and fluvio-lacustrine clays and siltstones, alternating with fluvial and fluvio-estuarine sandstones and conglomerates. The northernmost exposures of the member in the Sengkang Anticline are found in the vicinity of Celeko. Hooijer (1954a) mentioned Celeko as one of the sites where van Heekeren collected vertebrate fossils. Though the exact site of van Heekeren could not be rediscovered in the field, it is thought to be located near the place indicated as FVL-27 on Encl. A, based on indications of our guide, Mr. Anwar Akib. On the aerial photographs it was observed that the upper part of the westward dipping sequence disappears below the floodplain deposits of the Walanae River further north of Celeko (Encl. A).

In the claystones and siltstones of the Beru Member sedimentary structures have been usually obliterated by bioturbation and/or soil formation. The muds show a wide variety of colours, but are normally gray or olive, frequently with orange-brown mottling. Upon weathering, the colour of the gray muds changes to yellowish-gray. Palaeosols are characterized by intensely mottled intervals, sometimes with dark-red, purple or chocolate-brown colours. Caliche concretions are widespread in the muds, but are rarely seen to follow the original bedding plane. They might be partly of (sub)Recent origin. In the lower part of the Beru Member gray silts and silty clays are locally alternating with yellow calcified siltstones containing reworked marine molluscs and echinoid fragments, suggesting a lagoonal depositional environment for at least some of the muds (where indications for a lagoonal environment are present, these layers or intervals have been marked with l in Encl. C). In some marine-terrestrial transitional intervals near the base of the member, lag deposits occur at places. These consist of pebbles and rounded vertebrate bones in a poorly sorted sandy clay matrix. These deposits are matrix-supported. Some of the pebbles and bones have been encrusted by bryozoa and subtidal molluscs (*Chlamys* sp., *Ostrea* sp.) and/or crustaceans (*Balanus* sp.). These are subtidal marine organisms, which depend on rocky substrates. Such transitional deposits can be found near Sompe (FVL-25 in Encl. A & C), Padali (FVL-30; this is the only fossil vertebrate locality outside the mapped area shown in Encl. A) and Bulu Barere (FVL-28 in Encl.A). At other places, like Lonrong (FVL-24), terrestrial vertebrates occur in sandy layers together with shark teeth and calcified wood fragments with borings of marine molluscs. Also well cemented sandy layers with densely packed fragmented and reworked *Ostrea* remains occur locally in the transitional zone (e.g. in the layer stratigraphically 3 m below the lowermost fluvial sandstone of the Beru Member in section I). Such layers have been interpreted as littoral or beach-rock deposits and are indicated with b in Encl. C.

The fluvial sandstone layers vary in thickness between 10 cm and 30 m. The thinnest sandstone layers usually occur in the middle of a mottled interval of silty muds. They are irregularly bedded and sometimes wedge out locally to reappear again laterally over distances of several meters. Nevertheless, they can be usually traced over considerable distances of tens of meters. They are composed of very poorly sorted clasts (including granules) with a considerable amount of clay matrix. Such thin sandstone layers are interpreted as unchannelized sheetflow deposits. The thicker, single- or multistorey sandstone beds have erosive bases, and often tend to show one or several fining-upward intervals, separated by erosional surfaces (multistorey layers). The fluvial sandstone beds can be easily distinguished from the fine-grained, marine sandstones in the lower part of the sequence. The fluvial layers are coarser-grained, usually with admixtures of granules or isolated pebbles and rather poorly sorted: they contain abundant angular to subangular grains, and show rapid alternations of middle-grained and very coarse-grained sand layers. They do not contain marine fossils.

The sandstone beds consist of characteristic irregularly bedded stacked layers of up to tens of centimeters thick, often without internal structures preserved. Parallel or low-angle laminations are the most frequently occurring structures in the sandstones. Crossbedding can occasionally be observed in the fluvial sandstones, usually in the less well cemented intervals. Both tabular and trough-crossbedding occur. The trough-crossbedded foresets have a maximum preserved height of 15 cm. Tabular foresets of up to 1 m high have been found locally intercalated with 10-40 cm thick layers, consisting of either massive sandstone or of sandstone with low-angle cross-laminations (section III, Encl.C). In the generally weakly consolidated sandstones hard, irregular concretionary bands of siderite- or calcite-cemented sandstone are common. Large-scale inclined heterolithic bedding, indicative of laterally migrating channels, has not been encountered anywhere, but this may be related to the poor outcrop conditions, as the layers can seldomly be studied in detail over lateral distances larger than 10 m.

In the lower part of the Beru Member the fluvial sandstones locally contain partly preserved cream-coloured mud drapes of less than one to several centimeters thick. Otherwise, rounded intraclasts of the same silty clay, supposedly representing reworked fragments of these mud drapes, can be found at some places. In the poorly sorted fluvial sandstones, mud drapes do not occur in well-organized bundle sequences such as those in the subtidal interval at the top of the Samaoling Member. In the fluvial sandstones mud drapes exhibit an irregular, interrupted or undulating pattern inside parallel and low-angle laminated sandstone intervals, the latter showing maximum grain sizes larger than medium grainsize, whereas in the subtidal sandstones near the top of the Samaoling Member the maximum grain size normally does not greatly exceed medium grainsize. It is thought that the mud drapes were deposited in river channels in a more inland setting, where tidal currents periodically counteracted the fluvial currents. In Encl. C such intervals are indicated with ft (fluvio-tidal).

Subdivision of the Beru Member — West of the Bulu Cepo Fault (BCF), in the Lakibong Triangle (LT) all strata that crop out can be included in the Beru Member. At some places fluvial layers were found intercalating with tidally influenced sandstone layers exhibiting sand/mud couplets, and other shallow marine clastics, sometimes containing marine molluscs. The shallow marine strata always occur along the western margin of the LT or in the river valley bottoms, topographically corresponding with the lowest areas in the LT. As the layers have a horizontal to subhorizontal orientation in the LT, contrary to the steeply westward dipping layers of the Sengkang Anticline east of the BCF, the interval showing intercalating of shallow marine and fluviatile layers corresponds with the stratigraphically lowest part of the sequence in the LT (e.g. at FVL-9, section X and at Palangiseng, section VII). The structural discontinuity formed by the BCF is also reflected in the different sequential development on both sides of this fault. In all measured sections east of the BCF (sections I-III) the percentages of fine-grained sediment (clay + silt) in the Beru Member vary between 47% and 78% of the total measured sequential thickness (Encl. C). Silts and clays representing low energy environments, such as lagoonal, lacustrine or floodplain settings, constitute a major part of the sequence here. In the Beru Member west of the BCF on the other hand, fine-grained low energy silts and clays are clearly less well represented (sections V-VII), and their total percentage amounts to 28% at most (Encl. C).

One possibility is that this sequential difference reflects syndepositional faulting and folding activity during the deposition of the Beru Member, with relative uplift of the area east of the BCF as compared to the western area, the latter being closer to the faster subsiding depositional axis of the WSB. Bridge & Leeder (1979) and Bridge & Mackey (1993) presented a computer simulation model of fluvial deposition under varying depositional constraints. It followed that when the basin floor is tilted, the sandy channel belt deposits tend to become concentrated near the most rapidly subsiding side of the basin, whereas on the less subsiding side mostly floodplain fines accumulate. Similarly, initial uplift of the Sengkang Anticline could have confined the palaeo-Walanae River system largely to the more rapidly subsiding depocenter of the basin, while the higher reaches of the palaeo-floodplain, that is in the less rapidly subsiding area east of the BCF (sections I-II), would be dominated by fine-grained mud deposition. If the sediment supply remained constant before and after the onset of the presumed differential subsidence, marine incursions would also be expected to occur in the more rapidly subsiding area, i.e. the Lakibong Triangle.

The presence of fluvial sandstones deposited under tidal influence in the upper 50 m of sections I and II indicates that this part of the basin was still under marine influence at the time of deposition, whereas in the upper part exposed in the LT tidally influenced facies is lacking and coarse clastics dominate the picture there. If differential subsidence took place, and if the upper parts of the section west and east of the BCF are considered as time-equivalent, then the observed sequential differences can be only explained by assuming increased sediment supply, forcing back marine influences from the basin depocenter, whereas along the less rapidly subsiding basin margins tidally influenced deposits could still accumulate.

However, there is a more plausible explanation for the observed sequential differences, as will be argued next. Probably the sequence exposed in the LT west of the BCF is younger in age than the Beru Member sequence as preserved in the west flank of the Sengkang Anticline, east of this fault. This interpretation would be in accordance with the seismic profiles presented by Grange & Davies (1983). It can be observed in these profiles (Fig. 35A-B) that west of the Sengkang Anticline successively younger layers come to the surface in western direction (note however, that the profiles shown in these figures were obtained north of the study area where the BCF is not developed). In Fig. 35B it can further be seen that the deltaic upper part of the Walanae Formation shows an onlapping sequence of constant thickness from east to west. This indicates a period of tectonic quiescence and subsidence of the entire basin during deposition. However, the sequence conformably overlying this deltaic sequence in the depocenter of the WSB pinches out towards the basin margins. These deposits were formed simultaneously with downwarping of the basin along its axis and indicate compressional tectonic activity during deposition, which continues to the present day. This youngest sequence was deposited along the depocenter of the WSB while the Sengkang Anticline Area experienced uplift and erosion simultaneously.

It is therefore assumed that the upper part of the sequence developed west of the BCF in the LT, which is dominated by conglomerates (Encl. C), was deposited after the onset of the EW compressional phase resulting in the downwarping of the WSB,

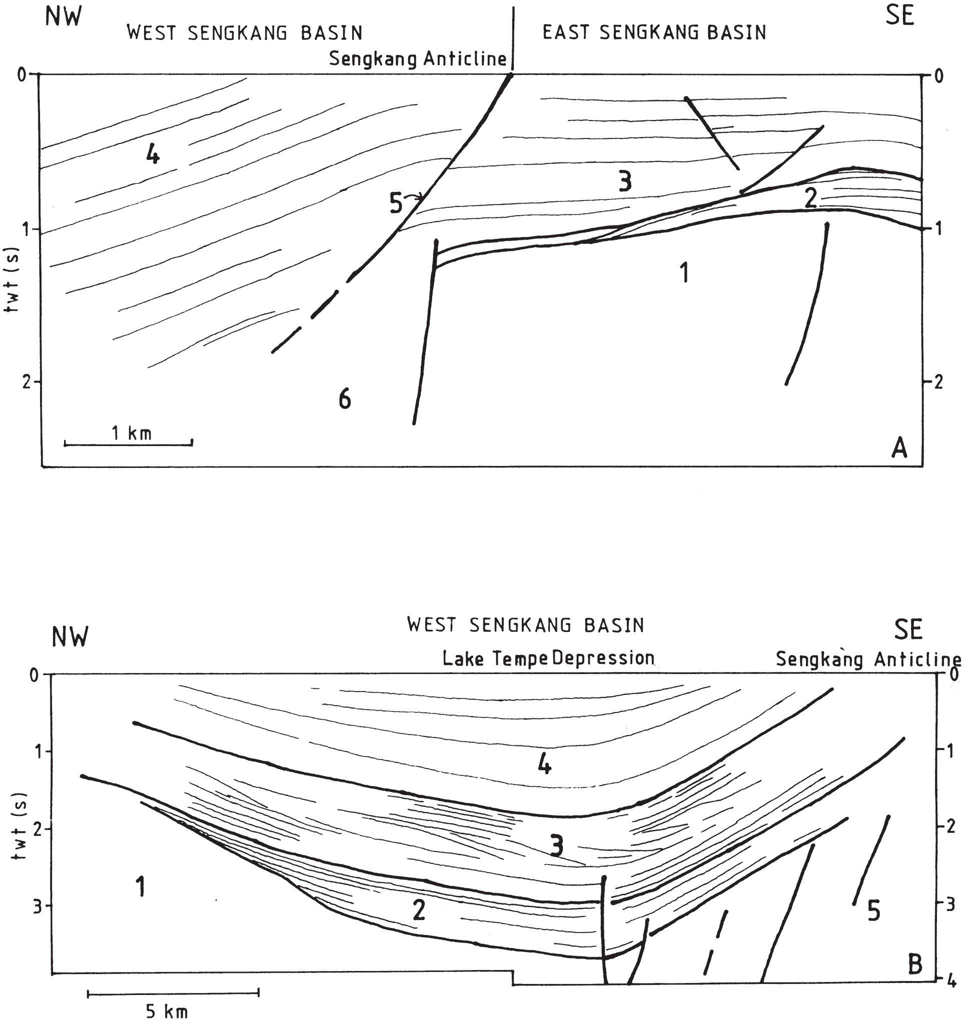


Fig. 35. NW-SE cross sections through the Sengkang Anticline and East Walanae Fault (A) and West Sengkang Basin (B), based on interpretations of seismic profiles presented by Grange & Davies (1983). A: 1 = Basement High; 2 = Tacipi Limestones; 3 = onlapping sequence of the marine clays of the Walanae Formation; 4 = down-folded layers of the Walanae Formation in the WSB; 5 = thrust fault underlying the Sengkang Anticline; 6 = zone of complex normal faulting with downthrowing to the west. B: 1 = pre-Miocene basement or Middle Miocene volcanics; 2 = onlapping Lower Walanae Formation (Burecing Member); 3 = large-scale delta foresets in Upper Walanae Formation (Samaoling and Beru Members); 4 = sequence deposited during tectonic downwarping of the WSB.

whereas the upper terrestrial part of the sequence in the west flank of the Sengkang Anticline predates this compression, and is thought to be deposited during the period of tectonic quiescence and delta progradation. This interpretation is shown in Figs. 30-31. The conglomeratic upper interval is thought to represent a later stage in the infill history of the WSB as compared to the youngest strata exposed in the west flank of the Sengkang Anticline. In the Sengkang Anticline this upper conglomeratic interval may never have been deposited due to the onset of uplift and folding there.

The latter interpretation, in which the fluvial deposits west of the BCF are being considered younger than the top of the sequence east of this fault, also fits better with the fossil evidence and ESR datings, as will be shown later. Following this interpretation, the conglomerate-dominated interval west of the BCF, is indicated as a separate subunit in Enclosures B and C (Subunit B of the Beru Member), while the lower part of the Beru Member, dominated by clays and silts, is indicated as Subunit A of the Beru Member. It must be stressed however, that because of the rather poor exposure of the sequence it is not possible to mark the exact boundary between both subunits. Their distinction is merely based on the overall sequential differences in combination with palaeontological evidence (see later) rather than on a clearly recognizable erosional or facies boundary. In the lower reaches of the Lakibong Triangle, fluvial sandstones occasionally exhibit sand/mud couplets indicative of tidal influence. This interval, though dominated by coarse-grained clastics, is more similar to the strata of Subunit A as developed in the west flank of the Sengkang Anticline. As a rule, the clastics exposed in the stratigraphically lower reaches of the LT were included in Subunit A when there were indications for tidal influence. The upper, conglomerate-dominated interval, lacking mud drapes and marine fossils, was mapped as Subunit B (Encl. B).

The upper part of Subunit B can easily be distinguished from Subunit A because of the predominance of pebbly sandstones and ortho-conglomerates and the absence of tidally influenced clastics with sand/mud couplets. The maximum clast diameter in the conglomerates of Subunit B is 4-12 cm, depending on the outcrop, with average clast diameters of between 2 and 4 cm. Sand lenses or layers are usually intercalated in the conglomerates and alternations of orthoconglomerates and pebbly sandstone layers are common. The pebbles in these conglomerates are for c. 90% of volcanic origin with minor amounts of chert and other sedimentary rocks. The composition of the conglomerates and sandstones will be discussed in more detail in the petrographic section of this chapter further on.

Palaeocurrent measurements — The amount of palaeocurrent directions that could be measured in fluvial sediments of the Beru Member is limited (only 10 measurements), partly due to the generally poor outcrop conditions, and partly due to the nature of the Beru Member fluvial deposits, in which fully preserved cross-bedding structures are rare. The palaeocurrent directions that could be measured were taken in fluvial sandstone layers with megaripple cross-bedding. Palaeocurrent measurements taken in steeply dipping west flank of the Sengkang Anticline were rotated to a horizontal position using the anticlinal axis as rotation axis. Though the amount of measurements is limited, there appears to be a consistent pattern. The 10 measurements were made at different localities and stratigraphic levels but indicate a consistent pattern of a northward flowing river system (Fig. 36A).

Nine palaeocurrent measurements could be taken in tidally influenced sandstones, characterized by cross bedding in which the sandy foresets alternate with thin mud drapes. Measurements were taken on both tabular cross bedding, like the example of the bundle sequence discussed earlier, as well as on trough-cross bedding with sand/mud couplets. All measurements were taken in the transitional interval between the Samaoling and Beru Members.

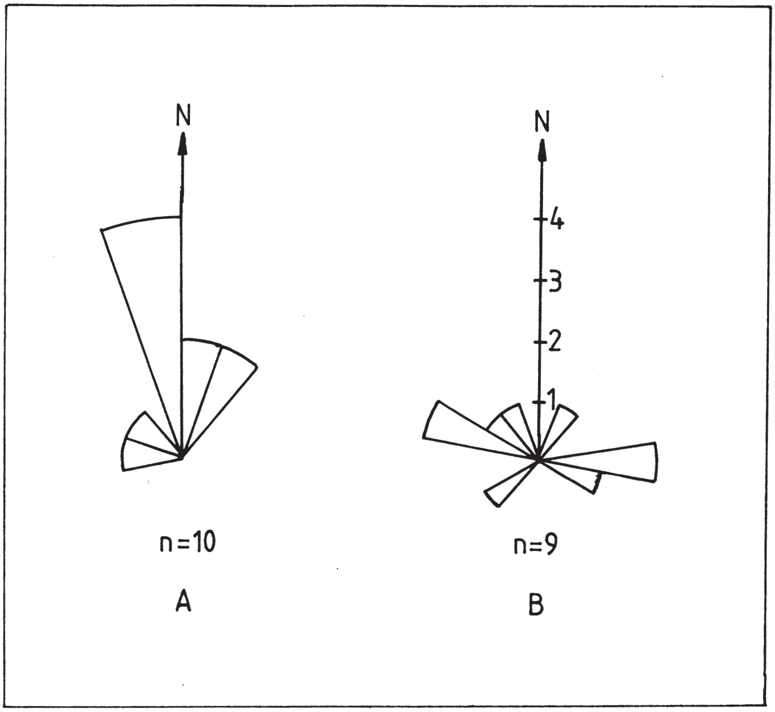


Fig. 36. Palaeocurrent measurements from various levels and locations in the Samaoling Member/ Beru Member transition zone and in the Beru Member. Measurements inferred from fluvial facies (A) have been separated from those inferred from subtidal facies (B).

The tidally influenced sandstones show more variable palaeocurrent directions (Fig. 36B) than the purely fluvial sandstone layers. Though the data are limited, they suggest an E-W trend, in which the eastward directed palaeocurrents may represent ebb currents and the westward ones flood currents, or vice versa.

Grange & Davies (1983) interpreted large-scale westward dipping strata visible on a NW-SE seismic profile of the northern part of the WSB as delta foresets (Fig. 35B). The profile, which was taken north of the area studied here, shows that this deltaic sequence reaches the surface in the Sengkang Anticline and can be correlated with the Samaoling and Beru Members of the Walanae Formation. A southeastward prograding delta system is inferred for the northern part of the WSB, but the palaeocurrent data from the southern part of the WSB presented here, indicate a northward directed infill of the same basin along its southern margin.

As will be shown in the petrographic section further on, the different sediment influxes for the northern and southern basin margin are also reflected in the sediment compositions in both areas: the clastics of the Beru Member, derived from the Bone Mountains and Western Divide range, are dominated by volcanic products, whereas the clastics deposited along the northern margin of the Sengkang Basin are dominated by quartzose products and abundant metamorphic and plutonic components (Grainge & Davies, 1983; own observations). During and/or after E-W compression, which led to the relative uplift of the eastern margin of the WSB, deposition became restricted to the depocentral axis of the basin, where the present day Walanae River continues to transport its sediment load in northern direction towards the Tempe Lake Depression.

Old Alluvial Fan Gravels — In the West Sengkang Basin younger course gravel deposits, postdating the deposition of the Beru Member but predating the formation of the present-day Walanae River floodplain, are mainly confined to the southern part of the study area west of the Walanae River. On the east bank of the Walanae river only two levels of gravel have been observed near Batuasange (FVL-9 in Encl. B), both below the 25 m contour. These gravel layers are located at 3 and 7 m above the low water level of the Walanae River. They differ in composition from the conglomerates of the Beru Member, but also from gravelbars in the modern Walanae River, as will be discussed in the petrographical section later on. Another distinction with the Beru Member conglomerates is the maximum clast size. The lower gravel layer at Batuasange, consists of a 50 cm thick layer of poorly consolidated pebbly sands with an average clast size of 17 cm for the 10 largest cobbles encountered. Besides subrounded to rounded cobbles, also angular blocks of up to 50 cm in diameter are included, which consist of eroded sandstones of the Beru Member. The upper gravel layer at 7 m above the low-water level of the Walanae River, is 1.2 m thick; its composition is similar as that of the lower gravel layer. The average clast diameter of the 10 largest pebbles is 8 cm. Both gravel layers abut sandy strata of the Beru Member.

Other, unconsolidated gravel deposits can be found at several localities north of the Cipee River and west of the Walanae River near Lenrang and Jampu (Encl. A-B), where unconsolidated gravels and cobbles are exposed. North of the Cipee River and northwest of Lenrang these deposits appear as cobble fields, slightly elevated above the flat surface of the Walanae River floodplain. One km WSW of Lenrang the upper surface of the conglomerates is situated several meters above the Walanae floodplain. At this site the gravels lie unconformably against subhorizontal deposits of the Walanae Formation in the east. Near Jampu, gravels with cobble-size clasts lie unconformably on limestones of the Tacipi Member. This gravel deposit is preserved along the western fault boundary of the uplifted Puncakoro block and rests with an angular unconformity on marine sandstones of the Walanae Formation. The gravel deposit itself might have been slightly tilted as suggested by the roughly 8 NW dipping unconformable contact surface between the gravels and the underlying marine sediments.

The maximum clast size of these gravels decreases in northeastern direction from 28 cm (= average maximum diameter of the 10 largest clasts) west of Jampu to 18 cm southwest of Lenrang, 17 cm near Batuasange (lower level), and 15 cm northwest of Lenrang and north of the Cipee River. The distance between the gravels near Jampu and the outcrop north of the Cipee River is 5.5 km. The elevation above sea level of the preserved top surface of each gravel outcrop also decreases in this direction from 30 to 75 m (at Jampu; the wide range in elevation here must be attributed to the tilting rather than to the total thickness of the gravel unit), 25-35 m (SW of Lenrang), and less than 25 m NW of Lenrang and near the Cipee River.

These gravels can be clearly distinguished from the conglomerates of the Beru Member in containing lager clasts (with boulders up to 30 cm near Jampu) and showing a higher variability in source rock types (see petrography section further on).

A rapid decrease in clast diameter over a short horizontal distance is a diagnostic criterion for alluvial fan deposits (Bull, 1972). The decrease in maximum clast size of the above mentioned gravels in northern direction coupled with a decrease in elevation, and the apparent relation with a major fault-bounded block in the south can be explained as features reminiscent of an ancient, northwards prograding alluvial fan system. This fan system supposedly became active during uplift of the Puncakoro Block. If correct, this fan has later been partly eroded following further incision of the Puncakoro Block by the source river. Remnants of the proximal alluvial fan remain as terraces above the present floodplain of the Walanae River. The more distal parts of the alluvial fan now seem to have been buried beneath the floodplain of the Walanae River, following subsequent subsidence of the distal fan area. The most proximal fan deposit near Jampu has been tilted, presumably due to further uplift of the Puncakoro block.

The above described deposits, which appear older then the Holocene Walanae River floodplain deposits, will be further referred to as 'Old Alluvial Fan Gravels' (Encl. A-B; Fig. 31). No vertebrate fossils have been encountered in these coarse gravels.

Colluvium — Some isolated pockets of colluvium, with a lateral extension too small to be mapped on the scale used in Encl. B, were found at several places. The most important one, which has yielded several molars of *Anoa* sp., can be found south of the Cabenge-Pampanua road near Ciangkange (FVL-21, Encl. B). Hooijer (1972b) probably referred to this locality when he announced the finding of an *Anoa* molar near Ciangkange. The colluvial deposit, which consists of a loose mixture of sand, caliche nodules, small pebbles and angular clasts in a mud matrix, is unstratified and unconformably overlies steeply westward dipping sandstone layers of the Beru Member (section III, Encl. C). Angular fragments derived from the Beru Member sandstones are incorporated in the colluvial deposit. Besides the already mentioned *Anoa* fossils, small fragments of other fossils have been found on the surface of the colluvial deposit, including shark teeth, enamel of proboscidean molars and isolated *Celebochoerus* molar fragments, all being in a rather rounded and poor state of preservation. It must be stated that the *Anoa* molars from this locality show a fossilization different from all other fossils commonly encountered in the Beru Member. The crowns of the *Anoa* molars are rather fractured and micritic calcite has been deposited in these fractures as well as around part of the fossils. The *Anoa* specimens as well as the caliche concretions around them have a white colour. They are less well fossilized than the gray, brown or reddish fossilized vertebrate bones and teeth derived from the Beru Member.

These colluvial pockets are considered the youngest fossiliferous unit in the West Sengkang Basin. They seem to contain a mixture of reworked fossils from the Beru Member as well as some younger, presumably Late Pleistocene or Holocene specimens of *Anoa*. It is of importance to note is that *Anoa* has never been recovered in situ from the excavations in the Beru Member, where over two thousand fossil specimens have been collected.

Youngest Alluvium in the WSB — The floodplain deposits of the Walanae River represent the youngest unit exposed in the West Sengkang Basin. A sandy levee complex with crevasse splay deposits has built up along the river, while silts and clays have accumulated on the floodplain. Gravel bars have locally formed along the Walanae River channel in the southern part of the study area. These unconsolidated sediments are exposed along the eroded banks of small tributaries.

In and around Lake Tempe fine-grained sediments accumulated. Cores drilled north of Lake Tempe reveal a sequence dominated by organic clays and silts, with minor intercalations of sands up to a depth of 150 m (Kusbini & Najamuddin, 1991). This indicates that lacustrine and fluvial deposition has continued for a long period in this area in response to basin subsidence. From seismic profiles (Fig. 35B) it can be deduced that accumulation of clastic sediments was continuous along the depocentral basin axis after the deposition of deltaic deposits of the Beru Member (Grange & Davies, 1983).

Along the western margin of the Walanae River floodplain alluvial cones locally consist of clastic detritus supplied from the Western Divide Range. These deposits have not been studied.

East Sengkang Basin

Walanae Formation — East of the EWF marine beds of the Walanae Formation crop out in the weakly undulous terrain at places where they are not covered by younger alluvium. The best exposures are along the major streams here, like the Paciro River. The sediments of the Walanae Formation comprise a fully marine facies, except from one place: Bulu Barere. This is a small flattened topographic elevation (FVL-28, see Encl. A). Though outcrop conditions are poor at this spot, characteristic well consolidated blocks of coarse angular fluvial sandstones and pebbly sandstones can be found scattered over the surface. Vertebrate fossils, a.o. of *Celebochoerus heekereni* and *Stegodon sompoensis*, were found at this spot, suggesting that the basal layers of the Beru Member (Subunit A of the Beru Member) crop out here.

Tanrung Formation — The Tanrung Formation is only locally developed in the East Sengkang basin. It consists of terrestrial conglomerates unconformably overlying the Walanae Formation in the ESB. The unit is here named Tanrung Formation, after the Tanrung River (Encl. A), which cuts through these horizontally bedded conglomerates. The Tanrung Formation is at least 7 m thick in the west (Fig. 37; either the base or the uneroded top are not exposed in individual outcrops). Towards the east the formation seems to wedge out. In the upper reaches of the Tanrung River west of the village Manciri (Encl. A) and close to the EWF, it was observed that the Tanrung Formation is underlain by well sorted fine- to medium-grained sandstones (Fig. 38). These sandstones contain reworked foraminifera (see chronostratigraphy section below) and probably belong to the upper shallow marine part of the Walanae Formation. The unconformable basal contact occurs at an elevation of c. 65 m above sea level here, while 3.5 km to the northeast (where the base is not exposed), the eroded top of the Tanrung Conglomerate is at an elevation of c. 40 m. The considerable difference in altitude of the base of the Tanrung Formation between west and east, in combination with its limited thickness (Fig. 30), suggests tilting of Tanrung Formation after deposition.

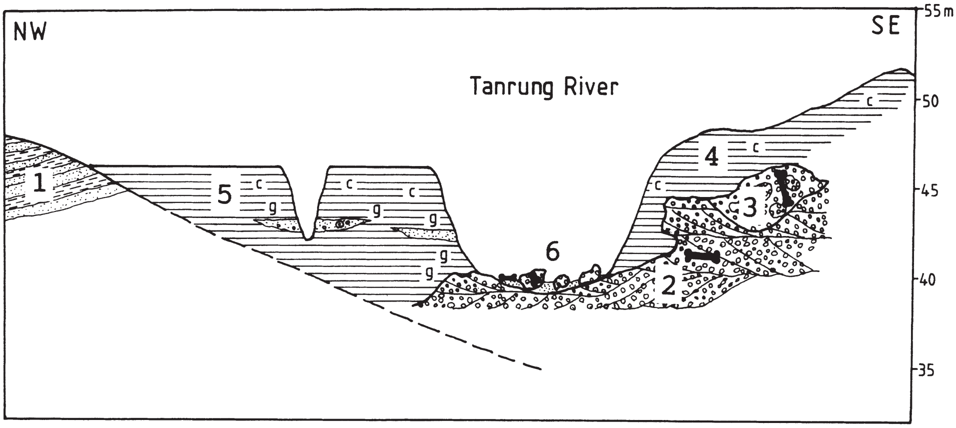


Fig. 37. Schematic NW-SE cross section along the Tanrung River showing the relationships between the various lithological units cropping out in the East Sengkang Basin near FVL-29. To the right is indicated the elevation above sea level. 1 = folded marine layers of the Walanae Formation; 2 = Tanrung Formation; 3 = redeposited calcareous gravel eroded from the Tanrung Formation; 4 = Older Alluvium unconformably overlying the Tanrung Formation; 5 = Younger Alluvium (Holocene?) unconformably overlying the Tanrung Formation; 6 = Recent Alluvium of the Tanrung River containing eroded blocks of the Tanrung Formation. Black bones indicate the occurrences of Elephantoidea fossils. They occur in the Tanrung Formation (primary deposition) and in reworked units containing eroded material of the Tanrung Formation.

The top of the Tanrung Formation has been eroded and locally steep erosional palaeocliffs have been preserved at the top surface in several outcrops along the Tanrung River (Fig. 37). The Tanrung Formation is unconformably overlain by younger, unconsolidated gray or black muds and gray or brown sands. Locally, eroded limestone pebbles derived from the Tanrung Formation have accumulated in pockets in between the cemented Tanrung conglomerates and these younger muds (Fig. 37).

At FVL-29 a *Stegodon* maxilla fragment with dentition and two tusk fragments of the same individual were found embedded in the well cemented Tanrung conglomerates close to the vertical erosional surface of a 1.4 m high, vertical palaeocliff. The entire structure was subsequently covered by orange-brown/gray mottled silty clays of the Older Alluvium (see below).

The conglomerates of the Tanrung Formation contain mainly rounded carbonate fragments, which will be dealt with in the petrography section on below. No siliciclastic material coarser than granules is present in the Tanrung Formation. However, the sandy matrix of the larger carbonate clasts contains abundant quartz grains. Rounded, reworked oyster fragments and other bioclasts from the marine part of the Walanae Formation are present in the conglomerates (reworked oysters derived from the marine part of the Walanae Formation are also frequently found in the modern bedding of the Paciro River and other small tributaries in the area east of the Walanae fault). The maximum clast diameter does not exceed 5 cm. Locally, consolidated sand lenses are intercalated in the conglomerates. The entire formation is generally well cemented with sparitic calcite (no siderite, which is the most common cement type in the Walanae Formation).

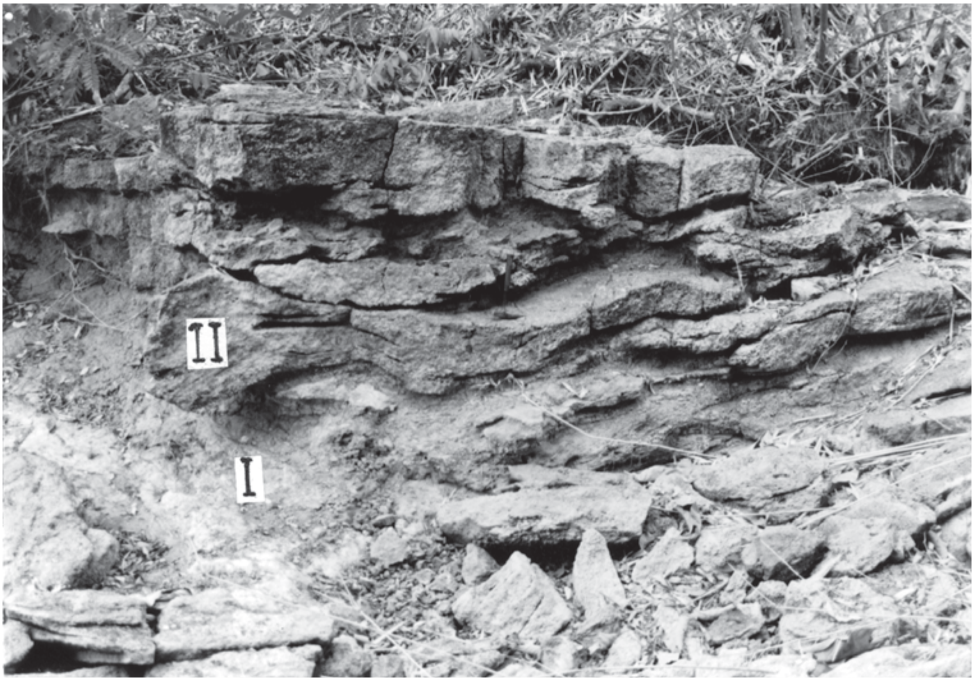


Fig. 38. Conglomerates of the Tanrung Formation (II) overlying fine-grained sandstones of the Walanae Formation (I) with an erosional contact. Sedimentary structures in the Tanrung Formation indicate longitudinal bars and small channel-fils. Palaeocurrent directions are perpendicular to the outcrop. Hammersize is ca. 30 cm.

Sedimentary structures in the Tanrung Formation indicate small channel fills, longitudinal bars (Fig. 38), and lateral accretion on small pointbars. A pointbar structure preserved in the upper reaches of the Tanrung river shows aligned scroll-bars on top of horizontally curved, gently dipping laterally accreted layers. The meander diameter of this pointbar could be measured at approximately 17 m. The palaeo-channel depth, as inferred from the height of the lateral-accretion layers and the scroll-bars on top, was c. 0.5 m. These structures indicate that the Tanrung Formation was deposited by a small-scale meandering channel system.

The fossil vertebrate fauna from the Tanrung Formation is clearly different from, and younger than the Walanae Fauna from the Beru Member, as will be discussed later.

Bartstra et al. (1994) included the deposits along the Tanrung River in the Walanae Formation. However, the Tanrung Formation represents a distinctly younger formation, which can easily be distinguished from the Beru Member on petrographical, stratigraphical and sedimentary grounds.

Older and Younger Alluvium — At least two distinct alluvial units can be distinguished in the ESB, which were deposited after deposition and subsequent erosion of the Tanrung Formation. They are designated as the Older Alluvium and Younger Alluvium.

The Older Alluvium rests unconformably on the eroded top surface of the Tanrung Formation. East of the Manciri River patches of the Older Alluvium are found directly on top of the inclined strata of the Walanae Formation, but these patches have not been mapped. The Older Alluvium consists of horizontal-bedded, unconsolidated dark-coloured muds and minor intercalations of sands. The Older Alluvium can be geomorphologically discriminated from the Younger Alluvium by its dissected, undulous upper surface. This undulous surface has its highest elevations up to several meters above the flat surface of the Younger Alluvium (Fig. 37).

The Younger Alluvium, presumably of Holocene age, occupies the lowest depressions in the ESB (Fig. 37; Encl. A). This Younger Alluvium is geomorphologically connected with the active floodplains of the Walanae River towards the north. The lithology of the Younger Alluvium is very similar to that of the Older Alluvium, also consisting of dark-coloured muds and unconsolidated sands. The Younger Alluvium locally covers the Tanrung Formation along the west bank of the Tanrung River, but its flat upper surface is 2-4 m lower than the dissected upper surface of the Older Alluvium along the eastern bank. Thus, the Older Alluvium has been shaped into a dissected terrace along the eastern bank of the river, whereas deposition of the Younger Alluvium still seems to continue during floodings.

As already mentioned, the lithologies of the Older and Younger Alluvium are similar, both units being dominated by unconsolidated dark gray or black/orange-brown mottled silty clays, with minor unconsolidated sands. The muds of the Older Alluvium frequently contain gypsum crystals in veinlets, which were not encountered in the Younger Alluvium. The dark-coloured muds of both the Older and the Younger Alluvium are thought to have been deposited in a coastal backswamp or mangrove environment. A mangrove environment is also indicated by data presented by Gremmen (1990), who analyzed pollensamples from a core taken in the Walanae River floodplain at Rawa Lampulung, 5 km east of Sengkang and north of the Walanae River (or Cenrana River as the river is also called along the transect from Sengkang to the Gulf of Bone). The pollenspectra provide clear evidence that the Walanae alluvial plain east of the Sengkang Anticline was covered by mangrove vegetation from 7100 ± 70 yr B.P. until 2610 ± 50 yr B.P. Pollenspectra from a core taken in Lake Tempe, west of the Sengkang Anticline, reflect the presence of a predominantly fresh-water vegetation from 4410 ± 100 yr B.P. onwards (the latter date was obtained from a sample taken at the base of this core). This suggests that the Sengkang Anticline prevented the sea from entering the Danau Tempe Depression at that time. The author further concluded that the relative sea level must have been around 5 m higher than at present to account for the occurrence of a mangrove environment 5 m above present day sea level at Rawa Lampulung.

At the most northeastern outcrops along the Tanrung River, 1 km NNE of FVL-29 (Encl. A) in the west bank of the river, large, angular conglomerate blocks, which were clearly derived from the Tanrung Formation, were found floating in a more than 90 cm thick chaotic layer of very poorly sorted, pebbly mud, lacking internal stratification. The layer is matrix supported. A possible explanation for the deposition of this layer may be formation by a tsunami, which invaded the coastal plain and was able to transport large blocks eroded from the Tanrung Formation. This chaotic layer is in turn overlain by a layer of 1.8 m thick, consisting of unconsolidated fluvial sands, which include a pebbly channel-lag with sub-recent terrestrial gastropods (Younger Alluvium).

In most outcrops along the east bank of the Tanrung River the irregular, eroded upper surface of the Tanrung Formation is covered by 6 to 4 m of Older Alluvium, consisting of mottled silty clays (Fig. 37). Locally, however, pockets of loose calcareous gravel derived from the Tanrung Formation, occur in between the Tanrung Formation and the overlying silty clays of the Older Alluvium (Fig. 37). These pockets of loose gravel seem to represent an episode of erosion that resulted in the dissection of the Tanrung Formation prior to deposition of the Older Alluvium.

Along the banks of the Walanae River east of Sengkang in the Eastern Sengkang Basin, slightly tilted, fine-grained marine sandstones of the Walanae Formation emerge at several places from below the unconsolidated gray muds and sands of the present-day Walanae River floodplain. At one place, however, near the village of Lagosi (Encl. A), a small outcrop of consolidated conglomerate occurs at the southern bank of the river. According to the local fisherman this indurated deposit also crops out in the bedding of the Walanae River at this spot. The conglomerate here is covered by the modern unconsolidated floodplain sediments. The composition of this conglomerate differs from that of the Tanrung Formation by lacking calcareous clast and containing abundant pebbles of volcanic origin. The maximum clast size does not exceed 5 cm. The conglomerate resembles the conglomerates of the Beru Member in composition, but its age must be younger, as follows from the in situ occurrence of an *Anoa* molar in this conglomerate. *Anoa* remains have not been found amongst the numerous fossils originating from the Beru Member, indicating that the Lagosi conglomerate is younger than the Beru Member. The correlation of this conglomerate with other lithostratigraphic units remains a problem. It probably represents a river system that was active after uplift and erosion had taken place in the ESB. It might be roughly time-equivalent to the Tanrung Formation or younger, but with a different source area in the north or west.

Petrography

Introduction

Thirty thin sections of samples from the various lithostratigraphic units described in the foregoing section, have been petrographically analyzed with the polarizing microscope. Most samples consist of sandstone, but also calcareous mudstones and caliche nodules have been studied. Pointcounts of hundred grains per sample were performed on the sandstones, in an attempt to characterize these sandstones and to distinguish compositional variations within and between the various lithostratigraphic units. The results of the pointcounts are presented in Table 2.

The stratigraphic position of most of the samples is indicated in the sections of Encl. C. One of the sandstone samples originates from the uplifted Puncakoro block (Encl. A) south of the study area (sample S-29B in Table 2). Detrital samples on which no pointcounts were carried out, as well as various non-detrital samples, have also been studied under the microscope. They comprise samples of very poorly sorted sediments and some samples of fossil bone and fossil wood (Table 3).

In order to define the composition of conglomerates and gravels, pebble counts were performed at several conglomerate levels from different lithostratigraphic units. The results will be discussed after the section on the composition of the sandstones.

Sandstones of the Walanae Formation

Cement — Most sandstones, particularly those from the Samaoling Member, are poorly consolidated. Samples were preferentially taken in well cemented layers or concretions, so that a bias towards well cemented sandstones is present in the studied samples. It was found that the majority of the studied sandstone samples from the Walanae Formation were cemented with siderite. Exceptions are sample S-49, the only sample from the basal Burecing Member (only one coarse-grained layer is present in the Burecing Member; see Fig. 40) and S-29B from the Puncakoro Block, which represents a marine facies thought to be roughly time-equivalent with the Burecing Member. Both samples have been cemented with calcitic cement. Furthermore, sample S-34 from the top of the Samaoling Member and samples S-23, S-42B, both from the Beru Member, have been cemented with blocky calcite and/or microsparite.

Siderite will form as a diagenetic mineral only where a very low dissolved sulfide concentration is coupled with high dissolved carbonate and a high Fe^{2+}/Ca^{2+} ratio (Leeder, 1982). These conditions usually restrict siderite formation to non-marine diagenetic environments (low sulphate) where abundant Fe^{2+} is present (tropical-zone weathering); it is particularly common in deltaic swamp facies. This is in agreement with the environmental interpretations given earlier.

Matrix — Substantial amounts of micritic or clayey matrix are restricted to a few samples from the Samaoling and Beru Members. In most samples matrix is entirely absent or has been replaced by neomorphic siderite or (micro)sparite cement. The total amount of matrix + cement varies between 24 and 51%. The highest matrix + cement percentages occur in the poorly sorted coarse sandstone samples and in well sorted fine to very fine sandstone samples. In the latter case many detrital grains must have been partly dissolved and replaced by cement, which may account for the unusually high amounts of cement in some of the fine-grained sandstone samples.

Detrital grains — Grains of volcanic origin predominate the detrital components of the sandstone samples of the Walanae Formation. The dominating volcanic grain types consist of glassy, aphanitic or porphyric rock fragments often with plagioclase phenocrysts. Volcanic rock fragments make up between 20 and 70% of the total amount of grains counted. The graintype usually second in abundance (4-43%) consists of clino-pyroxene grains in the upper part of the Walanae Formation. In samples S-41 and S-71 from the Beru Member, the amount of pyroxene grains even exceeds that of volcanic rock fragments. In the Burecing Member and the lower part of the Samaoling Member clino-pyroxene grains are rare, less than 3%, but clino-pyroxenes were found to be present in all samples. In sample S-41 (Beru Member) a considerable amount (19%) of magnetite grains is present, while only small amounts of magnetite grains occur in most other samples.

Quartz and feldspar tend to be well represented in the Samaoling Member, varying between 8 and 41% and between 9% and 18%, respectively. Perthite and quartz-feldspar aggregates also occur in the latter member, suggesting that at least part of the feldspars is of plutonic origin. Undulous and polyquartz grains occur in all samples of the marine interval, but they are rare or absent in samples from the Beru Member. Monoquartz grains are absent in samples S-49 (Burecing Member) and S-29B (Puncakoro, lower part of the Walanae Formation), but are well represented in the Samaoling Member in the most northern part of the study area (section XI, samples S-37 and S-39). In the latter section plutonic rock fragments tend to be more common than in those of the more southerly sections. This may reflect the different, non-volcanic source area north of the study area, where pre-Tertiary basement rocks and Eocene quartzose clastics are well exposed in the Latimojong Mountains north of the Sengkang Basin (Fig. 26).

Monoquartz grains from the Beru Member sometimes show euhedral crystal boundaries, suggesting that they have been derived from acid volcanic sources. The source of these acid volcanics remains unknown. Euhedral quartz crystals have not been observed in the Burecing and Samaoling Members.

Sample S-29B from the Puncakoro Block is strikingly similar to sample S-49 from the Burecing Member in the Sengkang Anticline. Both samples are the only ones with abundant bioclastic grains (mostly benthic foraminifera but also mollusc and echinoid fragments). The sediment of the coarse-grained and massive 10 m thick layer, from which sample S-49 originates, was probably derived from the south by means of mass-flow transport from the relatively high and shallow Puncakoro Block or from the shallow marine shelf of the ESB in the east.

On the other hand, bioclasts are totally absent in the samples of the sandstones of the Beru and Samaoling Members, though they have been encountered in the field in the claystones of the latter member. The absence of small calcareous bioclasts in the studied sandstone samples of the Beru Member reflects the terrestrial environments in which these sandstones were deposited, whereas the absence from Samaoling Member sandstones may have been caused by postdepositional dissolution of carbonate. Molds of bioclasts in the sandstones have been frequently observed in the field, indicating that indeed dissolution of carbonate has taken place.

The sandstone samples further contain minor amounts of sedimentary rock fragments (silt and claystones and some chert and chalcedony grains), weathered opaque grains (probably mostly of volcanic origin), and biotite. Biotite is always present in the Samaoling Member (also macroscopically), but it is rare in the overlying Beru Member. Biotite has also been reported from tuffaceous layers of the lower marine part of the Walanae Formation in the southern part of the Walanae Depression (van Leeuwen, 1983; Suminto, 1991).

According to Folk's (1968) classification, most sandstones of the Walanae Formation can be assigned to the group of volcanic litharenites, with the exception of samples S-49 and S-29B (Burecing Member), which, due to their high content of calcareous clasts in combination with volcanic grains, cannot be classified according to Folk's system.

Samples S-70 and S-71 (section IX, Encl. C), both collected near Sare Batue from a conglomeratic layer pertaining to Subunit B of the Beru Member, are composed mainly of reworked calcareous clasts. This conglomerate layer represents a local facies, which is distinct from other clastics of the same member. Some *Ostrea* and *Chlamys* shells, as well as vertebrate fossils that can be ascribed to *Celebochoerus* and *Geochelone* occur in this conglomerate. More than about half of the granule-sized clasts in these two samples consist of volcanic rock fragments, while the remaining part consists of calcareous peloids, which were not encountered anywhere else in the Walanae Formation. These peloids consist of regular, rounded microsparite aggregates, sometimes containing a few quartzose grains, and usually with a brown limonitic or hematitic rim. Their origin is not certain. These peloids clearly differ from caliche concretions, of which some samples were also studied (e.g. samples S-60 and S-25, Table 3). The caliche nodules consist of inhomogeneous aggregates of micritic carbonate often showing laminated crusts and characterized by cracks filled with blocky sparite, which cut through the entire concretion. These features are characteristic for caliche concretions (Fluegel, 1978). The peloids of samples S-70 and S-71, on the other hand, consist of homogeneous micrite (except for the inclusion of few silt-sized siliciclastic particles), lacking cracks and laminated crusts. These peloids do not contain microfossils, which makes their interpretation difficult. The microstructure of these peloids resembles that of the matrix of the calcareous pebbly mud layer of Bulu Barere (samples S-61A and B; Table 3), which has been interpreted as an intertidal lagoonal facies. A similar fossil association (a mixture of terrestrial vertebrates and subtidal molluscs) in the conglomerate layer at Bulu Barere and the layer at Sare Batue, suggests that the latter contains the reworked products of infra-formational erosion of a subtidal lagoonal deposit. The sandy matrix of samples S-70 and S-71 (point counts were carried out on the sand fraction of both samples; see Table 2) corresponds well in composition with the remaining sandstone samples from the Beru Member. The matrix is dominated by more or less equal amounts of clino-pyroxene grains and volcanic rock fragments. In addition, there are minor admixtures of plutonic rock fragments, magnetite, quartz, chert, and feldspar and sand-sized calcareous fragments similar to those in the coarser fraction.

The composition of the sandstones reflects the predominating volcanic source of the deltaic sediments. This source was located south of the study area. Only in the most northern section XI increased amounts of quartzose grains indicate different influxes from the north.

Composition of Beru Member Conglomerates and Old Alluvial Fan Gravels

Pebble counts were performed on eight conglomerate levels. In each of these levels 200 pebbles with a diameter of more than 2 cm were determined macroscopically. The results are presented in Fig. 39. Four of the counted conglomerate layers are believed to belong to Subunit B of the Beru Member. These are: the lowest and highest exposed conglomerate level near Palangiseng (FVL-2) in section VII and the conglomerates exposed near Calio at FVL-18 and FVL-20, respectively. The two counted conglomerate layers near Calio have been interpreted as remnants of the former alluvial plain of the Walanae River by previous authors (van Heekeren, 1958; Hooijer, 1972b; Bartstra, 1977, 1991; Keates & Bartstra, 1994), and were designated as the 50-m and the 75-m fluvial terrace, respectively. Here they are included in subunit B of the Beru Member (FVL-18 and FVL-20, respectively). Three counts were performed in gravels belonging to the Old Alluvial Fan Gravels. These are the gravels exposed 1 km WSW of Lenrang (Encl. B) and conglomerates exposed on the east bank of the Walanae River at Batuasange (FVL-9), which are in unconformable contact with the

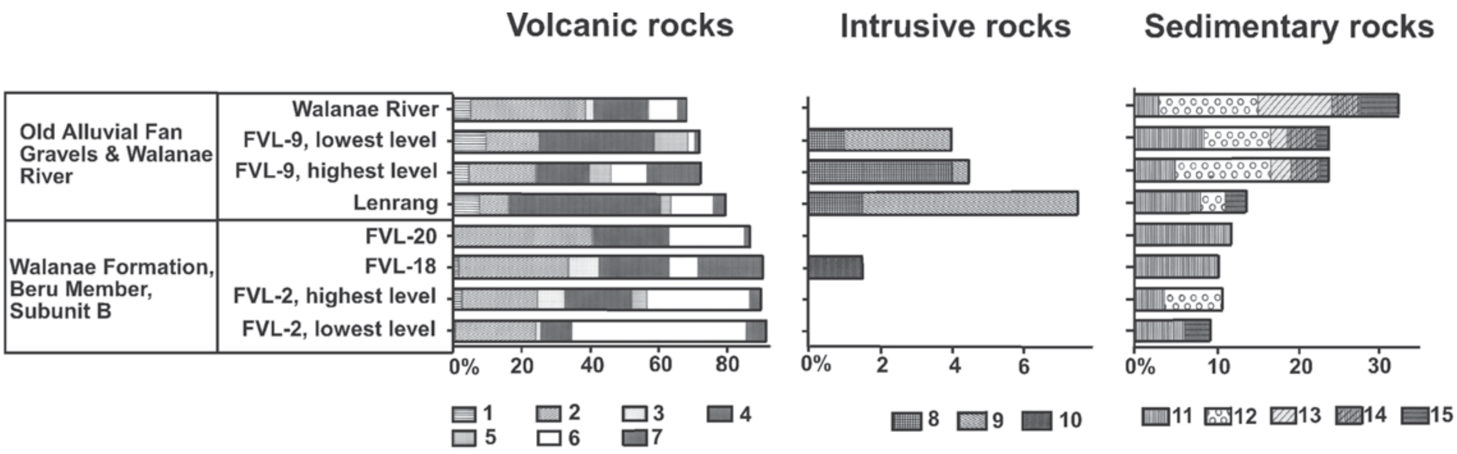


Fig. 39. Diagram showing the composition of various conglomerates and gravels in the study area, based on pebble-counts (200 pebbles were identified at each level represented). For further explanation see text. Legend: 1 = leucite tephrite; 2 = basalt; 3 = vesicular volcanic rock (including pumice); 4 = andesite; 5 = dacite; 6 = alterated volcanic rock (mostly silicified); 7 = weathered volcanic rock; 8 = granite, granodiorite; 9 = syenite, diorite; 10 = vein quartz; 11 = chert; 12 = limestones derived from the Tonasa Formation (sometimes partly silicified) and indeterminate massive limestones; 13 = porous limestones derived from the Tacipi Member; 14 = siliciclastic sedimentary rocks derived from the Walanae Formation; 15 = siliciclastic sedimentary rocks, indeterminate.

Walanae Formation. At the latter site two different layers were counted, one situated at 3 m above the low water level of the Walanae River (= lowest level at FVL-9 in Fig. 39) and one at 7 m above the low water level (= highest level at FVL-9 in Fig. 39). For comparison also a pebble count was performed on a gravel bar of the modern Walanae River, located downstream of Batuasange. The granule and pebble fractions of the Tanrung Formation conglomerates do not contain other components apart from calcareous clasts. They will be dealt with separately in the next section.

All counted conglomerate levels are dominated by volcanic clasts, mostly basalt and andesite. Andesitic and basaltic rocks are widely distributed in South Sulawesi. In the Beru Member conglomerates also considerable amounts of alterated rocks of volcanic origin are present (8.5-51%). These alterated rock pebbles mostly consist of silicified volcanics, but also a considerable amounts of green-coloured propylithized volcanics are present. In the Old Alluvial Fan Gravels the total amount of alterated volcanics is usually smaller (4-12.5%).

The alterated volcanics were probably derived from the older, Eocene volcanic formations, which crop out extensively in the Bone Mountains and to a lesser degree in the Western Divide Range (Fig. 26). However, the lower part of the Camba Formation also contains silicified volcanics (Sukamto, 1982).

Leucite-tephrite pebbles are very rare or absent in the conglomerates of the Beru Member, but they are always present in the Old Alluvial Fan Gravels, where they constitute between 5 and 10% of the total pebble composition. A microscopic study of these leucite-tephrites shows large phenocrysts of aegirien-augite and smaller ones of leucite embedded in a glassy groundmass. Macroscopically the most characteristic feature of these leucite tephrites is that large vesicles are filled with zeolites, which makes them easy to recognize when they occur as pebbles. The leucite tephrites were presumably derived from the upper part of the Middle to Late Miocene Camba Formation, which covers most of the older formations in the Western Divide Range (Sukamto, 1975; van Leeuwen, 1981). A large body of leucite tephrites related to an eroded caldera is situated 25 km SW of the study area (Fig. 2).

The most conspicuous compositional difference between the Old Alluvial Fan Gravels and the conglomerates of the Beru Member concerns the total absence of intrusive rock pebbles in the Beru Member conglomerates. In the Old Alluvial Fan Gravels, on the other hand, they are always present in small percentages (c. 5%). They consist of intrusive rocks with an equigranular texture. They partly consist of rock types characterized by low amounts of quartz, such as syenites and diorites. However, also granites and granodiorites have been identified. The intrusive rock types contain varying amounts of dark minerals such as biotite and amphiboles (10-50%). Most of the intrusive rock pebbles were probably derived from the Western Divide Range, where small intrusive bodies occur along the entire length of the mountain chain (Sukamto, 1982; van Leeuwen, 1981). A few dioritic intrusions have also been mapped in the Bone Mountains (Sukamto, 1982).

In the field special attention has been paid to the possible occurrence of intrusive rock pebbles in the Beru Member conglomerates, but such components have nowhere been found. On the other hand, they are always present in the Old Alluvial Fan Gravels. They are absent in the modern Walanae River as well.

There is another conspicuous compositional difference between the Beru Member and the Old Alluvial Fan Gravels. Siliciclastic and limestone pebbles, originating from erosion of the Walanae Formation, are absent in the conglomerates of the Beru Member, whereas they are commonly present in small amounts (< 12%) in the Old Alluvial Fan Gravels. Some limestone clasts in the Old Alluvial Fan Gravels have been clearly derived from the Tacipi Member of the Walanae Formation (which consists largely of porous limestones), while others must have come from the massive mudstones and wackestones of the Eocene to Middle Miocene Tonasa Formation, outcropping at numerous places along the Western Divide Range (Fig. 26).

Chert pebbles are present in all counted levels in small quantities varying between 4 and 10%. It is interesting that such chert pebbles and cobbles have been used for the manufacturing of Palaeolithic stone tools, which can be found at several places in the Old Alluvial Fan Gravels (near Jampu, Lenrang) and on the surface of the coarse clastics in the surroundings of Calio and Beru (Bartstra, 1991, Keates & Bartstra, 1994; own observations). The cherts often contain silicified marine bioclasts and were derived from the Eocene to Early Miocene Tonasa Formation. The Tonasa Formation crops out extensively in the Western Divide Range. Near Ralla (Fig. 26), southwest of the study area, Oligocene limestones of the Tonasa Formation can be found interbedded with concretionary chert layers in association with redeposited limestones (Wilson & Bosence, 1996; own observation). The cherts appears to be the result of secondary replacement of the fossiliferous wackestones and packstones, because the original carbonate bioclasts can still be recognized as ghosts in these cherts. A chert pebble with ghosts of bioclasts originating from the conglomerate at FVL-18 was sectioned for microscopic study. It contains larger foraminifera (*Pellotispira* sp. and *Discocyclina* sp.; Sudijono, pers. comm. 1994) and has a similar appearance as the chert layers interbedded in the limestones of the Ralla area.

Occasionally, rounded silicified wood fragments are found in the conglomerates of the Beru Member and in the Old Alluvial Fan Gravels (samples S-63 and S-64; Table 3). These wood fragments are always silicified and seem to have been reworked from older, unidentified strata. In the fine-grained sediments of the Beru Member also larger, non-rounded, calcified wood fragments occur. They usually consist of tree trunk fragments of various size. The calcified wood fragments are not reworked from older strata but occur in situ (e.g. sample S-62). The original cel structures of these calcified wood fragments have been poorly preserved, in contrast to those in the reworked silicified wood fragments. Near Sare Batue a calcified palmfruit was excavated from a silty layer. The calcified wood fragments found in a subtidal sandy interval of section II (Encl. C, section II, 45 m below the top of the section) contain borings made by marine bivalves (Teredinidae), which are still in situ. Mineralized wood fragments with such borings were also reported by Bartstra et al. (1994) from Ciangkange and further north.

The clastic sediment pebbles derived from the Walanae Formation consist of characteristic brown or yellow, immature, carbonate-cemented sandstones and siltstones, sometimes containing calcareous bioclasts. They are distinguished from other sedimentary rocks, classified in Fig. 39 as ‘sedimentary undeterminable’. The latter category includes quartzitic sandstones and dark-coloured shales. Though pebbles from the Walanae Formation were not encountered in the Old Alluvial Fan Gravels near Lenrang, they are present in small quantities in all other outcrops of this unit. On the other hand, they are always absent in the conglomerates of the Beru Member.

Composition of the Tanrung Formation conglomerates

Because of the large amount of rounded calcareous clasts the conglomerates of the Tanrung Formation (Samples S-54, S-55, S-64 and S-65; Tables 2-3) look macroscopically quite similar to those of the Beru Member near Sare Batue described above (samples S-70 and S-71, section IX). Closer inspection however, shows some essential differences between the clastics of the Tanrung Formation and those of the Beru Member. The most conspicuous one is that the Tanrung Formation contains abundant fragmented and rounded marine bioclasts, in addition to rounded calcareous clasts. The latter are of a more diverse origin than the calcareous clasts in the Beru Member near Sare Batue. The bioclasts in the Tanrung Formation consist mostly of benthonic foraminifera fragments. Subordinate amounts of coral, bivalves, and echinoid fragments are also present. Some of these bioclasts are partly or entirely embedded in micritic lumps, others occur as isolated bioclasts.

The rounded calcareous clasts in the Tanrung Formation vary from sand- to small pebble-sized (maximum diameter 5 cm). The clasts are usually subspherical, but also more elongate clasts are present. They are rounded, and most of them are coated with a thin Fe-oxide rim. The following types can be distinguished: 1) Rounded micrite clasts, with or without marine bioclasts and/or silt-sized quartz particles. Some of these are regularly laminated, the laminae cut off by the surface of the clast. 2) Transparent homogenous microsparite or sparitic peloids without internal structure. 3) Brownish micrite or microsparite peloids with an irregularly shaped core of transparent blocky sparite, in which some islands of micrite may occur. The crystal size of the sparite usually increases towards the center. In some peloids of this type concentric patterns can be distinguished at one or more sides of the peloid, caused by an alternation of light and dark microsparitic bands. 4) Microsparitic peloids in which the crystals are preferentially oriented with their long axes directed towards the center, causing a radiate extinction pattern under X-nicols.

Peloids of the first type originate from eroded calcareous sediments and were presumably derived from erosion of the marine part of the Walanae Formation, especially the Tacipi Member, which has extensive outcrops to the south. Type 3 clasts resemble algal oncolites (Fluegel, 1978). The blocky sparite core, which is often present, seems to have filled a central cavity after formation of the outer part. The laminated outer part is thought to have formed around fragments of organic matter, which subsequently decayed so that a cavity remained. These oncolites might have been eroded from older layers, but may as well have been formed in the fluvial channels in which the Tanrung Formation was deposited. Type 2 clasts may represent either recrystallized oncolites, or eroded fragments from marine calcareous sediments. Type 4 clasts are oolithes and must have been derived from erosion of marine limestones.

The sandy matrix of the pebbly sandstones and conglomerates of the Tanrung Formation also shows some clear differences with those of the Walanae Formation. Volcanic rock fragments are relatively rare in the former and pyroxene grains are completely absent. The most abundant siliciclastic graintype is quartz (mono- and polyquartz), totaling between 21 and 47 %. Feldspars are less frequently present. The remaining part is made up of weathered opaque grains, detrital hematite and a few chert grains.

The clastics of the Tanrung Formation are all cemented with large blocky sparite crystals, which are sometimes increasing in size towards the centers of the original porespace (cement type B of Fluegel, 1978). Cement type B forms in both marine and in meteoric environments, but in marine environments it is often preceded by the formation of radiaxial fibrous cement, which is absent in all samples of the Tanrung Formation. Thus, the Tanrung Formation conglomerates seem to have been deposited out of reach from the sea.

Discussion

Clinopyroxene and magnetite grains are very common in the sandstones of the Beru Member and the upper part of the Samaoling Member. They tend to be less common in the lower part of the marine Samaoling and Burecing Members. This difference in heavy mineral composition between the marine and terrestrial parts of the Walanae Formation may be due to differences in depositional environment. The single coarse clastic layer in the Burecing Member was probably derived by means of mass-transport from the shallow water carbonate platform of the Puncakoro High or the southern margin of the ESB.

The coarse clastics of the Samaoling and Beru Members on the other hand were mostly supplied from the south by the palaeo-Walanae River, and were deposited in a mixed tide-fluvial controlled deltaic environment (see below). Especially samples taken from the marine-terrestrial transition zone, such as sample S-41 from a fluvial sandstone just overlying lagoonal clays at the base of the Beru Member, seem to be relatively enriched in heavy minerals.

The relatively higher contents of quartz in some of the Samaoling Member sandstones, especially those from the most northern section XI, might be accounted for by sediment influxes from the north. The marginal Neogene Basin facies north of the Lake Tempe Depression is represented by more mature clastics with metamorphic and igneous components (Grange & Davies, 1983; own observations). Seismic data also suggest a different source area in the northwest for the northern parts of the West and East Sengkang Basins (Grange & Davies, 1983).

The relatively high proportion of Eocene volcanics in the Beru Member conglomerates probably reflects a main provenance area in the Bone Mountains to the SE, whereas the Old Alluvial Fan Gravels may have had their main source area in the Western Divide Range, where Eocene volcanics are less well represented (Fig. 26). Other compositional differences that point in this direction are the higher proportion of leucite tephrites in the Old Alluvial Fan Gravels and the inclusion of intrusive rock pebbles, which are absent in the Beru Member. Presumably, uplift of the Puncakoro Block facilitated the formation of an alluvial fan against the hanging walls of the boundary faults. The greater variability in source rocks of these fan deposits (as compared to the Beru Member clastics), particularly of the sedimentary clasts derived from the Walanae Formation, mirrors the uplift and erosion of the Walanae Formation itself in the southern part of the Walanae Depression during deposition of these gravels.

The clastics of the Tanrung Formation are in many ways also different from those of the Beru Member. In comparing the composition of the sand fractions of both units, marked differences are apparent. The Beru Member sandstones are dominated by volcanic rock fragments and clinopyroxene grains, whereas the sandy matrix of the Tanrung Formation conglomerates (samples S-54, S-55, S-64 and S-65) is dominated by quartz grains besides calcareous grains. In the Tanrung Formation volcanic rock fragments are rare and heavy minerals are lacking all together, apart from some rounded detrital hematite grains. The Beru Member clastics on the other hand, are dominated by grains of volcanic origin whereas calcareous bioclasts are absent. The compositional difference between the Beru Member clastics and the Tanrung Formation clastics, both of fluvial origin, clearly reflects a different source area: it seems that the Beru Member clastics were derived mostly from erosion of volcanic products. The Tanrung Formation clastics seem to be of more local provenance, with hardly any influxes of volcanic material. Most of the carbonate fragments of the Tanrung Formation were probably derived from erosion of the Tacipi Member limestones, which crop out extensively on the southern margin of the ESB (Fig. 26). Presumably, pyroxene minerals eroded from the Walanae Formation did not survive a second erosion cycle and consequently, the most resistant quartz grains became enriched in the Tanrung Formation as compared to the Walanae clastics.

Age control

Following the chronostratigraphic scheme of Berggren et al. (1995), the Pliocene/Pleistocene boundary corresponds with the top of the Olduvai Event at 1.77 Ma. The Early Pleistocene/Middle Pleistocene boundary corresponds with the base of the Brunhes Epoch at 0.78 Ma. The boundary between the Middle and Late Pleistocene is placed here at 125 ka, corresponding with the beginning of the Eemian Interglacial.

Vertebrate remains

Beru Member of the Walanae Formation — Vertebrate fossils occur in the fluviatile sandstones, pebbly sandstones, conglomerates and in the floodplain and lacustrine siltstones and claystones of Subunits A and B of the Beru Member. They also occur occasionally in lagoonal mudstones around the shallow marine/fluvial transitions near the base of this member. Fossils from lagoonal mudstones are often covered with molluscs and bryozoa, and have been found in association with other shallow marine molluscs, shark teeth, stingray remains and calcified wood fragments.

Aziz (1990) introduced the name Walanae Fauna for the terrestrial assemblage exclusively derived from the upper part of the Walanae Formation (= Beru Member) as exposed in the Sengkang Anticline. Our excavations and in situ collecting in the area has shown that this fauna includes *Celebochoerus heekereni*, *"Elephas" celebensis*, *Stegodon sompoensis*, *Geochelone atlas* and two types of crocodiles. Possibly a large-sized representative of *Stegodon* originates from Subunit B of the Beru Member, but this could not be substantiated by in situ findings. The name Walanae Fauna was chosen to replace the term *Archidiskodon-Celebochoerus* Fauna, which was originally introduced by Hooijer (1954a). The term *Archidiskodon-Celebochoerus* Fauna subsequently came into use to designate a composite fauna, which included all fossil species found in the area, marine and terrestrial. Amongst these faunal elements were also species from lithostratigraphic units younger than the Beru Member, such as *Anoa depressicornis* (Hooijer, 1948c, 1972b) and *Sus celebensis* (Hooijer, 1969b). The term Walanae

Fauna used here, refers exclusively to the fauna of terrestrial vertebrates from the Beru Member of the Walanae Formation.

Though Hooijer never paid much attention to the stratigraphy, he originally followed van Heekeren's assumptions that the fossils of his *Archidiskodon-Celebochoerus* Fauna originated from terrace deposits and were found associated with stone artefacts (Hooijer, 1972b, 1975). For example, he mentioned (Hooijer, 1975, p.51) that a skull portion of *Elephas celebensis* originated from the `highest terrace' along the Walanae River in the Tjabenge area. Later it was assumed that the *Archidiskodon-Celebochoerus* Fauna was much older than the artefacts, and that the fossils that dìd occur in association with artefacts in what were believed to be terraces, were in fact reworked from the underlying Walanae Formation (Bartstra et al., 1994).

Based on the occurrence of the dwarfed *Elephas [Archidiskodon] celebensis*, which is generally thought to have been derived from *Elephas planifrons*, a Late Pliocene or Early Pleistocene age was inferred for the *Archidiskodon-Celebochoerus* Fauna (e.g. Bartstra, 1977; Bartstra & Hooijer, 1992). *E. planifrons* is known from the Upper Siwaliks in the Indian Subcontinent. It has been shown that *E. planifrons* in the Siwaliks ranges from at least 3.3 Ma until 2.7 Ma, when it was replaced by *Elephas hysudricus* (Hussain et al., 1992). This suggests that the Walanae Fauna could range as far back as 3.3 Ma. It may also be much younger, as the possibility remains that on Sulawesi *"E." celebensis* survived for a longer period as a relict. It may also be older than 3.3 Ma on the contrary, because the phylogenetic relationships of *"E." celebensis* are not so clear, and it may be derived from a more primitive species than *E. planifrons*. This is the reason why it is here preferred to place its generic name between quotation marks. This matter will be discussed in the palaeontological section later on.

The dwarfed *S. sompoensis* appears closely related to the group of stegodonts designated as the *Stegodon trigonocephalus* group by Saegusa (1996). Besides *S. trigonocephalus* from Java this group includes *S. ganesa* and *S. pinjorensis*. The time range of the species from the Indian subcontinent is uncertain, but is thought to lie roughly between 3.5 Ma and 1.7 Ma, while *S. trigonocephalus* from Java ranges up into the Middle Pleistocene. This long time range makes *S. sompoensis* also less suitable for dating the Walanae Fauna more precisely. Based on faunal correlations alone it can be only stated that the age of the Walanae Fauna probably lies between Late Pliocene and Middle Pleistocene.

Tanrung Formation — Twenty-seven identifiable vertebrate fossils have been recovered from the Tanrung Formation. It concerns both in situ findings and fossil remains attached to blocks of the characteristic conglomerate of the Tanrung Formation found in the Tanrung River. The composition of the assemblage, though of moderate extent, can clearly be distinguished from that of the Walanae Fauna. Pygmy Elephantoids and *Geochelone* remains were not found. The dental Elephantoidea remains originating from the Tanrung Formation belong to a large-sized *Stegodon* species, provisionally referred to as *Stegodon* sp. B by van den Bergh et al. (1992). In the present thesis it is shown that *Stegodon* sp. B is different from *Stegodon trigonocephalus*, but seems to have affinity with *Stegodon florensis* from Flores, the latter having an early Middle Pleistocene age. All the Elephantoid postcranial elements from the Tanrung Formation are also large-sized (see chapter 4). Isolated molars and canine fragments of *Celebochoerus* also occur *in situ* in the Tanrung Formation, but these have all a rounded appearance and may have been reworked. A rolled fragment of a high-crowned molar of a large-sized *Elephas* species was found on the surface in the bedding of the Tanrung River in 1993. The matrix attached to this fossil fragment suggests that it was derived from the Tanrung Formation (van den Bergh et al., 1994). The *Elephas* species, which corresponds in hypsodonty with *E. namadicus* or *E. maximus*, (van den Bergh et al., 1994), suggests a maximum age of Middle Pleistocene. The Middle Pleistocene or younger age suggested by this *Elephas* molar fragment is in accordance with the observed unconformable contact between the Walanae Formation and the Tanrung Formation. Concerning the upper age limit of the Tanrung Formation, a Late Pleistocene age can be considered as unlikely, because its deposition was followed by at least two periods of low base-level (low sea level), resulting in erosion, followed by periods of high sea level (deposition of coastal sediment), in the ESB. The last period of erosion is assumed to have corresponded with the latest glacial period and was followed by the deposition of the Younger Alluvium in the ESB following the Holocene sea-level rise.

Colluvium — The colluvial deposits have yielded small fragments of Walanae Fauna elements, which seem to have been reworked from the Beru Member, as they are always very fragmented and rounded. In addition, dental and postcranial remains attributable to *Anoa* sp. were also found in the colluvium. The fossils of this still extant dwarf buffalo differ markedly in fossilization as compared to the fossils originating from the Beru Member. They are considered younger, which is in accordance with the unconformable lithostratigraphic relationships.

Micropalaeontological results

Sartono (1979) analyzed foraminifera from a sample collected in his Beru Formation (which corresponds to our Samaoling and Beru Members together). Though he did not present detailed sections, it is suggested that the sample was taken below the terrestrial vertebrate zone. Based on the foraminifera assemblage, Sartono concluded a Late Pliocene age (zones N19 or N20 of Blow, 1969) for his Beru Formation. Van den Bergh et al. (1992) concluded that the land vertebrates from the upper terrestrial part of the Walanae Formation should be younger than 3 Ma, assuming that Sartono's sample was obtained from a marine level underlying the terrestrial, vertebrate-bearing deposits. Sartono's (1979) fauna includes *Globigerinoides fistulosus*, which occurs widely distributed in the Upper Pliocene of the tropical Indo-Pacific (zones PL5 and PL6 of Berggren et al. (1995)).

In the course of the present study, various samples from the Burecing and Samaoling Members were studied for foraminifera contents by Sudijono and for calcareous nannoplankton by Adi Priadi Kadar, both of the GRDC. The micropalaeontological results are given in Table 4. The stratigraphic levels of the samples are indicated in Fig. 40.

Of the microfossil samples from the Sengkang Anticline only one was found to contain a planktonic foraminifera assemblage suitable for age assessment. The sample, F-9B, was taken from The Burecing Member at the base of section III at the core of the Sengkang anticline. Stratigraphically, it is c. 1600 m below the base of the Beru

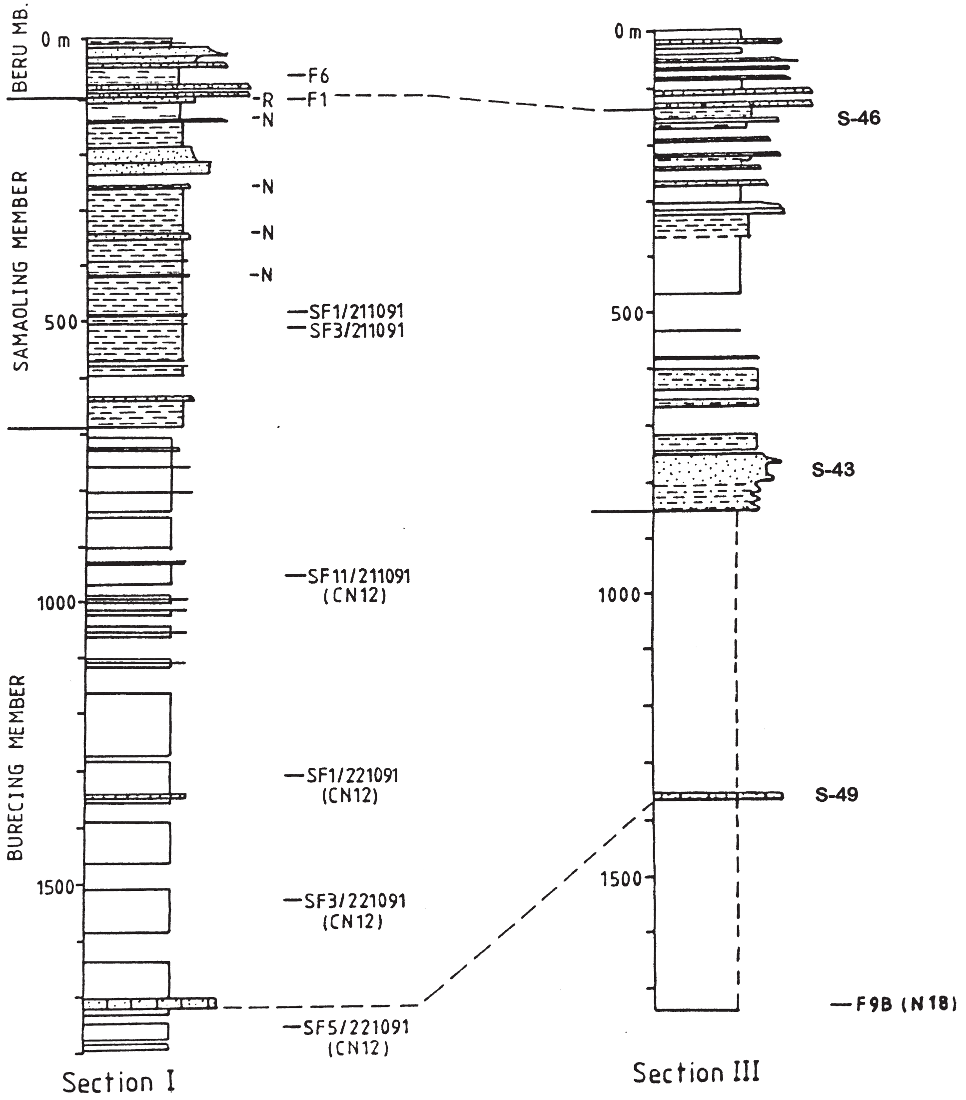


Fig. 40. Sections I and III with the levels of micropaleontological and palaeomagnetic samples indicated. S-numbers in section III refer to the sandstone samples discussed in the petrography section of chapter 3. SF-numbers indicate nannoplankton samples, F-numbers indicate foraminifera samples.

Member. The foraminifera assemblage (Table 4) is indicative of Zone N18 (Blow, 1969). According to the stratigraphic scheme of Berggren et al. (1985) this indicates an age of c. 5 Ma. The assemblage contains amongst others *Globorotalia tumida* and *G. margaritae*, which allows a correlation with zones PL1-PL2 of Berggren et al. (1995). This zonal interval ranges between c. 5.6 and 3.58 Ma. The benthic foraminifera association of the same sample can be interpreted as representing an open marine, outer sublittoral to upper bathyal environment (Sudijono, pers. comm.). A sample from the sandy upper marine part of the Walanae Formation in the ESB, taken in a fine-grained sandstone immediately below the unconformable contact with the Tanrung Formation conglomerates (sample F-13, see Fig. 38) contained reworked foraminifera, amongst others *Spaeroidinella dehiscens*. This taxon is indicative for an age not older than Early Pliocene (Sudijono pers. comm.). The foraminifera from this sample appeared to have been reworked so that this sandstone could still be younger than Early Pliocene.

Two samples (F-1 and F-6) taken from the base of the Beru Member in section I (Fig. 40) contained only benthic foraminifera, besides echinoid fragments and ostracodes. The benthic assemblages are not suitable for dating; they indicate rather restricted lagoonal conditions.

Eight samples from section I were also analyzed for calcareous nannoplankton contents. Two samples of the middle reaches of the Samaoling Member were found barren and two others contained only few poorly preserved nannofossils, which could not be used for dating. Four samples from the Burecing Member (Table 4 and Fig. 40) are indicative of Zone CN12 of Okada & Bukry (1980). These four samples can be stratigraphically placed above the foraminifera sample F-9B mentioned above (Fig. 40). According to the scheme of Berggren et al. (1995) zone CN12 ranges from about 3.75 to 1.95 Ma BP.

It is interesting to note that the prodelta of the Recent Mahakam delta on the east coast of Borneo consists of massive homogeneous muds incorporating beds of carbonaceous clay and silt. Phytoplankton is absent in these prodelta muds while decayed phytoclasts are common (Gastaldo et al., 1995). This facies association corresponds well with some of the fine-grained intervals of the Samaoling Member.

Palaeomagnetism

In order to obtain alternative and more accurate ages for the Walanae Fauna, palaeomagnetic dating was attempted in combination with the analyses of the foraminifera and calcareous nannofossil samples from the Burecing and Samaoling Members. Palaeomagnetic samples have been analyzed by Bondan Mubroto of the GRDC. The Natural Remanent Magnetization (NRM) was measured using a Schönsted DSM-2 Spinner Magnetometer and a stepwise alternating field (AF) demagnetization method in steps of 5-20 mT up to a maximum peak field of 100 mT. For the analyses oriented block samples were cut from fine-grained layers, using non-magnetic tools. The samples taken vary in grain size from silty clay to very fine sandstone. The block-samples were then prepared in the laboratory, where 5-6 cores were drilled in each of the blocksamples. The cores were then put into acrylic cubes, preventing them from drying out or being broken. Study of thin sections revealed that the clastics of the upper part of the Walanae Formation contain detrital magnetite grains.

Samples from only 5 of the sampled layers, all in the upper half of the Samaoling Member exposed in section I (Fig. 40), gave satisfactory demagnetization results. During successive AF demagnetization the total intensity dropped rapidly removing the spurious unstable magnetization, and then decreased exponentially after obtaining a stable magnetic direction. The lower four samples provide a normal polarity, whereas the upper one, taken from a fine sandy lens at the top of a reworked oyster bed 1 m below the lower boundary with the Beru Member, showed a reverse polarity (Fig. 40).

Thus a magnetic reversal from normal to reverse polarity seems to correspond roughly with the transition from the Samaoling into the Beru Member. In the Beru Member it was hard to find well consolidated, unweathered, fine-grained layers that were not bioturbated, and the samples taken from the Beru Member in the same section did not give reliable results.

The transition from normal to reverse magnetic polarity in section I at the transition between the Samaoling and Beru Member can be interpreted in several ways: 1) This transition represents the top of the Olduvai Event, with an age of 1.77 Ma BP according to the magnetostratigraphic scheme in Berggren et al. (1995). 2) The transition represents the Gauss-Matuyama transition at 2.58 Ma. 3) The reversed sample corresponds with the base of the Mammoth Event with an age of 3.33 Ma.

As mentioned above, the four nannofossil samples obtained from the Burecing Member are indicative of Zone CN12. This biozone spans the entire Gauss Chron and the lower part of the Matuyama below the Olduvai normal Event (the period between 3.75 and 1.95 Ma: Berggren et al., 1995). Thus the time interval in which the entire Burecing and Samaoling Members were deposited has to be fitted within the time limits set by zone CN12. This makes the third palaeomagnetic interpretation, in which the transition between the Samaoling Member and the Beru Member would be about 3.3 Ma old, highly unlikely. In that case a 1650 m thick sequence would have been deposited in a period of only 420 ka or less, which would mean a deposition rate of 4 mm/year or more. This seems much too high for a sequence that is largely made up of marine muds.

As we do not have a clear time constraint dictated by micropalaeontological biozonation in the upper part of the section, it remains difficult to choose between interpretations 1 and 2. Attempts to correlate the sequence with eustatic sea level curves would also be hazardous in a tectonically active region such as Sulawesi. Geohistory data from several islands along the unstable Banda Arc have revealed that vertical movements caused local perturbations on the depositional sequences that were of an order of magnitude larger than eustatic oscillations (Fortuin & de Smet, 1991).

Seismic data from the ESB in combination with micropalaeontological analysis (Grange & Davies, 1983) indicate that the youngest marine deposits in the central part of the basin correspond with zone N21, Late Pliocene. Around that time E-W oriented compressional deformation began, resulting in uplift in the ESB. This renders the first interpretation too young, because the transition between the Samaoling and Beru Members represents a stable phase of delta progradation prior to this E-S compressive phase, during which the Sengkang Anticline was uplifted as well.

Therefore, it is concluded that the second palaeomagnetic interpretation is the most likely one; as a consequence the base of the vertebrate-bearing Beru Member in section I would have and age of c. 2.6 Ma. This would correspond with an average deposition rate of 1.4 mm/year. This interpretation also fits well with the ESR results treated below.

ESR dating

Three fossil molar enamel samples from Sulawesi were sent to Japan for ESR analysis, with the kind help of David Reese. They were dated together with two samples from Flores and a large series of fossil teeth samples from various sites on the

Mediterranean islands of Crete, Mallorca, Sardinia and Cyprus. The ESR datings were carried out by a student of Dr Motoji Ikeya at Osaka University. The obtained ESR dates are based on a tentative dose rate: radiation assessment of the samples only. Radiation assessment of the sites would be necessary to determine the ages more accurately. Therefore, the ESR ages only suggest the order of magnitude. Seven ages obtained on fossil tooth samples from Crete have been recently published (Reese et al., 1996).

One of the Sulawesi samples is a molar fragment of *"Elephas" celebensis* (GRDC Coll. no. BC-2958) originating from the Beru Member as exposed in the west dipping flank of the Sengkang Anticline collected in the surroundings of FVL-11, east of the BCF. Two molar samples of *Celebochoerus heekereni*, also originating from the Beru Member were analyzed, one from the excavation at Lonrong (GRDC Coll. no. LR-2695 from FVL-24c) and one from the excavation site at FVL-5 (GRDC Coll. no. 1209). The seven samples from Crete yielded relatively young ages of less than 0.85 Ma, which could be divided in two groups: an older group of three ages lying between 846 ± 20% ka B.P. and 475.55 ± 20% ka B.P., and a younger group of four ages lying between 127.45 ± 20% ka B.P. and 32.53 ± 20% ka B.P. These two age groups fit well within the frame of previously inferred relative ages of the two successive endemic faunas recognized on Crete (Sondaar et al., 1996).

Two Sulawesi samples (from FVL-24c and FVL-11) gave relatively old ages of c. 2.1 Ma ± 20% (ED of 4323 Gy and 4255 Gy, respectively). The Lakibong sample suggests a rather young age of 0.5 Ma ± 20% (ED = 1026 Gy). Because no background radiations were measured in the field, the obtained radiometric ages can not be directly compared with the results from the Mediterranean islands. However, the results are in accordance with the assumed younger age of Subunit B of the Beru Member as exposed in the LT, compared to Subunit A exposed in the west flank of the Sengkang Anticline. The ages of 2.1 Ma ± 20% also seem consistent with the palaeomagnetic results presented above, which resulted in an age assessment of 2.5 Ma for the transition between the Samaoling and Beru Members.

Palaeogeographic reconstruction of the Sengkang Anticline area

Introduction

The Walanae Formation as exposed in the Sengkang Anticline represents a coarsening- and shallowing-upward deltaic sequence. The marls from the Burecing Member were deposited in a marine, outer sublittoral to upper bathyal environment, with minor course-grained clastic influxes from a marginal carbonate platform. Based on the seismic data (Grange & Davies, 1983) and sequential development the upper part of the Walanae Formation (Samaoling and Beru Members) are interpreted as a delta-progradation sequence, .

Palaeoenvironments

The marine sandstones and siltstones at the base of the Samaoling Member were deposited in a shallow, open-marine shelf environment subject to wave action and storm currents. The deposition of the upper sandstones of the same member on the other hand, was clearly influenced by tidal currents, and probably took place in an estuarine outer delta or deltafront environment. The tidal regime was presumably diurnal as has been argued before. Most recent tidal ranges in the Indonesian region are microtidal or mesotidal. Macrotidal ranges occur only in the Malacca Strait and along the south coast of Irian Jaya. The tides around most of Sulawesi are mixed prevailing semi-diurnal. Around the southwest peninsula the tides are mixed prevailing diurnal (Whitten et al., 1988). If the palaeo-tidal system in the area was indeed formed under a prevailing diurnal regime, it is the more remarkable that the dominant tidal currents were strong enough to propagate megaripple migration at all. Probably, the subtidal channel in which the described bundle sequence was formed, constituted part of a funnel-shaped embayment or strait (perhaps corresponding with the Walanae Depression?) with a large resonance effect, causing an amplification of the local tidal range. The presumed embayment may also explain the absence of wave-ripple structures in this part of the sequence.

The fluvial system active during deposition of the Beru Member is not easy to reconstruct due to the lack of large outcrops and the generally weathered condition of the outcrops. Such conditions could have prevented the recognition of large-scale lateral accretion surfaces. The fluvial sandstone layers frequently alternate with lagoonal mudstones (foraminifera samples suggest restricted lagoonal environments: Sudijono, pers. comm., 1994) and mudstones deposited in low-energy lacustrine and floodplain environments. One important feature is that the coarse-grained sandy fluvial sandstones often show tidal influences in the form of closely alternating sand/mud couplets.

Combining the various observations, a tide-dominated deltaic system emerges, with estuarine embayments strongly influenced by mesotidal currents and extensive supratidal flats and lagoons of low energy. Tidal influence reached landinwards in the fluvial channels on the upper delta plain. Deposition in the prodelta was probably mainly characterized by silts and muds containing plant debris, locally interrupted by sandbars, whereas such sandbars were lacking in the deltafront environment.

To substantiate this interpretation a comparison can be made with Recent examples of tropical tide-dominated deltas. A well studied Recent example of a mixed tide- and fluvially controlled delta in the same region is the Mahakam River delta on the east coast of Borneo (Verdier et al., 1980; Gastaldo et al., 1995). The Mahakam Delta is c. 50 km ‘long’ from the initial Mahakam River bifurcation towards the prodelta slope. It has an extension of c. 5000 km^2, comprising subaerial deltaic plain, distributary channels, tidal channels, delta front platform with a water depth 5 m and an extension of between 5 and 10 km, and a prodelta slope. Wave action on the delta front is minor (mean wave heights < 0.6 m), due to the narrowness of the Makassar Strait. The tidal regime in the delta area is mixed semi-diurnal with a mean tidal range of 1.2 m and a maximum amplitude of 3 m during spring tides (Gastaldo et al., 1995). The distributary channels are 7-10 m deep on average. They have a low sinuosity and their positions have been stable over the last 50 years. The thalweg within the channels exhibits a meandering pattern due to the development of sidebars. The distributaries are incised into clayey delta plain sediments, which are in turn covered by supra and intertidal swamps. The distributaries are floored by fine-medium grained sands. Meandering tidal channels, not connected to the river distributaries, cut through the lower delta plain. In the lower delta plain the distributary channels become funnel-shaped under the influence of tidal currents, and mid-channel bars separate ebb- and flood-dominant channels. The sediments in the channels of the lower delta plain are generally more muddy and the sands finer-grained than in the channels in the middle and upper delta plain.

Cores taken from the distributary channels have shown that the sediment accumulations within the distributaries (sidebars and mid-channelbars) are characterized by the occurrence of sand/mud couplets (Gastaldo et al., 1995). Medium sand dominates the upper reaches of the distributaries, whereas fine- to very fine-grained sands are characteristic of the more distal parts. Primary structures in the sandy layers include trough cross-bedding, small-scale ripple and lenticular and wavy bedding. Sand/mud ratios were found to vary between 15:85 and 25:75 in the upper reaches of the distributaries, and between 40:60 and 80:20 in the middle reaches. In the lower delta-plain channels the sediments are composed mainly of alternating silt and mud layers, with local intercalations of sand/mud couplets. Cores obtained from the delta-front exhibit a greater diversity of facies. The sand/mud couplet facies is more often strongly bioturbated, while isolated macrofaunal shell fragments and intraclasts are often encountered. Sands containing abundant reworked shell fragments and representing distributary mouth-bar deposits often underlie the sand/mud couplet facies in this outer deltaic environment, whereas the latter was found often overlain by organic rich muds signaling a tidal flat environment. Sulphurous black muds with horizontally bedded phytoclasts are characteristic for the interdistributary marshes.

Similar facies types have been encountered in the Samaoling and Beru Members of the Walanae Formation. In addition, the delta deposits of the latter include a conglomeratic sandstone facies, which is not present in the recent example of the Mahakam River delta. The Mahakam River does not supply course bed-load material. However, in the estuaries of coarse bed-load rivers entering the sea under a mesotidal regime, a facies characterized by an alternation of gravels and coarse sands can be found in the uppermost, fluvial dominated upper reaches of the estuaries landwards of the first bifurcation (Borrego et al., 1995). Seaward of the first bifurcation, and thus in the upper delta realm, the channel deposits become better sorted, with mean grain sizes in the medium to coarse sand range.

A significant difference between the Walanae deltaic sequence and the Recent Mahakam delta deposits concerns the total thickness of the sequence. The present Mahakam delta, formed after the Holocene transgression, comprises a relatively thin sequence of c. 50-60 m thick, which overlaps older Pleistocene palaeodeltas (Gastaldo et al., 1995). The regressive deltaic sequence topping the Walanae Formation, on the other hand, is more than 700 m thick (combined thickness of the Samaoling and Beru Members). As recorded in section III, two progradational phases can be recognized, separated by a transgressive interval as represented by the middle fine-grained interval of the Samaoling Member. The overall thicker Pliocene deltaic sequence from South Sulawesi may be explained by a combination of distinct factors compared to the recent Mahakam Delta sequence. Firstly the Mahakam Delta progrades over older Pleistocene delta complexes and the present substrate is relatively shallow, whereas the palaeo-Walanae Delta probably prograded into a relatively narrow but deep basin. Secondly, the sediment supply of the palaeo-Walanae River was certainly much lower than that of the present Mahakam River. The catchment area of the latter encompasses 75000 km^2, which is five times greater than the entire surface area of South Sulawesi. The thickness of single-storey fluvial sandstones in the Beru Member is usually between 1 and 4 m, whereas the sandy lateral bar sequences deposited in the distributaries of the Mahakam River are typically 7-8 m thick (Gastaldo et al., 1995). This also indicates that the river channels of the palaeo-Walanae were of a comparatively small size.

The relatively small sediment supply, in combination with the fact that progradation took place into a deeper basin, must have resulted in slower progradation of the palaeo-Walanae River delta. Reworking of sediments deposited in the outer deltaic environments was probably much stronger than in the present Mahakam Delta. In the palaeo-Walanae Delta periodic drowning of the lower delta plain marshes presumably resulted frequently in the development of lagoonal environments. This is in accordance with the observed intercalation of fluvial and lagoonal sediments (sections I, IV) and the occurrence of shallow marine lag deposits containing terrestrial vertebrate fossils (FVL-25b, FVL-28, FVL-30). This interpretation means that more precise time-stratigraphic correlations between the various sections are practically impossible without information from shallow seismic data.

During deposition of Subunit B of the Beru Member, deposition is thought to have occurred more landinward, outside the reach of tidal influence, as follows from the lack of sand/mud couplets in this subunit. The increased presence of pebbly bedload material that characterizes subunit B, is probably related to this more proximal position rather than to tectonic uplift in the source areas. Indeed, the maximum pebble diameter is equal in both the shallow marine lag gravels at the transition of the Samaoling and Beru Members and in the fluvial conglomerate layers of Subunit B.

However, besides representing a more inland depositional environment, Subunit B is probably also younger than Subunit A of the Beru Member, as has already been discussed above. At the time subunit B was deposited in the area west of the Bulu Cepo Fault, incipient uplift of the Sengkang Anticline had possibly started in combination with downwarping of the WSB along its depocentral axis in response to a E-W compressional regime. While at this stage deposition may have been intermittent in the marginal basin area occupied by the LT, deposition probably had ended at the position of the Sengkang Anticline. Only during the later culmination of this compressive phase, coarser material was being newly supplied and deposited, as represented by the Old Alluvial Fan Gravels.

The limited outcrop conditions do not allow tracing individual layers laterally over long distances. There are no indications in the field of a major hiatus in the sequence, except in the uppermost fluvial part of the Beru Member. From the field observations alone, however, it is impossible to assess whether the erosional bases of coarse-grained fluvial layers represent short term hiatuses of an order of magnitude of hundreds to thousands of years, which are usually related to the process of lateral shifting and avulsion of rivers, or whether they mark major periods of erosion related to base-level fluctuations or tectonic movements. Angular unconformities could be noticed neither in the field, nor on the aerial photographs. The first marked glacio-eustatic sea level fluctuations related to northern hemisphere glaciation started around 3.6 Ma (e.g. Vrba et al., 1991). It is possible that some depositional hiatuses that related to eustatic sea level fluctuations do occur in the deltaic Beru Member, the base of which has an age of c. 2.5 Ma. The presence of mottled palaeosols at several levels indeed points to prolonged depositional hiatuses. Further, as has been discussed in the chronostratigraphic section, a fossil sample originating from Subunit B, yielded an Electron Spin Resonance dated age conspicuously younger than a sample from Subunit A. Considering the limited thickness of Subunit B, this also adds to the assumption that pronounced gaps are present between Subunits A and B and perhaps within Subunit B.

Palaeogeography

Combining the stratigraphical, sedimentological, seismological, and chronostratigraphic results, the palaeogeographic history of the Sengkang Anticline area during the Pliocene and Quaternary has been reconstructed as depicted in Fig. 41. This figure shows four successive stages of the basin evolution preceding the present situation as shown in the geological map of Encl. A.

During the Late Miocene to Early Pliocene (Fig. 41A) the area, now occupied by the Sengkang Anticline, formed the transitional area between a marine trough in the west and a more shallow marine platform to the east, where pinnacle-reef growth could locally keep up with basin subsidence during the Early Pliocene. Along the Sengkang Anticline deposition occurred under generally calm conditions at a water-depth of c. 200 m. The palaeodepth along the central axis of the WSB is not known, but the seismic profiles indicate absence of pinnacle-reefs as developed in the ESB. This basin configuration was generated earlier during Middle to Late Miocene times, due to normal faulting along the Walanae Fault zone, with downthrowing of the WSB. Besides the East Sengkang Basin presumably also the Puncakoro Block remained relatively shallow, facilitating carbonate deposition.

Coarse-grained sediment influxes were limited and are represented by a single layer in the Burecing Member only. This coarse bioclastic packstone represents a mass-flow deposit that moved from the shallower shelf in the east into the deeper West Sengkang Basin. From late Early Pliocene to early Late Pliocene subsidence was reduced largely, and the WSB and ESB became gradually filled in by prograding deltas. Some volcanic activity took probably place in the region during this period, as evidenced by the presence of euhedral biotite and pyroxene crystals.

During the Late Pliocene the WSB had been largely filled with clastics, and along the northern and southern margin of the WSB deltas prograded into a marine gulf, where relatively strong tidal currents were active. From the south the palaeo-Walanae River supplied sediments (Fig. 41B). The downstream areas of this river system were influenced by tidal currents, and the delta was presumably of the low-wave-energy mixed tide- and fluvially controlled type, characterized by the development of estuaries at the mouths of the delta distributaries (similar as the present Mahakam Delta).

During the Early Pleistocene (Fig. 41C) an E-W compressive regime resulted in reverse faulting along the EWF and possibly along the WWF. E-W compression is thought to have resulted in the uplift of the Sengkang Anticline and the ESB above the depositional baselevel. The main deformation was concentrated along the pre-existing faults of the Walanae Fault zone. In the WSB the compressive regime resulted in the downwarping of the basin along its depocentral axis, while in the ESB fold-

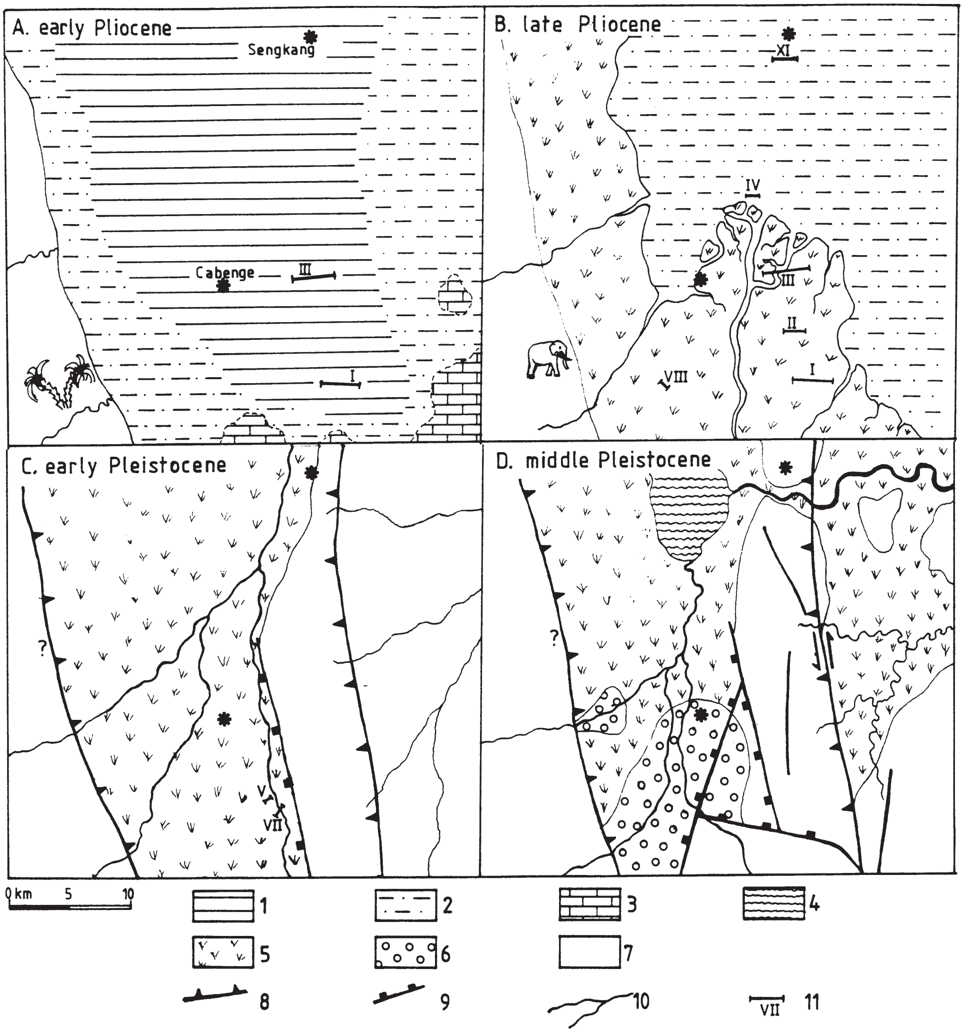


Fig. 41. Basin infill history of the Sengkang Anticline area represented by four successive stages. The approximate positions of the towns Sengkang and Cabenge are indicated by stars. Legend: 1 = deep marine (>200 m depth); 2 = shallow marine clastic; 3 = shallow marine carbonate; 4 = lacustrine; 5 = coastal/alluvial plain; 6 = alluvial fan; 7 = terrain subject to erosion; 8 = thrust fault (triangles in upthrusted block); 9 = fault (tick-marks in downthrown block); 10 = rivers; 11 = section with section-number; 12 = wrench fault. Partly based on data presented by Grange & Davies (1983).

ing and faulting resulted in uplift. Due to this uplift the upper part of the Walanae Formation was largely eroded in the central part of the ESB. Structurally, the ESB became separated from the WSB by thrusting along the EWF, which resulted in the generation of the Sengkang Anticline. The downwarping of the WSB facilitated continuous deposition along the basinal axis of the WSB, whereas in the narrower southern part of the Walanae Depression deformation was more severe, resulting in folding, faulting and uplift of the Walanae Formation.

During culmination of the compressive phase that had started in the Early Pleistocene, alluvial fans developed in the WSB (Fig. 41D). The rivers depositing their sediment loads in the WSB started to supply erosion products from plutonic rocks in the adjacent mountain ranges and also of consolidated rocks from the locally uplifted Walanae Formation. The Puncakoro Block was uplifted, and in the southwestern part of the study area an alluvial fan system became active near the fault-bounded margins of the uplifted Puncakoro Block, which is located at the hinge line of the uplifted Walanae Depression, and the further subsiding WSB.

In the ESB, intermittent deposition occurred on the eroded and largely leveled Walanae Formation. Periods of deposition (Tanrung Formation and overlying Alluvial Units) are thought to have been related to periods of high sea level (interglacials), whereas erosion affecting the area was related to periods of low sea level (glacials). The source area of the Tanrung Formation clastics was of limited extent because the Sengkang Anticline acted as an efficient barrier for clastic influxes supplied by the palaeo-Walanae River, similar as the present day situation. The clastics of the Tanrung Formation were derived from erosion of the Walanae Formation, including the Tacipi Member limestones. The source area of the Tanrung Formation might largely correspond with the present-day catchment area of the Tanrung River (Encl. A). At least two cycles of erosion and deposition followed the formation of the Tanrung Formation (Old and Young Alluvium in the ESB). The latest cycle is thought to include erosion during the last glacial and subsequent filling of the eroded valleys during the Holocene sea-level rise (Youngest Alluvium).

The so-called ‘terraces’: delineation of the problem

Some of the weathered gravels and conglomerate layers exposed in the surroundings of Beru have been interpreted as representing remnants of a terrace system of the Walanae River by various authors (e.g. van Heekeren, 1958; Bartstra et al., 1992; Keates & Bartstra, 1994). Van Heekeren (1958) originally distinguished seven terraces in the Beru area, which is equivalent with the northern part of the area defined here as the Lakibong Triangle (LT). The two oldest and most frequently mentioned terraces were reported to correspond with the 50-m and 75-m contour levels, and the youngest to (inactive?) parts of the Walanae River floodplain. Van Heekeren (1958) considered the vertebrate fossils and artefacts, both found in the same area, to be of the same age. Hooijer (1972b) followed van Heekeren by stating that the fossils from Beru and Calio originate from these terraces. Later it was suggested (Bartstra, 1977) that at the maximum three or four terraces could be recognized, one year later further reduced to two or three (Bartstra, 1978). More recently, it is again stated that on the basis of height alone, no more than three or four terraces can be recognized in the Beru area (Bartstra et al., 1991, 1994), the highest terraces corresponding with the 50-m and 75-m level.

River terraces are part of many river systems and constitute the remains of former, abandoned floodplains. River terraces usually constitute elongated plateaus, remnants of partly eroded older deposits, along valley slopes above the present river bed. Three major external factors are usually mentioned as responsible for terrace formation: climate fluctuations, base level fluctuations and tectonics (Veldkamp, 1991).

Climate fluctuations can result in variable discharges and sediment loads in river systems through time, and these fluctuations may lead to alternating periods of aggradation and incision of the floodplain. Base-level changes in a depositional basin can both occur in response to glacio-eustatic sea level fluctuations, as well as due to tectonic uplift or subsidence. During periods of low base level rivers start to cut into their own floodplain and non-eroded parts of the older deposits can afterwards be recognized as terraces.

The various authors that have dealt with the terrace stratigraphy in the Beru area (van Heekeren, 1958; Bartstra, 1977, 1978; Bartstra et al., 1991; Keates & Bartstra, 1994) do not mention anywhere which of the above mentioned factors is thought to have been responsible for the terrace formation. In absence of suitable materials for radiometric dating techniques, understanding the underlying processes of terrace formation becomes of crucial importance when one wants to assign an age to the deposits now remaining as terraces. Bartstra et al. (1991: 319) merely state that 'in view of the rate of denudation these [terrace fills] cannot be older than Upper Pleistocene at the most'. However, the artefacts themselves seem to play a more important role in the dating of the terraces. In the same paper (Bartstra et al. 1991: 320) they mentioned that the artefacts from the Walanae Valley could be divided into three groups (assemblages). This division is maintained in a more recent paper (Keates & Bartstra, 1994). In these papers the authors stated that the supposedly oldest of these 3 temporal groups was classified on the basis of heavy patination and fluvial wear. This group, recognized as based on a flake and core tool technology, was thought to be in primary context in the gravels of the 75-m and 50-m levels, although this could not be confirmed by direct evidence from test pits (Bartstra et al., 1991: 320). A second group of artefacts, morphologically not unlike the Upper Pleistocene Leang Burung 2 cave industry, for which C^{14} dates go back as far as c. 30 ka B.P. (Glover, 1981), was thought to be younger than the gravels of the 75-m and 50-m levels, based on their better preservation of flake scars. A third group consists of small cores and flakes with no signs of fluvial transport at all. This group was thought to be Holocene in age and synchronous with the later cave artefacts of the Maros region, the so-called 'Toalian'.

It is further noted that the first group, the heavily patinated artefacts, have not been found anywhere else in Sulawesi, and therefore may represent the earliest evidence for human occupation in Sulawesi (Keates & Bartstra, 1994: 27). The assumption that these artefacts were made by modern *Homo sapiens*, as was stated various times (e.g. Bartstra et al., 1991: 120; Keates & Bartstra, 1994: 28), seems to have prompted the presumed Late Pleistocene age of the 50-m and 75-m terrace fills, rather than geomorphological or geological observations.

Beru is located in the area here designated as the Lakibong Triangle (LT), a fault-bounded structural block separated from the Sengkang Anticline to the east by the Bulu Cepo Fault (BCF) (Encl. B). As has already been discussed, the composition of the so-called terrace-fills is not significantly different from other conglomerates in the area, which pertain to the fluviatile Beru Member of the Walanae Formation. On the other hand, the composition of these presumed terrace fills dóes differ from those of the stratigraphic unit designated in this thesis as the Old Alluvial Fan Gravels. The latter unit represents an eroded alluvial fan system of presumably Middle Pleistocene age, at places covering strata of the Walanae Formation unconformably (e.g. west of

Jampu and west of Lenrang, Encl. A), or remaining as up to several meters elevated terrace remnants surrounded by the modern floodplain of the Walanae River (e.g. north of the Cipee River Encl. B).

As shown in Encl. A, the LT is fault-bounded in the east and south and presumably in the west. Horizontal to subhorizontal layers of the Beru Member of the Walanae Formation crop out in the LT. The terrain consists of hilly E-W running ridges that decrease in elevation towards the west. The main ridges are dissected by a dendritic pattern of small erosional V-shaped valleys, which debouch into roughly west-flowing small rivers, which in turn flow westward and debouch in the Walanae River. East of the BCF fault the valley pattern changes into a feather type, due to the parallel westward dipping sandstone layers of the Samaoling and Beru Members on the westflank of the Sengkang Anticline.

The highest elevation in the LT is 103 m at Bulu Cepo Hill, just west of the Bulu Cepo Fault. Towards the west the elevations gradually decrease and the ridges gently slope down towards the Walanae River floodplain. The delineation of the western boundary of the LT is less sharp. Older rocks of the Beru Member have become covered with alluvium of the modern Walanae River in the west, but locally, on the southernmost part of the Walanae River Floodplain, inliers exposing horizontally bedded rocks of the Walanae Formation crop out, e.g. near Lenrang (Encl. A).

The Walanae River flows through two depositional basins, the WSB and the ESB, before debouching into the Gulf of Bone. Before entering the ESB, the river passes through a narrow break-through valley near Sengkang. Therefore, the influence of Pleistocene sea level fluctuations has been probably less marked in the WSB than in the ESB. If river terraces were formed in the WSB, they would probably have resulted from tectonic uplift rather than from sea level fluctuations. The Lakibong Triangle lies on the hingeline between the uplifted southern Walanae Depression and the still subsiding WSB, and thus remnants of the former Walanae River floodplain, younger than the bedrock strata of the Walanae Formation, might indeed have been preserved as terraces in this transitional area. Because of the marked elevations of the two most frequently mentioned high terraces above the present Walanae River banks (c. 30 and 55 m above the banks of the modern Walanae River, and c. 50 and 75 m, respectively, above present-day sea level), an Middle Pleistocene age for the gravels can not be excluded, if indeed they could be shown not to pertain to even older strata of the Walanae Formation. In order to solve this problem, several approaches can be made.

Criteria for identifying the gravels associated with artefacts

The recognition in the Beru area of a Walanae river terrace system by Bartstra (1977, 1978), Bartstra et al. (1991, 1992, 1994) and Keates & Bartstra (1994) is based on three criteria: 1) elevation (the 50 and 75 contour near the village of Beru are considered as terraces), 2) terrace gravels are unconsolidated, although Bartstra et al. (1994) also distinguish unconsolidated gravels which are the residue of weathered conglomeratic bedrock or a mixture of eroded bedrock conglomerates and terrace fills, and 3) the association with artefacts. These, and other criteria, will be discussed below in view of our own investigations.

Elevation — Due to the poor outcrop conditions in the Lakibong Triangle (LT), contacts between lithological units are often obscured by colluvium and soils, apart from the steeper slopes and in the bedding of rivers. However, the outcrops along the valleys do show one important fact: layers of the Beru Member, characterized by fluvial facies types which are also developed in the west dipping flank of the Sengkang Anticline, have an (sub)horizontal orientation in the LT. Therefore the layers come to the surface at constant elevations over considerable distances. At the lowest stratigraphic levels exposed in the LT in the east-west cutting valley bottoms, fluvial and tidally influenced layers alternate with each other. This interval has been included in Subunit A of the Beru Member (sections VII, VI, IX, and X). Clast-supported conglomerates, on the other hand, which are here included in the younger interval because of the lack of tidally influenced deposits (Subunit B of the Beru Member), crop out roughly above the 37.5 m contour in the northern part of the LT, whereas in southwestward direction, near Sare Batue, the sequence has been slightly tilted under influence of the uplift of the Puncakoro Block further south. The lowest conglomeratic levels of subunit B can be traced there to elevations of up to c. 75 m (Encl. B). However, the dip of the layers never exceeds 10, contrary to what was stated by Bartstra et al. (1994: 11), namely that 'the various deposits at Lakibong are steeply folded'. Somehow, this remark contains some truth because Lakibong is the name of a small E-W flowing river with its origin on the summit of the Sengkang Anticline, where indeed the layers are steeply inclined. However, on the accompanying map (Bartstra et al., 1994: fig. 2) the name 'Lakibong' is placed in the area here designated as the LT. Because of the horizontal orientation in the substratum exposed in the LT, including fluvial sands and conglomerates, the recognition of terraces based on elevation alone has considerable limitations.

Consolidation — The conglomerates in the LT are locally found to be poorly consolidated, for example at FVL-18 (Encl. B), which is one of the former excavation sites of van Heekeren and referred to as Beru II by Keates & Bartstra (1994). The same site, located on top of a small rounded hill, has also been designated as Calio II or Marale, depending on the author or paper[1]. At some places the Beru Member conglomerates show irregularly cemented horizons (e.g. near Palangiseng, section VII), but this can be also observed several meters below the excavation pit of van Heekeren, at FVL-18. At still other places the conglomerates have even been completely lithified by carbonate cement, for example at FVL-16 and FVL-17 near Marale (Encl. A). The top of section II near FVL-11 (Encl. A-C) comprises poorly cemented clast-supported conglomerates, which dip steeply in western direction. Because of the steep inclination, there can be no doubt that these conglomerates belong to the Beru Member at this place.

Such variations in degree of cementation, as observed at the various conglomerate outcrops, are not uncommon in coarse-grained fluvial sediments, especially under tropical conditions, and they may reflect local, early diagenetic cementation around former ground-water tables. Many factors such as porosity variations, interconnectedness of the coarse-grained lithosomes, infiltration of clays etc. may have influenced early diagenetic cementation (Leeder, 1982). Other unconsolidated gravels might have resulted from dissolution of cement due to percolating meteoric water. Especially where conglomerates crop out at the top of hills or ridges, such as at FVL-18, secondary dissolution by percolating meteoric water may have dissolved the carbonate cement. On this hill a 6.8 m thick interval of matrix and clast-supported conglomerates covers the highest reaches. Though the surface of this hill is covered with loose gravel, small outcrops with consolidated pebbly sandstones can be observed in erosional gullies at the lower reaches of the hill, suggesting that the core of the hill is made up of (partly?) consolidated deposits. It can be concluded that consolidation is not a suitable criterion to distinguish bedrock conglomerates from younger terrace fills.

Artefacts — It thus seems that the only criterion to discriminate between relatively young deposits shaped into terraces and older conglomerates pertaining to the bedrock, remains point 3, the association with artefacts. However, this criterion is only valid when the artefacts occur in situ in the gravels, which could not be proven so far as has already been mentioned above. Still, I would agree with Bartstra et al. (1991: 320) that the postulated in situ occurrence of the group 1 artefacts is likely, because of the very pronounced patination and fluvial wear. But then, could these artefacts not have an age older than Late Pleistocene and with them the gravels with which they are associated? As was concluded by Keates & Bartstra (1994: 28) the group 1 artefacts concerned here were 'manufactured by modern *Homo sapiens*, but lack the complexity which researchers familiar with European and Near Eastern assemblages cite as a characteristic component of the cultural character of this species.' Could these group 1 artefacts not be the work of an earlier hominid?

Stone tools were excavated from a sandstone layer of the Ola Bula Formation at the site Mata Menge on the island of Flores. Apart from stone tools, the layer, which was palaeomagnetically dated as early Middle Pleistocene, has also yielded a fossil island fauna (Maringer & Verhoeven, 1970; Sondaar et al., 1994; van den Bergh et al., 1996; chapter 5 of this thesis; Morwood et al., 1997, 1998). Based on these data it is concluded that *Homo erectus* may have been able to cross sea barriers more than half a million years ago. If this controversial hypothesis can be substantiated by additional research, this would imply that early humans could also have reached South Sulawesi during the Middle Pleistocene. Though it is clearly too premature to speculate on the latter possibility unless artefacts will be found in situ in the Beru gravels and unless their age can be proven by reliable dating methods, the point here is that the association with artefacts does not necessarily imply a relatively young, Late Pleistocene age of the gravels, the more as the artefacts appear to be rather 'primitive'.

In addition to the criteria mentioned above, there is a number of other features that might provide information about the status of the gravel deposits associated with artefacts. These have not yet received much attention from other workers and will be discussed next.

Spatial distribution — When looking at the spatial distribution of the so-called 'terraces', it follows that they have not been reported by others or observed by ourselves from localities north of the point where the BCF disappears below the Walanae floodplain, 2 km N of Calio (Encl. A). North of this point the fluvial deposits of the Beru Member are dipping westward along the westflank of the Sengkang Anticline. If younger deposits would have been laid down on the eroded surface of these inclined strata and would have become dissected subsequently into terraces, it would be easy to recognize them as terrace remnants because of the unconformable contact below.

However, the 'terraces' that have been recognized are restricted to the LT and the margin of the uplifted and fault bounded Puncakoro Block (the latter corresponding with the Old Alluvial Fan Gravels distinguished in this thesis). Both the LT and the Puncakoro Block can be considered as structural units, which have been tectonically active synchronous with or after deposition of the Beru Member, as deposits of this member have been deformed by the faults that delineate these structural units. It is thus possible that former Walanae River floodplain deposits remained as remnants in the LT as a result of recurrent episodes of uplift and erosion of this structural unit. This would explain the absence of terraces north of the LT. If so, these terraces should be referred to as tectonic terraces. On the other hand, if glacio-eustatic sea level fluctuations induced the base-level lowerings that resulted in the formation of terraces, it would be expected to find recognizable terraces also more to the north along the Sengkang Anticline, which is not the case. The interpretation of tectonic terraces would imply that the gravels associated with the artefacts may have an age much older than Late Pleistocene, because the precise timing of uplift is not known.

Composition — Another aspect, which can help in testing the two opposing hypotheses, is composition and texture of the gravels and conglomerates. The pebble count results discussed earlier clearly show that the conglomerates of FVL-18 and 20 (corresponding with the van Heekeren archaeological sites Beru II and Beru III, respectively) match other conglomerates of the Beru Member, also those which certainly predate the deformation phase and which are exposed in the west-dipping flank of the Sengkang Anticline. An important aspect in the gravel composition at FVL-18 and 20 is, that they do not contain pebbles derived from erosion of the Walanae Formation. This is in sharp contrast with the composition of the gravels near Jampu, Lenrang, Kecce and Batuasange, which unconformably overlie Walanae Formation deposits and contain erosion products of the Walanae Formation. They have a larger maximum and average clast size (cobble size dominates) than the gravels at FVL-18 and 20 and all other conglomerate deposits from the LT which were examined (pebble size dominates). These compositional and textural differences seem to reflect spatial and/or temporal differences in source area. Particularly the absence of reworked Walanae Formation clasts (such as Tacipi Member limestone clasts) in the conglomerates cropping out at the 50-m and 75-m levels in the LT, strongly suggests that they largely predate the compressive tectonic phase which occurred at the Pliocene-Pleistocene transition, whereas the gravels mapped here as Old Alluvial Fan Gravels, clearly postdate this event as indicated by their more varied composition and coarser texture. The latter also more resemble the gravels in the modern Walanae River bedding, although here again intrusive rock clasts appear to be absent.

Fossil contents — Scattered fossil vertebrate remains do occur in the conglomerates cropping out in the LT, but were not found in the Old Alluvial Fan Gravels. According to Bartstra et al. (1991, 1994) fossils are relatively rare in the coarse-grained deposits, irrespective of their interpretation as terrace fills or as layers belonging to the Walanae Formation. Our own findings confirm that vertebrate fossils are relatively rare indeed, which is to be expected in conglomeratic deposits. However, skulls of pygmy proboscideans have been found in situ in the Beru Member conglomerates near Marale (sensu stricto: FVL-17) and south of the Lakibong river (FVL-2). The maximum pebble diameter does not exceed 10 cm in these conglomerate layers. Large objects such as largely intact fossilized skulls are unlikely to have been reworked from older deposits. On the other hand, the absence of reworked terrestrial vertebrate fossils in the Old Alluvial Fan Gravels, which do contain reworked rocks of the Walanae Formation, may be explained by a lack of vertebrate-bearing beds in the source area, i.e. in the southern part of the Walanae Depression.

Remains of a large-sized *Stegodon* have been found neither in situ in our excavations in the LT, nor anywhere else outside the LT in subunit A of the Beru Member. However, some surface-collected findings in the LT clearly represent a *Stegodon* of large-sized dimensions (see chapter 4). Fragmentary dental remains that were surface-collected in the surroundings of Palangiseng (FVL-2) can be attributed to a large-sized *Stegodon* sp. They cannot be allocated under *S. sompoensis*, the common dwarfed species which is present in many localities that certainly pertain to Subunit A of the Beru Member. Other large-sized *Stegodon* remains, though not discovered in situ, originate from the localities FVL-12 and FVL-17. All three localities display exposures of Subunit B of the Beru Member.

A *Celebochoerus* metapodial of clearly shortened proportions was surface-collected at FVL-15 near Marale, where strata corresponding with Subunit B of the Beru Member crop out. All other *Celebochoerus* metapodials collected in older strata of the Beru Member are elongated. Shortening of the distal limbs is a common evolutionary trend amongst island artyodactyla (Sondaar, 1977).

These data suggest that the layers, here included in Subunit B of the Beru Member and cropping out in the upper reaches of the LT, are indeed younger than the youngest layers exposed in the west flank of the Sengkang Anticline or in the lower reaches of the LT. The presence of a large-sized *Stegodon* in these inferred younger layers may seem contradictional to the model of dwarfing of elephants on islands. However, it is not uncommon on islands to find large-sized Elephantoidea in layers that are younger than strata containing dwarfed species of the same genus (e.g. Mol et al., 1996). On the island of Flores, a fauna with a dwarf *Stegodon* is succeeded by a fauna with a large-sized *Stegodon* (see chapter 5). The large-sized but younger species is thought to represent a new immigrant from elsewhere.

Though the data presented above support the view that the layers mapped here as Subunit B of the Beru Member are younger than Subunit A, they can not solve the terrace problem. In both hypotheses the upper reaches of the LT may be considered younger than the youngest layers cropping out in the Sengkang Anticline or in the lower reaches of the LT.

Sedimentology — Let us consider the excavation site of van Heekeren south of Calio in more detail (FVL-18). This excavation would correspond to the so-called 50-m terrace (though conglomerates and gravels also occur at elevations below the 50-m contour and between the 50-m and 75-m contour in the close vicinity of the excavation). This excavation, at present still present, is located on top of a small rounded hill with a N-S elongation. On this hill a 6.8 m thick interval of matrix- and clast-supported gravels covers the highest reaches. Though the surface of this hill is covered with loose gravel, at the lower reaches of the hill small outcrops with weakly consolidated

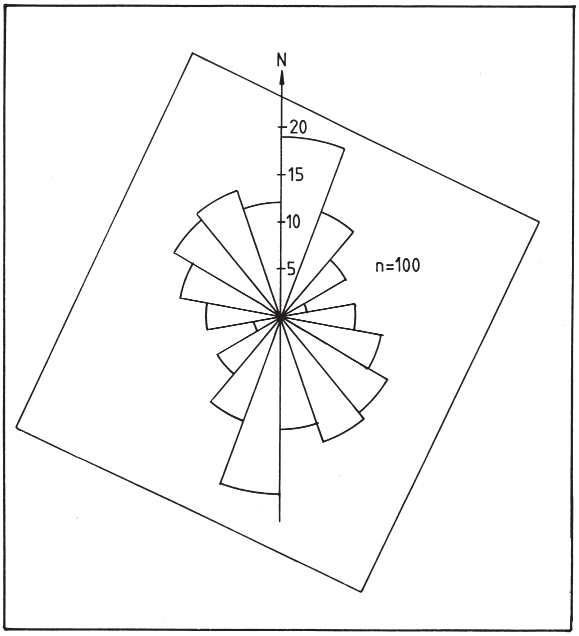


Fig. 42. Rose-diagram showing the orientations of the longest a-axis of 100 pebbles in the conglomerates outcropping at FVL-18. The measurements were performed in the walls of the original excavation pit of van Heekeren. Inner box indicates the orientation of the excavation pit. On each side of this pit 25 measurements were taken to avoid selective bias as much as possible.

pebbly sandstones, with a horizontal layering, can be observed in erosional gullies. The average diameter of the ten largest pebbles from the walls of the excavation pit near the top amounts 9.7 cm, the largest pebbles consisting of both andesites and brown cherts (for further details on the composition see Fig. 39). No pebbles larger than 11 cm in diameter were found on the slopes of the hill. In the excavation the conglomerate appears to be clast-supported with a coarse-grained, poorly sorted and unconsolidated sandy matrix without admixtures of clay, except in some small pockets. Sedimentary structures cannot be clearly distinguished. The unconsolidated and loose nature of these gravels can be explained by the action of percolating rain water, which supposedly has acted severely near the most weathered part of the outcrop, that is near the top of the hill.

The orientations of the longest a-axis of hundred pebbles from the four walls of the pit were recorded. Because flattened pebbles are rare, imbrication is not obvious at first sight. However, the pebbles appeared to have their longest axis in a preferred N-S orientation (Fig. 42). Preferred orientations in a water current-produced fabric, such as this conglomerate, depend critically upon the mode of transport. In gentle bedload transport with clasts rolling or sliding, the clasts tend to lie with their long a-axis normal to flow. During stronger flows, in which clasts tend to saltate, they take up the a-axis parallel to the flow (Johansson, 1976). As the conglomerate at FVL-18 is rather well sorted, gentle bedload transport seems to have been the most likely mode of deposition. This would suggest an E-W palaeocurrent direction.

Such a palaeocurrent direction seems at odds with the main transport direction of the Beru Member fluvial system as inferred from other palaeocurrent measurements, which indicate a south to north flowing Beru Member palaeo-river system (Fig. 36A). The deposit may have been deposited in an E-W transect of this fluvial system, at times when the Sengkang Anticline did not yet constrain the course of this river system. If on the contrary the gravels at FVL-18 are interpreted as marginal remnants of a former floodplain of the Walanae River, deposited at a time when the Sengkang Anticline was already uplifted, a northwards directed current should have been responsible for the deposition of the gravels, unless the river would have flown 'into' the hills in the east.

Alternatively, the preferred orientation might have resulted from creep processes on the sloping hill surface. In debris flows elongate clasts take up orientations with their long axis parallel to flow (Johanssen, 1976). Because the hill slope at van Heekeren excavation is dipping in western direction, the latter possibility seems unlikely.

In conclusion, I would suggest that the occurrence of the so-called 'terraces' at the 50-m and 75-m levels near Beru couldn't unambiguously be proven. If they do represent remnants of the former Walanae River floodplain, they must have been shaped by uplift of the LT, and should be designated as tectonic terraces. In that case the age of the gravels and the associated group 1 artefacts could be easily older than Late Pleistocene. It is thought much more likely however, that the gravels near Beru pertain to the youngest exposed levels of the Beru Member of the Walanae Formation. These deposits are thought to have been deposited along the southwestern margin of the WSB at a time when uplift of the Sengkang Anticline had started to take place in response to E-W compression, as depicted in Fig. 41C. The horizontally layered deposits exposed in the LT are thought to have been deposited in a normal succession. Subsequently, the LT has been uplifted, probably in relation to the uplift of the Puncakoro Block to the south. Following uplift of the Puncakoro Block the Old Alluvial Fan Gravels were deposited. The compositional similarity between Subunit A and Subunit B gravels, and their different composition as compared to the Old Alluvial Fan Gravels, corroborate this model.

Plio-Pleistocene faunal succession of South Sulawesi

Fossil Vertebrate Localities of the Beru Member

The total of 31 fossil vertebrate localities (FVL) sampled during the successive field campaigns have been numbered and the numbers are indicated on the geological maps (Encl. A-B). If the FVL occurred in one of the measured sections, their locality numbers are also indicated on Encl. C. Only FVL-30 near the small river Padali, is situated outside the area covered by Encl. A and is not indicated on the maps. FVL-30 represents the only FVL located west of the Walanae River floodplain. There, fossils were collected in poorly exposed agricultural fields on the weakly sloping foothills of the Western Divide Range.

Around 3000 vertebrate fossils have been collected at the various FVL, of which 2525 can be identified to at least genus level. Of these identifiable specimens 27% were collected in situ from the bedrock. Most of these in situ collected fossils (22% of total amount of identifiable fossils) were excavated at two rich localities, FVL-24c and FVL-5. The importance of these two localities lies in the fact that they give a good impression of the composition of the Walanae Fauna during two short time intervals. The taphonomy of these two excavated sites and some other relatively rich localities will be discussed further on, but first the general description of these and some other fossil vertebrate localities, which have yielded important fossil specimens and/or data on the local biostratigraphy, will be treated.

FVL-24a-c: Lonrong — One of the excavations was carried out at FVL-24c, stratigraphically representing the highest fossiliferous level of a 14 m long exposed interval. This small section is situated 1 km N of the village of Lonrong (Encl. A) in slightly south-dipping (less than 5) layers pertaining to the Beru Member. This is the southernmost fossil vertebrate locality discovered in the area so far. It was discovered in 1990 in a teakwood plantation during a survey in that area. In total 390 fossils, all of terrestrial vertebrates, have been collected here, of which 251 in situ. Stratigraphically 12 m below FVL-24c there is another fossiliferous layer exposed, FVL-24a. The latter, though less rich in fossils than FVL-24c, contains a mixture of terrestrial and marine vertebrates. Stratigraphically in between FVL-24a and FVL-24c a few fossils were collected from the surface (FVL-24b). The petrography of the sandstones at Lonrong (Table 2, sample S-50) corresponds with the Beru Member sandstones as exposed in sections I-III. In the surroundings of Lonrong only marine layers have been found stratigraphically below the layer of FVL-24a, suggesting that the latter can be considered as the local base of the Beru Member.

FVL-24a-c are located along the depositional axis of the WSB but near the southern margin of this basin, and not in the Sengkang Anticline. This makes any chronostratigraphic correlation with the base of the Beru Member (Subunit A) in sections I-III uncertain. The fossiliferous interval might be older or younger than the lowest marine-terrestrial transition (= lower boundary of the Beru Member) as developed in the Sengkang Anticline sections. The ESR dating results suggest, however, a similar age for the fossiliferous layers near Lonrong and Subunit A of the Beru Member as exposed in the west flank of the Sengkang Anticline.

The three successive fossiliferous intervals developed near Lonrong provide important information concerning the size variability of *Celebochoerus heekereni* through a relatively short interval of time. The three fossiliferous levels south of Lonrong are located on the eastern slope of a N-S trending eroded ridge. On the slope from FVL-24c stratigraphically downward a poorly exposed section of 14 m could be logged connecting the three fossiliferous intervals encountered near Lonrong (section VIII, Encl. C). FVL-24a is situated at the valley bottom of a small stream, in which a poorly sorted, fossiliferous pebbly sandstone layer on top of well sorted fine-grained sandstones crop out. Most abundant in the fossiliferous sandstone layer are dental elements of Elasmobranchii (65 dental elements of both sharks and eagle-rays) and teeth of a crocodile species with narrow, slightly curved teeth, similar to teeth of *Gavialis* (9 specimens). The layer also yielded 8 rolled molar fragments of *"Elephas" celebensis* and 11 isolated molars of *C. heekereni*. *Geochelone* and a Trionychidae sp. are both represented by a single carapace fragment. Wood fragments with Teredinidae borings can also be found in the same sandstone layer. Several meters above this fossiliferous sandstone layer fine-grained silty claystones crop out. Several fossils of *Celebochoerus* and one molar fragment of *"E." celebensis* and one of *S. sompoensis* were collected on the surface of this fine-grained interval (FVL-24b). This interval is c. 10 m thick, and is overlain by an alternation of fluvial sandstones and claystones. FVL-24c represents a rich fossiliferous level in this upper interval.

At FVL-24c a trench of 1 × 7 m was dug out to a depth of 1 m. In the bottom of the trench a core was taken to a depth of 5 m, in order to collect unweathered pollen samples (the samples turned out barren). Fig. 43 shows the SW-NE profile of the excavated trench. At the base of the trench gray clays were found (layer III), overlain by a fine-grained, 30-50 cm thick gray/orange-brown mottled sandstone layer(layer II). This sandstone layer is erosive at the base with a pebbly lag deposit. The upper part of this sand layer appears to have been partly eroded and is overlain by a darkbrown coloured, organic silty clay (layer I). The erosive contact between layers I and II is formed by an undulous surface, which cuts down into the gray clays of layer III as well in SW direction. Layer II only yielded a small, heavily weathered tusk fragment. All of the remaining in situ fossils at FVL-24c were collected from layer I, including a few poorly preserved wood fragments. As far as preserved layer I is 35-70 cm thick. In the upper part an irregular concretionary layer of yellow calcareous claystone is developed, from which also a few poorly preserved fossils were recovered. Laterally of this concretionary horizon towards the NE a 20 cm thick well-cemented pebbly sandstone with an erosive base is developed.

Identifiable in situ fossils comprise the following taxa in descending order of abundance: *C. heekereni* (148 specimens, amongst them several skull fragments); crocodile remains (12 specimens, comprising teeth of a short conical type, dermal scutes, limb bones and skull fragments); pygmy proboscidean (postcranial elements of either *"Elephas" celebensis* or *Stegodon sompoensis*, 13 specimens); *Geochelone* carapace/plastron fragments and limb bones (6 specimens); Trionychidae (4 carapace fragments) and *"E." celebensis* (1 molar fragment). One molar fragment attributable to *S. sompoensis* was found at the same spot on the surface and most likely originates from layer I, like the bulk of the in situ fossils excavated at FVL-24c. All surface finds were recovered within a radius of 30 m from the excavation site. FVL-24c did not yield marine vertebrates nor molluscs. The fossil contents at FVL-24a, in combination with the sedimentological data (section VIII), indicate that the fossiliferous layer was deposited somewhere near the transition between a marine and terrestrial environment, such as a mangrove swamp or intertidal channel. The fossiliferous layer I at FVL-24c must have been deposited in a more landinward located deltaic environment, such as an abandoned distributary or a supratidal swamp or lake.

FVL-5: Lakibong — The second excavation was carried out at FVL-5, situated in the LT, c. 500 m S of the Lakibong River (Encl. B). The fossiliferous layer occurred in a horizontally bedded silty clay layer pertaining to the Beru Member. The site was discovered in 1990 during a survey of the area and has yielded in total 534 determinable surface-collected fossils and 371 identifiable excavated fossils, all representing terrestrial vertebrates.

The fossiliferous layer crops out near the northern margin of a flat NW-SE elongated ridge, which toward the north bends down into a cliff eroded by a tributary stream

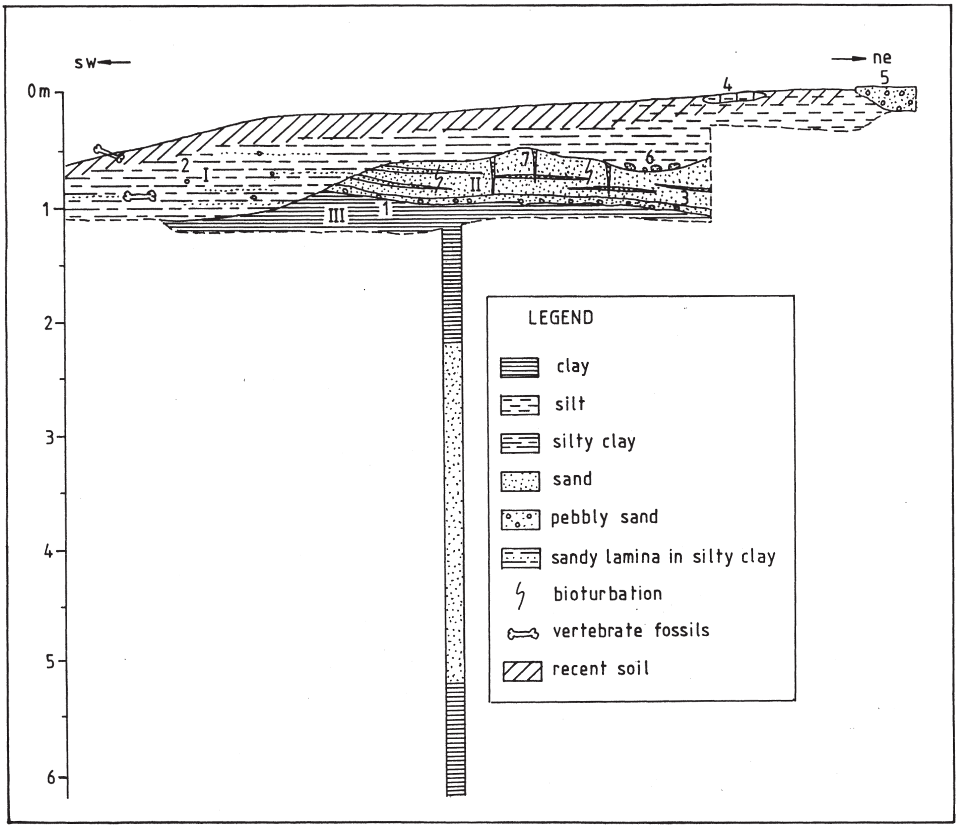


Fig. 43. Profile of the excavation at Lonrong (FVL-24c) and lithology of a 5 m deep core. In the excavation three main units can be distinguished. Layer I: brown silty clay with sandy streaks. All in situ fossils at FVL-24c originate from this layer. Layer II: gray-orange brown mottled sand. Layer III: gray clay, locally with orange-brown mottles. Explanation of the lettercodes: 1 = erosional contact between layers III and II; 2 = main concentration of vertebrate fossils; 3 = location of palaeomagnetic sample taken in fine-grained sandstone; 4 = calcareous concretions; 5 = pebbly sandstone with erosive base; 6 = erosional contact between layers II and I; eroded fragments of layer II are incorporated locally near the base of Layer I; 7 = vertical cracks filled with brown silty clay.

of the Lakibong River. A short section could be measured in this cliff upwards to the top of the ridge (section V, Encl. C). The base of the section occurs at an elevation of 40 m above sea level. The layers have a horizontal orientation. The lower 11.5 m of the exposed sequence consists of an alternation of conglomerates, pebbly sandstones and sandstones, with a few lenses of silty claystone. The maximum size of the pebbles is 3 cm near the base, decreasing to granule size at the top of the interval. Tabular cross-bedding was observed in one layer, which indicated a northwestern palaeocurrent direction. However, parallel and low-angle laminations are the dominant structures in the sandstones. The pebbles consist of volcanic rock and chert. Fossil wood fragments in the sandstones are surrounded by iron oxide halo's, indicating that they are not reworked from older formations. Irregular carbonate cemented bands are developed at several levels. This interval of coarse clastics is overlain by 4.5 m of gray claystone. The claystone is characterized by caliche concretions and orange-brown mottles. It is in the top of this claystone that fossil vertebrate remains are concentrated in a c. 30 cm thick interval, which appears to be more silty than the underlying clays.

The fossil rich clay level can be laterally traced over a distance of c. 25 m. Two pits were dug 10 m apart at the same level. One pit measured 3.5 × 9 m and the other 4 × 5 m, both c. 1 m deep. In general the fossils are poorly preserved due to breakage prior to fossilization. *Celebochoerus* skulls were found squeezed as a result of clay compaction. Also dissolution and caliche formation (Table 3, sample S-25) has severely damaged some of the specimens. In any case, a large fossil sample could be obtained from one level. 88% of the in situ assemblage consists of identifiable *Celebochoerus* fossils. Other taxa from the excavation comprise, in descending order of abundance: crocodile (7%), *Geochelone* (3%), pygmy proboscidean postcranial remains (1%) and *"E." celebensis* (1%). Poorly preserved freshwater gastropods (*Viviparus*) were also recovered from the claystone. A few postcranial elements of pygmy elephantoids and one molar fragment of *"E." celebensis* originate from a 30 cm thick yellow sandy siltstone, which overlies the gray silty claystone from which the bulk of the fossils at FVL-5 originated. This yellow sandstone is in turn overlain by a 15 cm thick fine-grained sandstone with a dark-red colouration, indicating soil-formation. The transitions between the various layers are gradual. Though *S. sompoensis* molar fragments were not found in situ, this taxon is represented by 5 dental fragments, which were found on the surface of the plateau and must have been derived either from the main fossiliferous level or from the overlying sandy interval. The fossiliferous part of the sequence can be interpreted as representing the marginal facies of a lake or swamp.

ESR dating on enamel of a *"E." celebensis* molar fragment gave a rather young date of 0.5 Ma ± 20%, as opposed to a date of 2.1 Ma ± 20% for samples from FVL-24c and FVL-11. Based on the dominance of coarse-grained fluvial facies types in the sequence exposed at FVL-5, in combination with this relatively young age, the fossiliferous layer is interpreted as belonging to Subunit B of the Beru Member.

FVL-6: Lakibong — 250 m NE of FVL-5, and separated from it by the small valley in which section V was measured, another fossil accumulation had been discovered already in 1986 by F. Aziz. So far, only vertebrate fossils have been collected at the surface here (FVL-6). In 1990, fossils were collected from a small surface area of c. 100 m^2, and the locality seems suitable for a future excavation. A coarse sandy matrix was attached to some of the fossils, but dense vegetation prevented the study of the geological context. FVL-6 occurs at an elevation some 10-20 m higher than FVL-5, and might be stratigraphically slightly higher in the sequence.

Some of the skeletal and dental elements of *C. heekereni* found at FVL-6 indicate the presence of individuals with the largest bodysize of this species observed amongst fossils from the Beru Member. Apart of *C. heekereni* fossils, 3 postcranial elements of pygmy elephantoids and a molar and tusk fragment of *"E." celebensis* originate from this locality.

FVL-25a-b: Sompe (old spelling: Sompoh or Sompo) — Another important locality where vertebrate remains have been collected is situated 800 m E of the village of

Sompe (FVL-25). This is one of the localities discovered originally by van Heekeren in 1947. Most of the fossil material described by Hooijer (1948a,b, 1949, 1953a,b,c, 1954a,b,c,e,f, 1955b) originates from this site. It is the type locality of *Celebochoerus heekereni*, *Stegodon sompoensis* and *"Elephas" [Archidiskodon] celebensis*. The locality is situated on the western flank of the Sengkang Anticline at a place where the layers dip 15° W; c. 20 m of section could be measured (section IV, Encl. C).

Eastward of section IV, stratigraphically lower in the sequence, only fine-grained shallow marine sandstones and silty claystones containing plant remains and rare marine molluscs have been observed. These have been included in the Samaoling Member. The lower 4.30 m of section IV consist of gray and brown claystones with a layer of yellow clayey calcareous concretions near the top. *Chlamys* shells can be found inside these concretions. The claystone is overlain by two stacked fining upward sandstone layers with slightly erosive bases. These fluvial sandstone layers represent the base of the Beru Member. Numerous vertebrate fossils, mostly rather fragmented, originate from these sandstones (FVL-25a). The sandstone contains abundant volcanic components (sample S-41, Table 2), but also a few conspicuous detrital lateritic fragments, which were not encountered in other samples. Interestingly, Hooijer (1949) mentions that the matrix of one of the fossils reportedly originating from Sompe consists of detrital grains of lateritic sandstone. This suggests that this is indeed the same level where van Heekeren collected fossils in the nineteenforties. Pebbles occurring in the sandstones consist mostly of altered volcanic rocks besides a few chert pebbles. Besides vertebrate fossils, several thick-walled *Polymesoda* shells were found in the sandstones. These bivalves are indicative for brackish water conditions (K. Mano, pers. comm.).

The vertebrate-bearing sandstone interval is overlain by a 12 m thick interval of claystones and sandy siltstones. Several horizons in this interval contain abundant echinoid fragments and reworked shells (*Chlamys* and *Ostrea*). The highest level of this interval also yielded several in situ *Celebochoerus* fossils (FVL-25b), some with encrustations of bryozoa. Thus, there are at least two vertebrate-bearing levels exposed east of Sompe. The sequence of section IV can be interpreted as representing a distributary channel prograding over shallow marine deltafront deposits. The absence of sand/mud couplets in the terrestrial vertebrate-bearing layer and its poor sorting suggest an upper deltaic, fluvially controlled environment. After abandonment of the distributary and/or continuing subsidence the sea invaded the delta locally and a lagoonal or tidal flat environment was established at the same spot.

At FVL-25a five vertebrate fossils were found in situ in the basal sandstones of the Beru Member. The bulk of the fossils (127 identifiable specimens) were found scattered over the slightly sloping surface below the sandstone interval. Many of the surface collected fossils have still some coarse-grained sandstone matrix attached and they can only originate from the basal sandstone layers of the Beru Member. Many fossils are rather rolled and fragmented due to transport. Our collection from FVL-25a contains 11 molar fragments and 3 tusk fragments attributable to *"E." celebensis*. Most of the collected fossils, however, can be attributed to *Celebochoerus* (104 specimens, mostly isolated dental elements). Furthermore 7 specimens represent crocodile remains (teeth, scutes and coprolites), 7 are carapace fragments of Trionychidae and there are also 3 teeth of Elasmobranchii. The latter may originate from the marine siltstones below or above the sandstone layer. One rather poorly preserved plastron fragment can be attributed to *Geochelone*. The Trionychidae carapace fragments are rather small and do not allow identification at the species level.

FVL-3/4/4a: Sare Batue — Three fossil localities are located close to one another at distances between 300 and 700 m S of the village of Sare Batue (FVL-3, FVL-4 and FVL-4a) in the southern part of the LT. The fossil bearing layer at these three localities constitutes a characteristic conglomeratic facies, and forms a local marker bed. The layer is rich in fossil vertebrate remains, most of them rather fragmented and some rounded due to transport. Apart of vertebrate remains also rolled marine shells (*Ostrea* and *Chlamys*) can be encountered in this layer. Fossils from the three localities represent the same stratigraphic level. The layers show a consistent dip of 7-9° ENE in the entire area south of Sare Batue, and the marker bed crops out at an elevation between 55 and 70 m (the most northeastern FVL-4a having the lowest elevation). The tilting is locally developed and may be explained by the proximity of the uplifted Puncakoro Block towards the south.

One short section has been measured at FVL-3 (section IX, Encl. C). The lower part of section IX shows gray/orange brown mottled claystones and silty claystones with a red-brown coloured palaeosol horizon at the base of the section. This claystone interval is overlain by 2.7 m of poorly consolidated coarse sands intercalated with muddrapes, marking tidal influence. This interval is in turn overlain by the conglomeratic markerbed, which only varies in thickness between 20 and 40 cm. The top of the section consists again of gray/brown mottled claystone.

Roughly half of the small pebbles of the marker bed consist of calcareous mud clasts. These calcareous pebbles are thought to represent concretionary intraclasts derived from erosion of intertidal lagoonal mudstones (see previous part of this chapter concerning the petrography). The maximum clast size is not greater than 3 cm. The remaining part of the pebbles consists of altered volcanics and chert. The base of the conglomerate is flat and the thickness does not change much laterally. The sandy matrix of the conglomerate shows a similar composition as other sandstones of the Beru Member, but is distinct from the calcareous conglomerates of the Tanrung Formation (Table 2). The conglomerate is locally strongly cemented but at other places only loosely consolidated.

At FVL-4 and 4a, both c. 250 m apart, 9 *Celebochoerus* fossils were recovered from the conglomerate, amongst them a rather eroded skull. At FVL-3 a large scapula of *Geochelone atlas*, a cervical vertebra of a pygmy proboscidean and 3 identifiable *Celebochoerus* fossils came out of the conglomerate. Besides these in situ findings, 58 identifiable fossils were recovered from the area as surface finds, some of which might originate from the under and overlying clays and sands. Others, however, with calcareous clasts still attached, clearly originate from the marker bed. Amongst the fossils collected on the surface there are some tusk fragments and four molar fragments of a *Stegodon* species, that could not be attributed with certainty to *S. sompoensis*. Other surface finds from Sare Batue include molar and tusk fragments of *"E." celebensis*, postcranial elements of pygmy elephantoids and crocodile remains, including some coprolites. A very large proximal humerus of *G. atlas* was collected in the same area by F. Aziz in 1986 (GRDC No. STL/010186-1). In its large dimensions this humerus would fit quite well with the scapula found in situ in the conglomerate at FVL-3 (GRDC No. SB-3195). Also an almost complete *Geochelone atlas* plastron (GRDC No. SCL/030186-2) was excavated by Aziz in 1986 from a medium to fine-grained sandstone layer in the same area, possibly the sandstone layer below the marker bed.

The fossiliferous layer of FVL-3/4 can be stratigraphically placed at the top of Subunit A, as shown on Encl. B. West of FVL-3 and FVL-4 marine mollusc fragments were surface collected and isolated outcrops showed fine-grained clastics, some with sand/mud couplets, indicating tidal influence.

Other fossil vertebrate localities of the Beru Member — The richest fossil localities in the Beru Member have been described in some detail above. There remain a number of other localities which did not contain large quantities of fossils, but which have yielded some rare and important fossil specimens such as pygmy elephantoid skulls. These FVL will be briefly treated below.

Two localities showed evidence for marine influences. One is FVL-28 at Bulu Barere, which is the only Beru Member locality in the ESB. The other is FVL-30 at Padali on the west side of the WSB. Correlations between these localities and the sections in the Sengkang Anticline and Lakibong Triangle are uncertain. At both localities encrustations of vertebrate fossils with shallow marine molluscs (*Ostrea*) and crustaceans (*Balanus*) indicate that the fossils were submerged in the sea either before or after fossilization. At both localities outcrop conditions are extremely poor and in the surrounding fields only loose blocks of the original sedimentary rocks can be found. At Bulu Barere an agent selecting for small size seems to have acted on the concentration of fossils. Most fossils represent highly fragmented and often rolled dental elements of *C. heekereni* and a few small-sized postcranial elements like phalanges of that same species (33 specimens). Next in abundance are isolated crocodilian teeth (26 specimens pertaining to two different types, one with narrow curved teeth and one with short conical teeth), Elasmobranchii teeth (7 specimens) and one very worn dP2 fragment attributable to *S. sompoensis*. In addition there are various small and unidentifiable bone fragments. At FVL-30 near Padali also larger fossils occur. Here 19 *Celebochoerus* fossils were collected. In addition, there are a lower M3, two molar lamella fragments and two tusk fragments, either attributable to *S. sompoensis* or *S.* cf. *sompoensis*, and one molar fragment belonging to *"E." celebensis*. Like at Bulu Barere, some fossils are encrusted with *Balanus*, *Ostrea*, or *Chlamys*.

Several FVL can be stratigraphically placed at the base of the Beru Member in the west dipping west flank of the Sengkang Anticline. These are thought to be roughly of similar age as FVL-25. One is FVL-1a, which represents the lowest fluvial sandstone layer in section I near the village of Lepangen. This sandstone layer is 4 m thick and dips 65 W. A juvenile mandible of *"E." celebensis* was found embedded in sandstone.

The next one is FVL-23, which represents the basal Beru Member sandstone in section III near the village Ciangkange. FVL-26 is situated near the village Sabbang Baru 3 km N of Sompe, where a sandstone layer overlies a 60 cm thick beach-rock layer consisting of reworked shell fragments.

FVL-1b represents a 12 m thick sandstone interval 25 m above the base of the Beru Member in section I and 21 m above the layer of FVL-1a. A second juvenile mandible of *"E." celebensis* was found at FVL-1b in a block of sandstone.

FVL-11 is not a single layer but represents an interval comprising the upper 90 m of section II east of the Bulu Cepo Fault in the west dipping flank of the anticline. Most of the 51 identifiable fossils from this interval are surface finds. Aziz (1990) reported an almost complete sinistral mandible with M3 of *S. sompoensis* from the pebbly sandstone halfway this interval (Encl. C). A sinistral *C. heekereni* mandible with canine was found from the sandstone level indicated with '11' in section II. The sequence comprises an alternation of fluvial and fluvio-tidal deposits. Apart from vertebrate fossils also calcified wood fragments were encountered at several levels (sample S-63, Table 3). Identifiable vertebrate fossils from this interval are: *C. heekereni* (44 specimens), *Geochelone* (2 carapace fragments), crocodile (1 scute), Trionychidae (1 carapace fragment), *"E." celebensis* (1 molar fragment, which was used for ESR dating), *S. sompoensis* (1 sinistral mandible with M2 and M3 fragment originating from the same pebbly sandstone as the mandible found by Aziz as indicated by the matrix of this fossil).

FVL-22 is situated near the village of Ciangkange and is represented by a 4.5 m thick medium to coarse-grained, parallel laminated sandstone layer in section III, stratigraphically 58 m above FVL-23. The layer crops out at an elevation of c. 80 m above sea level and dips 45 NW. Only a few fossils were surface collected at this level by our team, but it is quite possible that the *"E." celebensis* skull fragment described by Hooijer (1972b), which is stated to come from an elevation of 80-85 m along the same road, originates from this level.

FVL-9 represents an outcrop on the concave east bank of the Walanae River near the village of Batuasange. A complete dP^4 of *S. sompoensis* was found in a consolidated, pebbly sandstone layer overlying an interval exhibiting stacked tidal bundle sequences (section X, Fig. 10). The pebbly sandstone layer has a scouring base and the maximum clast diameter is 3.5 cm at its base. Pebbles consist of altered volcanic pebbles and chert. The layers dip around 5° N. They are being eroded by the Walanae River and are exposed from the low-water level upwards. These observations indicate that these strata belong to the Beru Member of the Walanae Formation. At the same spot 2 layers of coarse gravel, belonging to the unit here designated as Old Alluvial Fan Gravels, are locally unconformably overlying these Beru Member strata. The 1-1.2 m thick consolidated gravel layers, which contain clasts of intrusive rocks and erosion products of the Walanae Formation, are attached to the sloping concave bank of the river. The bases of these two layers are at elevations of 3 and 7 m, respectively, above the low water level of the Walanae River.

FVL-14 is located 1 km NW of Paroto and represents a small rounded hill north of the road Cabenge-Paroto, with a maximum elevation of around 55 m above sea-level. The upper part of the hill is covered with loose gravel, which is weathered from consolidated conglomerates beneath. These have a subhorizontal oriented beddingplane. The average clast diameter of the 10 largest clasts is 7.2 cm, and the composition is similar to that of the conglomeratic levels excavated by van Heekeren near Beru. A *Celebochoerus* skull (Coll. GRDC No. PR-3145) was found on the slope of the hill with some pebbly sandstone matrix still attached. The conglomerate has been included in Subunit B of the Beru Member. Towards the southeast along the road to Paroto and lower in the Beru Member sequence, tidally influenced sandstones with mud-drapes crop out, which have been included in subunit A of the Beru Member (Encl. B).

Towards the northeast, the hills are bordered by the alluvial plain of the Cipeë River. At the southwestern foot of the same hill a very poorly sorted colluvium covers the older strata. It is of the type encountered at FVL-21 (see below). It is a mixture of unconsolidated sandy mud with isolated pebbles and small rounded fossil fragments. The colluvial deposit yielded several small rounded fossil fragments, presumably reworked, and a molar fragment of *Anoa*.

FVL-2 is located 500 m SE of the village of Palangiseng. It has only yielded one in situ fossil, which happens to be a *S. sompoensis* premaxilla with part of the left orbital. The conglomeratic level from which this skull fragment originated is indicated in section VII with '2' (Encl. C). The bedding plane of the layers is subhorizontal. At the base of the 34.5 m long section we find a 4 m thick interval of tidally influenced bundle sequences (Subunit A of the Beru Member). The upper 17 m of the section are dominated by pebbly sandstones and conglomerates (Subunit B of the Beru Member). The maximum clast diameter varies between 3 and 8 cm.

FVL-7 was discovered in 1985 by Aziz. He collected an almost complete skull of *"Elephas" celebensis* near the summit of a hill, located half a kilometer north of FVL-6 on the opposite side of the Lakibong River. Pebbly sandstones and sandstones crop out on top of this hill. The skull originates from a pebbly sandstone layer at approximately the same elevation as locality 6 (65-70 m above sea level).

FVL-19 is stratigraphically the lowest one of the three fossil localities near Marale. The elevation is 50 m above sea-level in an outcrop a few meters above the Cipeë River alluvial plain. The bedding plain of the Beru Member is again subhorizontal here. The exposed lithology consists of a several meters thick interval of well consolidated pebbly sandstones with some orthoconglomerate lenses, the latter with a maximum average clast diameter of 6.8 cm. The only interesting vertebrate remains encountered here are two distal femur fragments of *Geochelone*, with the pebbly matrix still attached to the fossils.

FVL-15 is located 250 m WSW of FVL-19, and at an elevation c. 10 m higher in the sequence. Some well cemented fluvial sandstone layers crop out in a poorly exposed field. The most interesting finding at this locality is a sinistral metacarp IV of *Celebochoerus*, which is relatively shortened compared to all other *Celebochoerus* metapodials from the Beru Member. A *Celebochoerus* skull collected by Aziz in 1985 originates from the same locality, as well as a complete upper M^2 of *"E." celebensis*.

FVL-10 is located between Bulu Cepo and the village Pajalela. In 1989 a skull of *S. sompoensis* (BC-3050) was recovered from a coarse sandstone interval cropping out between the Cipeë River in the north and the road Paroto-Tetewatu in the south at an elevation of between 55 and 60 m.

FVL-13 is located around 300 m E of FVL-10 at about the same elevation and 300 m W of the BCF. An interval of poorly consolidated sandstones and pebbly sandstones is overlying at least 10 m of silty clay, with a subhorizontal bedding plane. Pebbles have a maximum clast diameter of 4 cm and are made up of altered volcanic clasts and chert. Irregular calcite cemented bands occur in the coarse clastics and small fossil vertebrate fragments and pieces of fossilized wood can be found in the clastics. Below the pebbly sandstones several fossils were collected on the surface with a pebbly sandstone matrix still attached. These include two fragments of presumably the same upper molar, which can be attributed to *Stegodon* cf. *sompoensis*, and 3 carapace fragments of *Geochelone*, which could be fitted together. Other surface findings without any sign of matrix, are a proximal femur fragment of a pygmy proboscidean and several dental elements of *Celebochoerus*.

FVL-16 and FVL-17 represent two small conical hills with outcrops of pebbly sandstones and conglomerates near Marale. Siltstone layers are intercalated locally in the coarse clastics. Several small rounded hills all near the 75 m contour form the highest points on the elongated E-W trending ridge here. These hills are covered with loose weathered gravels, but locally outcrops of well cemented sandstones and conglomerates with a maximum clast diameter of 10 cm can be observed in erosional gullies. Apart of volcanic rock and chert pebbles also a few silicified limestone pebbles derived from the Tonasa Formation were found in these conglomerates. The bedding is subhorizontal. A *S. sompoensis* mandible (MPC no. C3/2/79) and skull fragment (MPC no. C3/27-A/251286), both partly covered with a pebbly sandstone matrix and kept in the Museum of Prehistory at Calio, were collected from these highest conglomerate levels near Marale (FVL-17). In the MPC is also a rather rounded molar fragment of a large-sized *Stegodon* species (MPC no. C3/27/86). This molar fragment is figured in Bartstra et al. (1994: fig. 3). A *Celebochoerus* frontal skull fragment (GRDC no. Ma-3197) was picked up from the surface south of FVL-16 at an elevation of c. 60 m.

FVL-12 corresponds with the highest elevation west of the BCF in the LT. The locality is situated just 150 m W of the BCF at an elevation of 95-100 m above sea-level and just north of the road Paroto-Tetewatu. It is thought to represent the youngest level preserved in the LT. The locality has yielded only a few surface finds, notably an humerus diaphysis of *Geochelone* and, more interestingly, a poorly preserved *Stegodon* tusk fragment with a diameter of 12 cm. This tusk represents one of the few indications for the occurrence of a large-sized *Stegodon* in the highest levels of Subunit B of the Beru Member.

FVL-27 is the northernmost locality of the Sengkang Anticline near the village of Celeko (old spelling: Tjeleko). 2 km N of Celeko the Beru Member disappears below the floodplain deposits of the Walanae River (Encl. A). Van Heekeren collected several interesting fossils near Celeko, which have been described by Hooijer (1954e). Amongst them is a sinistral mandible of *"E." celebensis* with an alveole for a lower tusk (Hooijer, 1954e: pl. XXI, fig. 4; pl. XXII, fig. 2). Also mentioned are a scapula fragment and xiphiplastral cornu attributed to *Geochelone atlas* (Hooijer, 1954c) and a posterior fragment of a dextral upper molar, which was originally determined as an M^3 of *S. sompoensis* (Hooijer, 1964a), but which was later interpreted as an M^1 of *Stegodon* cf. *trigonocephalus* (Hooijer, 1972b). Here it is concluded that the molar represents an M^3 and falls within the size range of *S. sompoensis*. When visiting the surroundings of Celeko, we only found one *Polymesoda* shell in the poorly exposed farmlands near Celeko.

Fossil vertebrate localities younger than the Beru Member

FVL-29: Tanrung River — The Tanrung Formation cropping out along the Tanrung River, has a thickness of at least 7 m (either the uneroded top or base are not exposed in single outcrops). Its top surface is in erosional contact with overlying alluvial deposits. The formation probably represents a relatively short interval of time as compared to the 100 or more meters thick Beru Member of the Walanae Formation. The

Tanrung Formation is younger than the Beru Member. The various fossil localities along the Tanrung River have been indicated together as FVL-29 on Encl. A. A description of the Tanrung Formation has been given earlier (see also Figs. 37-38). Fossils were first discovered by our team in 1990, and during the two successive years more material has been collected, most of it belonging to medium- or large-sized elephantoids. In situ findings from the conglomeratic Tanrung Formation include a juvenile maxilla fragment with the worn out dextral and sinistral dP^4 remnants, a complete sinistral M^1 and the anterior portion of the dextral M^1, besides two tusk fragments, all of the same individual of a large-sized *Stegodon* species. These *Stegodon* molars are distinct from *S. trigonocephalus* and from *S. sompoensis*, and are attributed to *Stegodon* sp. B (van den Bergh et al., 1992; this thesis). Surface collected postcranial elements of large-sized elephantoids are represented by two distal scapula fragment, a proximal humerus fragment, a proximal tibia and three vertebrae thoracales, originating from an erosional gully eroding a pocket of loose, reworked calcareous gravel consisting of erosional products of the heavily cemented Tanrung Formation on the south bank of the Tanrung River (Fig. 37). Fossil remains found semi-in situ in the Tanrung Formation (in eroded conglomerate blocks clearly derived from the Tanrung Formation), include three *Stegodon* tusk fragments with a diameter of c. 12 cm and a dextral mandibular ramus with the posterior part of an M_3. Rounded and possibly reworked fossils occurring in situ in the Tanrung Formation comprise several canines and molar fragments of *Celebochoerus*, a large-sized *Stegodon* molar lamella fragment and several shark teeth. Besides the above mentioned fossils, which were certainly derived from the Tanrung Formation (though some of the rounded specimens might actually have been reworked from older deposits), some isolated fossils were surface collected in the Tanrung River bed. These are two large sized *Elephas* metacarpals, two *Anoa* molar fragments, three rounded *Celebochoerus* canine fragments, a humerus fragment of a small suid, and, most interestingly, a molar fragment of an advanced, high-crowned *Elephas* species. Except for the *Anoa* molars these specimens are all heavily fossilized.

FVL-21: Ciangkange — This locality represents a colluvial deposit along the road Cabenge-Pampanua near the village of Ciangkange. A loose, poorly sorted mixture of clastic material rests unconformably on steeply dipping layers of the Walanae Formation at this place. Though various colluvial patches exist throughout the hilly area of the Sengkang Anticline, only the one of FVL-21 will be treated here because it has yielded more than 10 *Anoa* molar fragments, all fractured and in a rather poor state of preservation. Caliche concretions have grown around some of these fossils and also in cracks. There is also one distal tibia fragment of a bovid with the size of *Anoa*. Likewise, this specimen is not heavily fossilized and severely cracked and damaged by caliche formation. Of importance is the fact that, though damaged, the specimens are not rounded by transport, unlike other small fossil fragments found at FVL-21, such as fragments of *Celebochoerus* molars and enamel fragments of proboscidean molars. The latter are clearly reworked from the Beru Member as they are very fragmentary though more heavily fossilized than the *Anoa* fossils and because they are not covered by caliche concretions. The *Anoa* remains are thought to be the only autochthonous fossils occurring in this colluvial deposit. Nowhere in the Beru Member has *Anoa* material been found in situ. Only 200 m S of FVL-14 in similar unconsolidated and poorly sorted colluvial deposits as developed at FVL-21, one *Anoa* molar was found on the surface, which had a similar type of fossilization as the *Anoa* fossils from FVL-21.

FVL-31: Lagosi — This locality represents a small outcrop of consolidated conglomerate on the westbank of the Walanae River near Lagosi in the ESB (Encl. A). The conglomerate contains mainly volcanic clasts and some chert and resembles those of the Beru Member. However, a single isolated fossil molar, which could be attributed to *Anoa* sp., was incorporated in the conglomerate. This indicates the deposit to be younger than the Beru Member as developed in the WSB. The eroded conglomerate was found to be covered by 'modern' alluvium.

Placing the various FVL in chronological order

One of the aims of this study is to see if small evolutionary changes within the various taxa can be observed during the time sequence in which they occur (for example size reduction of elephantoids trough time). For this purpose it is necessary to place the various FVL in a chronological order. In order to do so we can use the lithostratigraphic correlations discussed earlier (Encl. C). As follows from the sections I-III, the Beru Member is 100-130 m thick in the west flank of the Sengkang Anticline. The structural continuity within the Sengkang Anticline allows to make rough correlations between the various FVL occurring in this area. For example the FVL occurring in the lowermost, fully fluviatile layers of the Beru Member in the various sections can be considered to be the oldest. However, deltaic sequences are always more or less time-transgressive. In the case of the deltaic complex represented by the Samaoling and Beru Members, the coastal sediments are likely to have been reworked various times by marine invasions. As discussed above, the overall northward delta progradation was probably intermittent under the constraints of limited sediment supply and subsidence. The oldest fluviatile sediments that were deposited may have been fully reworked at one place but preserved at an other, so that more precise time correlations between the various sections based on lithostratigraphic correlations are uncertain.

In a general way we can conclude that the following FVL, all stratigraphically occurring just above the Samaoling/Beru Member transition, represent the oldest group: FVL-1, FVL-23, FVL-25a-b and FVL-26. Their age is c. 2.5 Ma, based on palaeomagnetic and micropalaeontological evidence.

Probably younger than any of the foregoing FVL are those situated stratigraphically various tens of meters above the base of the Beru Member (FVL-11 and FVL-22).

Time correlation between the Sengkang Anticline sections and the localities situated in the LT are more problematic. The sedimentary column in the LT can be estimated to be c. 80 m thick, which is the difference in elevation between the highest point near Bulu Cepo and the lowest point on the bank of the Walanae River. However, no continuous sections could be measured in this area and the longest section (section VII) measures only 34.5 m. Besides, there may be one or more depositional hiatuses developed in this sequence. As has been argued before, the uppermost, conglomerate-dominated part of the sequence in the LT (= Subunit B of the Beru Member) is probably younger than the entire sequence constituting the west flank of the

Sengkang Anticline (Subunit A of the Beru Member). Therefore, the FVL occurring in Subunit B are considered younger than any of the localities developed in the west flank of the Sengkang Anticline. Within the LT the older FVL are those occurring in the lower topographic reaches close to the Walanae River (FVL-9, FVL-3 and FVL-4). However, these FVL may still overlap in time with the localities in the west flank of the Sengkang Anticline. Younger are those occurring in the middle topographic reaches of the LT and corresponding with the lower part of Subunit B of the Beru Member (FVL-18 (lacking identifiable fossils), FVL-14, FVL-5, FVL-6, FVL-7 and FVL-2). Finally, the group of youngest localities of the Beru Member, are those occurring in conglomeratic facies in the highest topographic reaches of the LT, close to the BCF. These are FVL-20 (lacking identifiable fossils), FVL-19, FVL-10, FVL-15, FVL-16, FVL-17, FVL-12 and FVL-13. They have an estimated Early Pleistocene, perhaps even Middle Pleistocene age.

Some localities occurring in facies comparable to that of the Beru Member, but in different structural blocks than the Sengkang Anticline or LT, are FVL-24a-c, FVL-28 and FVL-30. These cannot be fitted with any certainty in the crude chronological sequence depicted above, with the exception of FVL-24a-c. ESR dating on a molar fragment from FVL-24c suggests an age similar to that of FVL-11 in the Sengkang Anticline.

The combined FVL occurring in the Tanrung Formation, indicated with FVL-29 are younger than any of the FVL occurring in strata pertaining to the Beru Member. The Tanrung Formation unconformably overlies the Walanae Formation in the ESB and is estimated to have a Middle Pleistocene age. Much younger is FVL-21 near Ciangkange, developed in colluvial sediments with an estimated age of Late Pleistocene or Holocene.

Three successive faunas

With the litho- and chronostratigraphic framework as a basis, the various FVL have been placed roughly in a chronological order in the foregoing paragraph. In Table 5 the total number of vertebrate fossils that could be attributed to one of the taxa distinguished, are listed for each FVL, the latter which are placed in the crude chronological order depicted above. In Table 5 the in situ and surface collected specimens are separated for each FVL. As follows from this table, the most marked difference in faunal contents is between the various FVL occurring in the Beru Member on the one hand and FVL-29 occurring in the Tanrung Formation on the other hand. Most of the Beru Member FVL yielded remains of at least one pygmy elephantoid species, except for FVL-22, 23, 14 and 19, which all have in common that they yielded only 4 identifiable fossils or less. Pygmy elephantoids were not encountered in FVL-29. Also *Geochelone* remains were not found in the Tanrung Formation, but are present in most of the FVL of the Beru Member that yielded more than 10 identifiable specimens (except FVL-28 and FVL-30). In addition, the Tanrung Formation (FVL-29) is the only stratigraphic unit with the proven occurrence of a large-sized elephantoid.

Based on these differences, at least three successive terrestrial vertebrate faunas can be distinguished in South Sulawesi, including the highly distinctive (sub)Recent one. These three successive faunas are named here from old to young: the Walanae Fauna, the Tanrung Fauna and the sub-Recent to Recent Fauna. The correlation to the lithostratigraphic record of these successive faunas and their inferred ages are shown in Fig. 44.

Walanae Fauna — The Walanae Fauna comprises all the fossil land vertebrates derived from the Beru Member of the Walanae Formation. This assemblage of fossil species has also been recovered from single layers at FVL-24c and FVL-5 (except for Trionychidae sp. in the latter). The highest age of the Walanae Fauna lies around 2.5 Ma. This age is reasonably well constrained now, based on the combination of micropalaeontological and palaeomagnetic data presented before. However, it can not be excluded that some or all of its faunal elements were present on emerged parts of South Sulawesi prior to deposition of the Beru Member. The upper time constraints of the Walanae Fauna are less certain. Deposition of Subunit B of the Beru member, which seems to have been influenced by compressional tectonic activity during the Early Pleistocene, may even extend into the Middle Pleistocene, as is suggested by the ESR dating results from FVL-5.

Celebochoerus heekereni, *Geochelone atlas*, Trionychidae sp., *Crocodylus* sp., and *"Elephas" celebensis* have all been encountered in the basal layers of Subunit A at FVL-25a near Sompe in the westward dipping flank of the Sengkang Anticline. The genera to which the above mentioned species belong are all still present in the younger layers pertaining to Subunit B of the Beru Member. As follows from Table 5, *C. heekereni* is clearly the most frequently occurring species in the Walanae Fauna. This suid appears to have evolved towards a short-legged variety or even a distinct species during the timespan covered by the Beru Member, as is suggested by a rare finding of a morphologically distinct metapodial at FVL-15 (in Subunit B of the Beru Member). This metapodial, a sinistral metacarpal IV, is shortened compared to all other *Celebochoerus* metapodials encountered at the older localities. Shortening of metapodials is a common trend in island artiodactyla (Sondaar, 1977), and *Celebochoerus* obviously also developed shorter legs in the insular environment. The occurrence of this metapodial with clearly derived features supports the view that Subunit B of the Beru Member is indeed younger than Subunit A.

Also a large-sized *Stegodon* may originate from Subunit B deposits, though it has to be mentioned that neither the short-legged *Celebochoerus* variety nor the large-sized *Stegodon* species are represented by in situ findings.

The fossil giant tortoise from South Sulawesi was originally named *Testudo margae* (Hooijer, 1948b). Later the author considered the tortoise as identical with the giant tortoise known from the Siwaliks, *Geochelone atlas* (Hooijer, 1971), an opinion shared by Auffenberg (1974).

The leatherback turtle carapace fragments from FVL-25a (Sompe) and a few other localities correspond morphologically to the carapace fragment from Sompe figured by Hooijer (1954c: fig.5) as Trionychidae, gen. et sp. indet. All fragments are characterized by their delicately pitted surface. This excludes the genus *Trionyx*, which has a more crudely sculptured carapace surface. Possibly the fragments belong to *Pelochelys*, a genus of leatherback turtles which is still widely distributed in SE Asia and which occurs in estuarine environments (Peter Paul van Dijk, pers. comm., 1996).

The crocodile from FVL-25a has been identified as *Crocodylus* sp. (Hooijer, 1954f). Its jaw and tooth size is similar to that of the Recent *Crocodylus porosus*, but differs in

AGE	RECENT	HOLOCENE-LATE PLEISTOC.		MIDDLE TO LATE PLEISTOC.	EARLY PLEISTOC.	LATE PLIOCENE 2,5 myr
FAUNA	RECENT	SUBRECENT		TANRUNG	WALANAE	
STRATIGRAPHIC UNIT / TAXA		CAVE DEPOSITS TOALIAN SITES	ALLUVIUM / COLLUVIUM	TANRUNG FORMATION	WALANAE FORMATION SUBUNIT B BERU MEMBER	 SUBUNIT A BERU MEMBER
Geochelone atlas					+	+
Crocodylidae	+				+	+
Tryonychidae					+	+
'Elephas' celebensis					+	+
***Elephas* sp. (advanced)**				+?		
Stegodon sompoensis					+	+
***Stegodon* sp. (large-sized)**					+?	
***Stegodon* sp. B**				+		
Celebochoerus heekereni						+
Celebochoerus sp.				+	+	
Babyrousa babyrussa	+	+				
Sus celebensis	+	+	+ ◀ ? ▶	+		
Anoa quarlesi	(+)	+				
Anoa depressicornis	(+)	+				
***Anoa* sp.**			+ ◀ ? ▶	+		
Phalanger ursinus	+	+				
Phalanger celebensis	+	+				
Macaca maura	+	+				
Macrogalidia musschenbroekii	(+)	+				
Homo sapiens	+	+				
Introduced mammals:						
Hystrix javanica	+					
Paradoxurus hermaphroditus	+					
Viverra tangalunga	+					
Cervus timorensis	+					

Fig. 44. Stratigraphic occurrences of large- and medium sized, fossil and (sub)Recent terrestrial vertebrate taxa from South Sulawesi. Contents of the Toalian cave deposits are taken from Hooijer (1950) and Clason (1976), those of the Recent Fauna from Cranbrook (1987) and Whitten et al. (1985). Taxa which have been reported as fossils from the 'Toalian' Cave sites, and which are presently not found in South Sulawesi anymore, but still live in other parts of Sulawesi, have been placed between brackets. Fossil taxa of which the stratigraphic occurrence is uncertain (e.g. based solely on surface collected fossils) are indicated with question marks.

that the teeth are more closely spaced compared to the Recent species. It may represent an endemic species, which is represented in many other FVL and is characterized by short and thick, conical teeth. In addition, at FVL-24a and FVL 28 also narrow, slightly curved and weakly flattened crocodile teeth have been found, resembling those of *Gavialis*. The two crocodile types have not been separated in Table 5, because many crocodilian remains represent dermal scutes, small skull fragments and even coprolites, on which the distinction could not be made.

The occurrence of *Stegodon sompoensis* in the oldest layers of Subunit A of the Beru Member could not be proven thus far, though a lack of evidence does not necessarily mean that it was not present in the fauna of South Sulawesi during the earliest phase of the Walanae Fauna stage. *S. sompoensis* was not amongst the 14 elephantoid dental elements recovered from FVL-25 at Sompe by our team. All these specimens could be attributed to *"E." celebensis* with certainty. In addition to the 14 *"E." celebensis* specimens from Sompe collected by our team, there are 24 elephantoid dental elements that were collected by van Heekeren near Sompe. These were all described by Hooijer (Hooijer, 1949, 1953a,c, 1954e, 1955b, 1972b), but amongst this material there are only 2 specimens that could be attributed to *Stegodon* (including the badly worn and incomplete holotype of *S. sompoensis*). The remaining 22 were all determined as belonging to *"E." celebensis*. Adding our own data from Sompe, it appears that *S. sompoensis* must have been comparatively rare at the time the Sompe sandstone was deposited. If the two *Stegodon* molar fragments in the van Heekeren collection were indeed derived from the main fossiliferous level at Sompe, the scarcity of this taxon there could have been the result of environmental factors. Perhaps *S. sompoensis* was not living in the coastal environments where *"E." celebensis* obviously dwelled. *S. sompoensis* may have occupied ecological niches more landinward, which are simply not represented by layers at the Samaoling/Beru Member transition zone. However, one result that speaks against this interpretation is the occurrence of *Stegodon* remains at FVL-30 and FVL-28. These are both localities where the vertebrate-bearing layers show evidence for marine depositional influences (by means of fossils from shallow marine organisms), but which cannot be directly correlated with the long sections I-III in the westflank of the Sengkang Anticline. *S. sompoensis* dental elements are relatively rare at these localities, but less so than *"E." celebensis* dental elements (Tables 5-6).

An alternative explanation may be that *Stegodon* invaded South Sulawesi at a slightly later stage than the age of FVL-25a. In that case the *Stegodon* material from Sompe present in the van Heekeren collection must have originated from an other, younger fossiliferous layer near Sompe or even from an other locality, but subsequently became mixed with the van Heekeren material from the basal Beru Member sandstone layer at Sompe. That mixing of fossils has actually taken place is proven by an *Anoa* fossil reportedly originating from Sompe (Hooijer, 1948c), but which was certainly not derived from the same layer from which the bulk of the Sompe fossils in the van Heekeren Collection did (see below). Whatever the right interpretation, *S. sompoensis* appears slighty more frequent in the coarser fluvial layers pertaining to Subunit B than in Subunit A of the Beru Member, though it is usually more rare than *"E." celebensis* fossils. At present, the data are too scarce to draw firm conclusions other than that *S. sompoensis* constitutes an element of the Walanae Fauna.

Another important result is that large-sized *Stegodon* remains have been found only at places where the youngest layers of the Beru Member, those of Subunit B, come to the surface (FVL-17 and FVL-12). In connection with this, it has to be mentioned that Hooijer (1972b: 10) attributed a molar fragment from Sompe and one from Celeko to *S.* cf. *trigonocephalus* (the fragment from Sompe is one of the two *Stegodon* molar fragments referred to above). Both these molar fragments had been attributed first to the pygmy *S. sompoensis* (Hooijer, 1964a). At the time when Hooijer (1972b) concluded that the specimens considered should be attributed to *S.* cf. *trigonocephalus*, only very limited material of *S. sompoensis* was known at all. The only complete *S. sompoensis* molar at that time, an M_3 from Calio described in the same paper (Hooijer, 1972b: 7), had a width of only 45 mm. Because the Sompe and Celeko fragments appeared to have a greater maximum width (60 and 63 mm, respectively), they were identified as fragments of a lower and upper M1 of *S.* cf. *trigonocephalus*. Since 1972 we have collected more molar material, which can be attributed with certainty to *S. sompoensis* (see chapter 4). There are now 7 posteriorly tapering M_3s or M_3 fragments from the Beru Member, which show that the variation in width of the M_3 of *S. sompoensis* lies between 45 and 65 mm (van den Bergh et al., 1994). It appeared that Hooijer's M_3 from Calio was actually the smallest (narrowest) *S. sompoensis* M_3 known to date. Also the M3 fragments from Sompe and Celeko fall within the range of variability of *S. sompoensis*. Thus, there is no proof for the presence of a large-sized *Stegodon* at Sompe and Celeko. In conclusion it can be stated that there is no evidence that large-sized *Stegodon* remains occur in the oldest interval of the Beru Member (= in Subunit A of the Beru Member in the West flank op the Sengkang Anticline). This might suggest a second dispersal of *Stegodon* to South Sulawesi during the time when Subunit B was deposited, but in situ findings would be required to prove this.

Hooijer (1948c) also described a set of teeth (P_4-M_3), which he attributed to *Anoa depressicornis* and which were reportedly originating from Sompe. Our team did not recover *Anoa* remains from any of the Beru Member localities. At FVL-25 near Sompe we recovered all the taxa that had also been reported earlier from this locality by Hooijer, with the exception of the already mentioned *S. sompoensis* and *Anoa*. It is very unlikely, however, that *Anoa* occurs in the Beru Member. First of all, *Anoa* remains are not present amongst the hundreds of fossils excavated or collected in situ or semi-in situ from the Beru Member deposits. *Anoa* teeth have only been found in situ in subrecent colluvial deposits (FVL-21) and in a small conglomerate outcrop near Lagosi in the ESB (FVL-31), which at present is difficult to correlate with any of the other distinguished lithostratigraphic units. In addition, several isolated subfossil *Anoa* teeth were found in the bedding of the Paciro and Tanrung Rivers, but these were certainly derived from strata younger than the Walanae Formation. Hooijer (1948c) mentions that the matrix of the *Anoa* teeth from Sompe consists of 'calcite grains of irregular form and containing some grains of quartz and alkaline feldspar'. This composition does not correspond to that of the sandstones commonly occurring in the Beru Member, which have usually only a very small percentage of quartz and feldspar, if present at all, and which usually contain considerable amounts of pyroxene grains and volcanic rock fragments. The matrix described by Hooijer agrees better with the caliche matrix encroaching *Anoa* fossils that were collected from colluvial deposits near Ciangkange (e.g. sample S-60, Table 3). Colluvial deposits have not been observed in the gently sloping surroundings of Sompe. Therefore, the *Anoa* molars described by Hooijer probably originated from another locality, but have become mixed with the Sompe sample of van Heekeren.

Resuming, the Walanae Fauna can now be defined as including only those land-vertebrate taxa, which unambiguously have been derived from the Beru Member of the Walanae Formation. The fauna list of the terrestrial Walanae Fauna then includes:

Celebochoerus heekereni Hooijer, 1948
Geochelone atlas Falconer & Cautley, 1844
"Elephas" celebensis (Hooijer, 1948)
Stegodon sompoensis Hooijer, 1964
Trionychidae sp.
Crocodylus sp. 1
Crocodile sp. 2, cf. *Gavialis*

It has already been mentioned that besides the common *C. heekereni* present in the lower part of the Beru Member, there is a distinct *Celebochoerus* variety with short metapodials. Whether this short-legged variety represents a distinct species that can actually be distinguished on cranial and/or dental elements, would require a detailed analysis of the material at hand, which is beyond the scope of this thesis. Tentatively, the two types can best be considered as successive chronospecies.

The Walanae Fauna as defined here does not include *Anoa*, *Babirusa* or *Sus*, and differs in this aspect from the concept of the *Archidiskodon-Celebochoerus* Fauna of Hooijer (1954e). In the youngest interval of the Beru Member (subunit B) a large-sized *Stegodon* may have been present in addition to the proven occurrence of the two pygmy Elephantoidea, *"E." celebensis* and *S. sompoensis*, but this remains to be confirmed by in situ findings. Furthermore, the presence of *S. sompoensis* in the lowermost, oldest strata containing the Walanae Fauna remains inconclusive.

Tanrung Fauna — A fauna clearly distinct from the Walanae Fauna and of presumed Middle Pleistocene age is represented by vertebrate fossils from the Tanrung Formation. This formation was deposited after the major Plio-Pleistocene deformation phase, and unconformably overlies gently folded sediments of the Walanae Formation in the ESB. The fauna is here called Tanrung Fauna. This fauna lacks pygmy Elephantoidea and *Geochelone atlas*.

A molar fragment, which was found in the Tanrung River and which was probably derived from the Tanrung Formation, was attributed to an advanced, high-crowned *Elephas* sp. (van den Bergh et al., 1994). The molar fragment is largely covered by a calcitic limestone crust, which suggests that it has been derived from the well consolidated and calcite cemented Tanrung Formation. This molar fragment is very important as it represents a high-crowned *Elephas* species with an hypsodonty index (length/width) of 2 (van den Bergh et al., 1994). Elsewhere in Eurasia such high-crowned elephants, like *Elephas hysudrindicus* from Java and *Elephas [Palaeoloxodon] namadicus* from the Eurasian mainland, appear for the first time during the Middle Pleistocene (Maglio, 1973). Therefore, this specimen puts a time constraint on the maximum age of the Tanrung Fauna: Middle Pleistocene.

The Tanrung Fauna further contains the intermediate to large-sized *Stegodon* sp. B. *Celebochoerus* occurs in the Tanrung Fauna (based on in situ but rolled fragments) and/or *Anoa* (surface findings only). The *Anoa* molars do not show any trace of matrix attached to them and they appear not so heavily mineralized as the fossils that originate with certainty from the Tanrung Formation and those of *Celebochoerus*. The *Anoa* molars are more likely derived from the unconsolidated alluvial deposits overlying the Tanrung Formation.

Two *Elephas* metacarpals from the Tanrung River have some well cemented sand-sized grains still attached. They were found close together on top of an emerged sandbank, as if they were left there by somebody. They may have been brought there from some other, unknown locality nearby. In any case it cannot have been derived from the Beru Member of the Walanae Formation, as in the present-day catchment area of the Tanrung River only the lower marine part of the Walanae Formation crops out besides the Tanrung Formation and overlying unconsolidated alluvial units.

The in situ findings of suid remains in the Tanrung Formation are all characterized by a relatively small size. Three upper canines (one in situ and two surface collected specimens) were found smaller than those of *Celebochoerus heekereni* from the Beru Member, though similar in morphology (DIRSP, 1995). Also an M_2 of this suid from the Tanrung Formation was found to be smaller in size than any of the 25 homologue specimens from the Beru Member localities. Though these specimens are rounded due to transport and may have been reworked from older deposits, this actual size difference suggests that they were originally derived from younger deposits than the Beru Member.

The Tanrung Fauna can now be defined as the assemblage of taxa derived from the Middle (or perhaps even Late?) Pleistocene Tanrung Formation. Only one taxon, *Stegodon* sp. B, can be included in the Tanrung Fauna with certainty. Other taxa, like the advanced *Elephas* sp. and a small variety of *Celebochoerus* probably occur in the Tanrung Fauna, while *Anoa* is unlikely to have been part of this fauna. The fauna is still insufficiently known and more material is needed.

Subrecent to Recent Fauna — The youngest faunal remains in the study area are represented by fossils from colluvial pockets (FVL-21 near Ciangkange, Encl. B). They yielded remains of *Anoa* sp. *Anoa* has also been reported from various Late Pleistocene to Holocene cave deposits (Hooijer, 1950; Clason, 1976). These caves are located around 25 km NE of Ujung Pandang. At one of these sites, Leang Burung, radiocarbon dating on shell remains yielded ages of up to 31 ka (Glover, 1981). *Anoa* molars have also been found in the Tanrung and Paciro Rivers in the ESB, but the lack of matrix made it uncertain whether they originate from the Tanrung Formation. More likely, these fossil remains were washed out from the Younger Alluvial units unconformably overlying the Tanrung Formation. It is also of interest to mention the fossilized skull fragment attributed to *Sus celebensis* by Hooijer (1969b). This skull was reportedly recovered from the Paciro River. Hooijer included this species in his *Archidiskodon-Celebochoerus* fauna, but there is no evidence whatsoever to do so. Our excavations at various localities have shown now that *S. celebensis* does not co-occur with *C. heekereni* in the Beru Member of the Walanae Formation, neither does *A. depressicornis*. The *S. celebensis* skull, which appeared heavily rolled, might have originated from the Tanrung Formation, because the Tanrung River flows into the Paciro River. However, it may also have originated from the younger alluvial units unconformably overlying the Tanrung Formation and now shaped into terraces along the Tanrung and Paciro Rivers. Both species are still extant in Sulawesi. Their oldest proven occurrence is in the Toalian cave sites described by Hooijer (1950) and in the colluvium locally developed in the Sengkang Anticline area. The (sub)Recent Sulawesi fauna is highly distinct from the Walanae and Tanrung faunas, in lacking elephantoids and *C. heekereni*. The modern fauna was probably established on South Sulawesi sometime during the Late Pleistocene. Some species, of which fossils have been found in the Toalian Cave deposits, are presently not occurring in South Sulawesi anymore but do live on other parts of Sulawesi. These species have been placed between brackets in Fig. 44.

Taphonomy

Introduction

In this section the taphonomy of the richest fossil localities of the study area will be discussed. The fossil assemblage as it is found at a specific site, is the result of a large number of factors that have acted on the bones before, during, and after fossilization, and which may have led to preferential preservation of certain fossil elements in the cluster of bones finally obtained at that locality (Behrensmeyer & Hill, 1980). These factors may include activities of carnivorous animals, trampling of bones by animals, physical influences such as drying and cracking of bones under influence of solar radiation and chemical processes such as dissolution of bones after burial. Furthermore, bones can become selectively removed by a depositional medium, but also by preferential recoverage during excavation. For example, it is expected that very small bones such as *Celebochoerus* phalanges will be underrepresented in the fossil assemblages from FVL-5 and FVL-24c, because the sediments have been sieved only to a limited extent at these excavation sites.

The taphonomic studies can provide information on whether a certain bone assemblage was transported or occurs in primary context. The best taphonomic information comes from the excavated FVL-5 and FVL-24, but also from the relatively fossil-rich FVL-25 and FVL-3/FVL-4.

Bone densities

At both FVL-5 and FVL-24c bone densities are relatively high compared to all other FVL. The occurrence of the bones in clayey deposits at both these sites indicates that transport by water currents must have been very small or absent. Both sites represent localities where fossil vertebrate remains were very abundant and where excavations have been carried out in order to obtain a large sample of in situ material. The density of identifiable specimens is estimated at 24 bones/m^3 for FVL-5 and 26 bones/m^3 for FVL-24c. These figures can be recalculated to bone density per 100 m^2, using a thickness of 9 cm for individual surface assemblages following the method of Potts (1988). The bone-bearing interval at FVL-5 is c. 0.3 m thick. Dividing 0.3 by 0.09 we obtain a figure of 3.33 buried 'surfaces' (9 cm is used as an average representative surface thickness). The total excavated surface area at FVL-5 is 51.5 m^2. Dividing up the total number of identifiable in situ bones (= 371) amongst these buried 'surfaces' and then dividing by the excavated surface area, we obtain a density of 2.2 bones per

m^2 = 220 bones per 100 m^2. For FVL-24c the calculation of the bone density per 100 m^2 would be more complicated because the thickness of the excavated fossiliferous interval is not homogeneous over the excavated area. However, a similar figure as for FVL-5 is expected because of the similar bone density per m^3 at both localities.

The bone density at FVL-5 is a factor 20 times greater than the highest concentration of 11 bones per 100 m^2 encountered on the surface in various modern natural habitats in Amboseli Natural Park in Kenya (Behrensmeyer, 1983). Amongst the studied habitats were swamps, dense wood, open wood, plains, lake beds and bush. The swamp habitat appeared to exhibit the widest variation in bone clustering. The highest density of 11 bones per 100 m^2 was found in a sub-area of the total area studied, whereas the average bone density of the entire swamp area sampled was estimated at 0.62 bones per 100 m^2. On the other hand, the FVL-5 bone density is a factor 7.6 to 10.7 smaller than three out of six fossil and artefact-bearing sites of Bed I Olduvai in Africa, in which hominids are thought to have contributed primarily to the bone accumulations (Potts, 1988). The FVL-5 bone density is similar compared to the figure of c. 3 bones per m^2 given for the c. 0.9 Ma old “Haupt Knochenschicht” at Trinil, east Central Java (Oppenoorth, 1911).

The bone densities of FVL-5 and FVL-24c in South Sulawesi are unusually high relative to those in various modern, high biomass, African habitats, but significantly lower than in some African sites influenced by early hominid activity. High concentrations of bones are usually related to sites of serial predation, e.g. around water holes, or due to mass deaths resulting from catastrophic events (Haynes, 1988, 1991a). Though the average bone densities at such sites are usually less than 1 bone per m^2, spot clusters of bones may approach 50 bones per m^2 in carcass loci (Haynes, 1991). Before drawing conclusions concerning the possible mechanisms that resulted in the high bone densities, it is necessary to consider other taphonomic aspects of these localities first.

Taxonomic diversity

Figure 45 shows 4 graphs representing the amount of determinable fossil elements of each taxon distinguished, as a percentage of the total bone assemblages from FVL-5 and FVL-24c. The surface collected (Fig. 45A) and in situ collected (Fig. 45B) bone assemblages from both FVL have been separated for comparison. Only the identifiable fossils have been considered for these graphs. There are only small differences in taxon percentages between the excavated fossils and those collected at the surface at both localities. The similarity between the in situ and surface assemblages can be explained by the fact that all fossils distributed on the surface were collected as much as possible. The graphs suggest that surface collected fossils can be considered as a good indicator of the original in situ assemblages. At those localities where no excavations have been carried out and where the fossil sample size is considerably smaller, like FVL-25a and FVL-3/4/4a, the surface and in situ assemblages have been combined in order to obtain the largest possible samples. These combined assemblages are thought to be representative for the original in situ assemblage. In Fig. 46A-F similar taxon percentage graphs are shown for the other FVL of the Beru Member that yielded more than 40 fossil specimens, lumping in situ and surface-collected fossils together in order to obtain the largest possible samples. It follows that the percent-

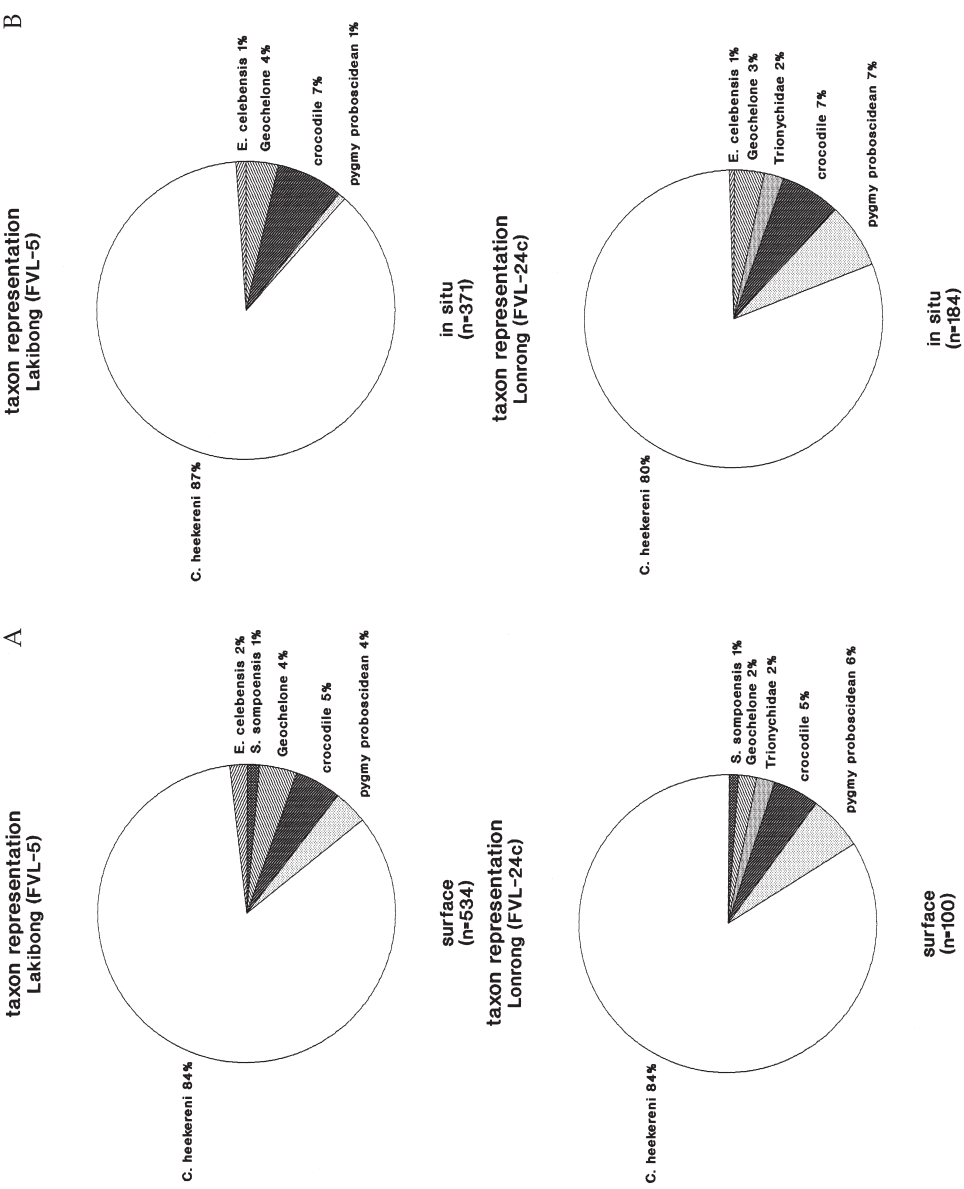


Fig. 45. Graphs showing the amounts of identifiable fossil specimens of each taxon distinguished, expressed as a percentage of the total number of identifiable fossil specimens (n) at FVL-5 (Lakibong) and FVL-24c (Lonrong). Surface collected fossils (A) and fossils excavated in situ (B) are represented in separate graphs for both localities.

ages of the various taxa are fairly similar in all Beru Member FVL where the surrounding sediment facies did not provide indications for marine influences (FVL-5, FVL-6, FVL-11, FVL-24c and FVL-3/4/4a). *Celebochoerus heekereni* fossils dominate the assemblages in these FVL, representing 75-87% of the total amount of identifiable fossils. The fossil assemblage of FVL-25a (Fig. 46A) includes a few Elasmobranchii teeth. These are surface findings, which were probably derived from the marine interval just underlying the main fossiliferous, fluvial sandstone layer at FVL-25a. Apart from these Elasmobranchii teeth, the assemblage at FVL-25a is similar in composition to the other, fully terrestrial assemblages.

The assemblages of FVL-28 (Fig. 46E) and FVL-24a (Fig. 46D) are clearly different. At these FVL terrestrial and marine vertebrates occur in the same fossiliferous layer. Some of the terrestrial vertebrate fossils at these FVL show encrustations of shallow marine organisms, indicating that the depositional environment was marine. The terrestrial vertebrate remains at the latter FVL must have been thoroughly reworked before entering in the marine depositional environment, and supposedly give no good representation of the Walanae Fauna composition.

The FVL with high proportions of *C. heekereni* fossils can be divided into two types. The first type is characterized by the fact that the fossils originate from fine-grained sediments, such as claystone or siltstone. It is expected that reworking by fluvial currents has been minimal in these low-energy environments (FVL-24c and FVL-5). At the second type of FVL, the fossils were concentrated in course sandy clastics (FVL-25a and FVL-3/4/4a). At FVL-11 the fossil assemblage was collected in an interval showing an alternation of fine- and coarse-grained layers. Also here, *C. heekereni* fossils dominate the assemblage. In the non-marine influenced localities the percentage of pygmy elephantoid remains varies between 2% and 18%, those of crocodiles between 2% and 7%, those of *Geochelone atlas* between 1% and 7%, and those of Trionychidae between 0% and 5%. The representation of the various taxa is surprisingly constant in the non-marine influenced localities, independent of their concentration in high- or low-energy deposits. Crocodile fossils, supposedly the main predator of the Walanae Fauna, constitute 1-7% of the total identifiable fossils. The pygmy elephantoids, with relatively large bodysizes compared to *C. heekereni*, must have had lower population densities than the latter, and their representation in the fossil assemblage is indeed lower than that of *C. heekereni*.

The percentages are quite distinct in the marine influenced sites FVL-24a and FVL-28. Here the percentage of *C. heekereni* fossils is considerable lower, 12% and 49%, respectively, compared to 75-87% in the non-marine localities. These low percentages seem to be partly due to the various amounts of Elasmobranchii teeth present at these sites, which suppress the percentages of the other taxa. If we leave Elasmobranchii teeth out of consideration than the percentages of *C. heekereni* fossils become 37% and 55%, respectively, which is still low compared to the fully terrestrial FVL. Besides the presence of Elasmobranchii teeth, the marine influenced sites show a relative enrichment of crocodile remains (almost exclusively teeth), which make up 30% of the assemblage from FVL-24a and 43% of that from FVL-28 (excluding Elasmobranchii remains). Especially at FVL-28, there seems to have been a preferential selection for small fossil elements, like *C. heekereni* isolated teeth, carpals and phalanges and isolated crocodile teeth. The only proboscidean fossil encountered at FVL-28 is a

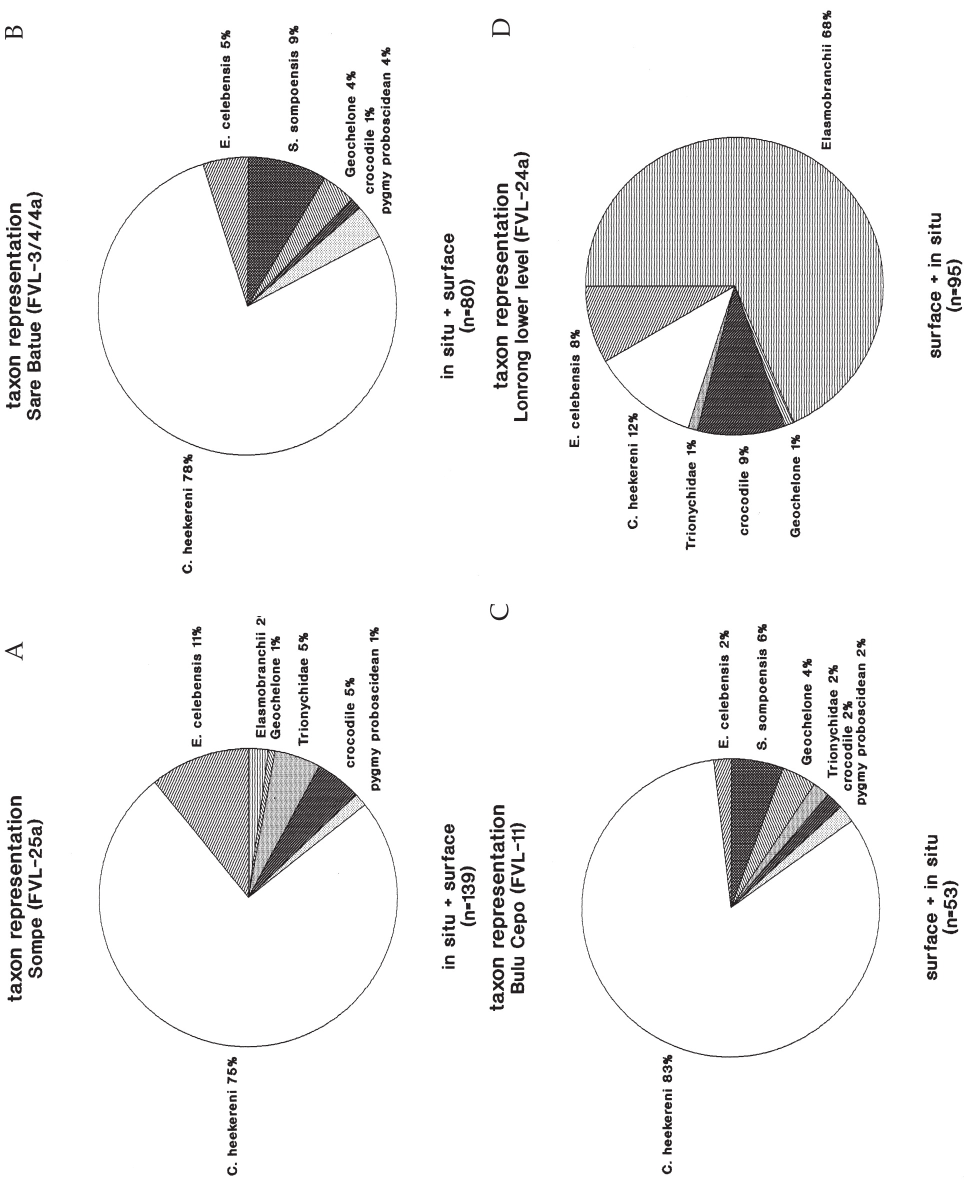
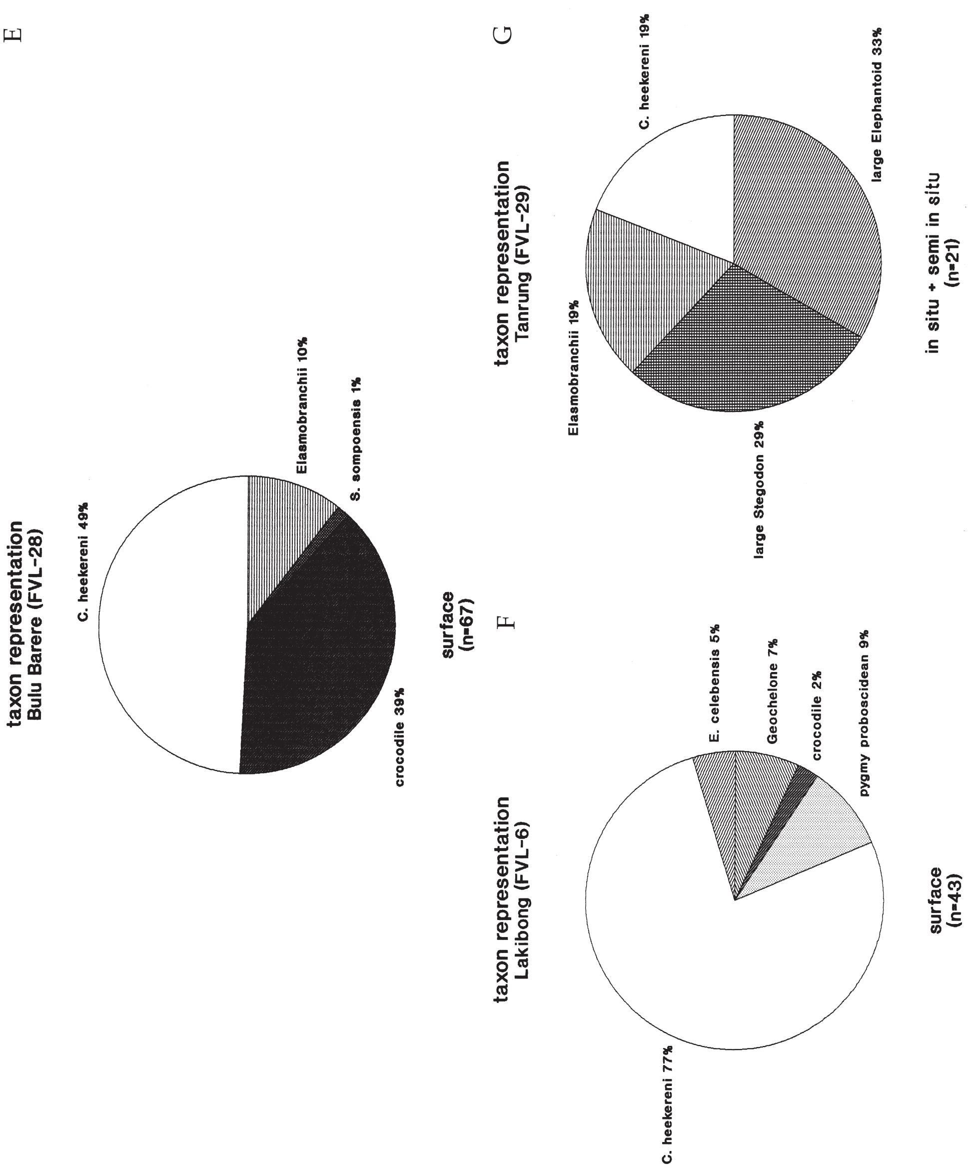


Fig. 46. Similar graphs as shown in Fig. 45 for FVL-25a (A), FVL-3/4/4a (B), FVL-11 (C), FVL-24a (D), FVL-28 (E), FVL-6 (F), all from the Beru Member, and FVL-29 (G) from the Tanrung Formation. Surface collected fossils and fossils excavated in situ have been lumped together in order to obtain larger samples, except for FVL-29, where only fossils have been included which were recovered in situ or semi in situ (the latter representing surface collected fossils with the characteristic Tanrung Formation matrix still attached).



tiny dP^2 of *S. sompoensis*. This size selection may have been due to reworking by waves or tidal currents. The crocodile teeth from FVL-24a are all of a narrow curved type, similar to teeth of fish eating *Gavialis* species. Teeth of this type have also been encountered at FVL-28, but never in the fully terrestrial sites, suggesting that this type of crocodile lived in an estuarine or coastal environment, whereas *Crocodylus* sp. may have lived in both the fluvial and marine domains.

In the Tanrung Formation (FVL-29) the representation of the various taxa is completely different from that of the Beru Member FVL (Fig. 46G). No bone concentrations have been found in the Tanrung Formation, except for 6 large elephantoid postcranial elements that were found close together in a small gully eroding the Tanrung Formation deposits. Some had the characteristic matrix of this unit still attached. The total number of in situ and semi- in situ (those with matrix still attached) fossils is only 21, which is unfortunately rather low compared to the Beru Member sites dealt with above. In Fig. 46G surface- collected fossils lacking matrix have been omitted, because some of them, in particular *Anoa* teeth, have been probably derived from the younger alluvial deposits overlying the Tanrung Formation. Large-sized elephantoid remains make up 52% of the combined in situ and semi-in situ assemblage from the Tanrung Formation. Remarkable is the absence of pygmy elephantoid and *Geochelone* fossils. In all Beru Member localities with 5 or more identifiable fossils, at least one pygmy elephantoid specimen is represented. *Geochelone* is usually more rare in the Beru Member localities, and may simply have been 'missed' up to now in the Tanrung Formation. *Celebochoerus* fossils constitute only 19% of the assemblage, which is lower than in any of the Beru Formation FVL. If Elasmobranchii teeth are left out of consideration, the total percentage of *Celebochoerus* remains from FVL-29 would still be 24%, lower than any of the Beru Member FVL. It follows that the taxa representation of the Tanrung Formation contrasts strongly with the Beru Member FVL, both in species and in percentages. These differences are perhaps due to the different faunal composition of both units, or due to different habitats, though the sample is actually too small to draw firm conclusions.

Bone representation of *Celebochoerus heekereni*

Bone representation graphs of *C. heekereni* fossils from the 4 Beru Member FVL with the largest numbers of fossils, are given in Fig. 47A (FVL-5), 47B (FVL-24c), 47C (FVL-25a), and 47D (FVL-3/4/4a). At FVL-5 and FVL-24c the accumulation of the bone assemblage must have taken place over a relatively short time span. Here the fossils originate from a clay deposit and were certainly not reworked from older deposits. At FVL-25a and FVL-3/4/4a the bones occur in a coarse clastic fluvial deposit and here the bone sample may represent a longer timespan, as bones may have been eroded and reworked by fluvial activity from older strata. The bone assemblage of FVL-3/4/4a was obtained from three different sites in the same layer, at distances of several hundred meters apart. Fossils from these three sites have been lumped together in order to obtain the largest possible sample from this locality.

The amount of each skeletal element in these assemblages is expressed as the percentage of the expected total amount of that element. The expected total amount of each skeletal element is calculated by multiplying the minimum number of individuals (MNI) of that locality with the number of that element present in one individual. The MNI is based on the most frequently occurring bone or tooth in the assemblage, either of the sinistral or of the dextral side. In all four samples this appeared to be the upper canine of either the sinistral or dextral side. For example, if there were 7 sinistral and 5 dextral upper canines in a certain assemblage, than the MNI was taken as 7. The expected total amount of upper canines in that assemblage would equal 2 × 7 = 14. In this example the real amount of upper canines present, expressed as the percentage of the expected total amount, would equal 12 × 100/14 = 85.7%. In the same example the expected total amount of cervical vertebrae (excluding atlas and epistropheus, which are treated separately in the graphs) would amount to 5 × 7 = 35. Skulls and costae have been omitted in the graphs because these elements tended to be very fragmented. Long bones have been separated in proximal (p) and distal (d) parts, while diaphyses have been omitted. Of the dental elements only the upper and lower M3s and canines have been included in the graphs. This includes both isolated M3s and canines as well as M3s and canines still placed in mandible or maxilla fragments. M3s and canines appeared to be the most frequently occurring dental elements of the tooth series. Of the generally rather fragmented pelvis only the preserved acetabulum fragments have been counted, either occurring as part of more complete pelvis specimens or as smaller fragments, whereas isolated pelvis fragments without acetabulum have not been included in the counts. Phalanges of the fore and hindlegs have been classified according to six groups, namely the first, second and third phalanges of the middle and side toes, respectively.

Selective bone removal — In the hypothetical case that no bone loss would have occurred at a certain locality and that all skeletal elements of all individuals present would have been recovered, the bone representation of all elements included in the bone representation graphs would equal 100%. The more bones would have been removed from the original assemblage by post-mortem processes, the larger the white area in the bone representation graphs would appear. With this in mind it is evident from Figs. 47A-D that of the four FVL represented, bone loss has been minimal at FVL-5 and maximal at FVL-3/4/4a and FVL-25a, whereas FVL-24c takes an intermediate position. In all four localities canines and teeth were the most frequently occurring elements. Teeth are commonly the most frequently occurring elements in a fossil vertebrate assemblage, because the high strength of dentine and enamel enhances their chance of fossilization more than bone. At sites where death bodies or parts of it became separated from the skulls, and subsequently were transported to different places, teeth may be underrepresented. As an example one could think of bone accumulations made by carnivores such as at hyena dens.

In all Beru Member FVL no bones were found in articulating positions. Disarticulation must have been complete prior to burial, even at FVL-5 with the lowest degree of bone removal. At FVL-5 almost all skeletal elements are present in the fossil assemblage except for the fragile atlas. Most long bones are represented for more than 40%, whereas the small distal elements of the limbs, like phalanges and carpals are mostly underrepresented, except for the astragalus and calcaneus. Vertebrae take an intermediate position with regard to their representation in the assemblage. To some extent the low representation of small distal elements may have been caused by the sampling method. Small elements may have selectively escaped attention during collecting. However, during the excavation large lumps of clay were fragmented into small pieces, and sieving of 5 large bags of residual clay from the fossiliferous layer did not yield any additional recognizable bone fragment, indicating that the recovery in the field was fairly complete. It therefore seems more likely that small bones with a relatively low density were selectively removed from the spot prior to burial, more so than the long bones and vertebrae. Removal of the smaller elements may have been either by weak water currents, predators (crocodiles?) or some other, unknown agent. The agent or agents selectively removing the smaller bones obviously have acted more severely at FVL-24a than at FVL-5. At FVL-25a and FVL-3/4/4a also long bones

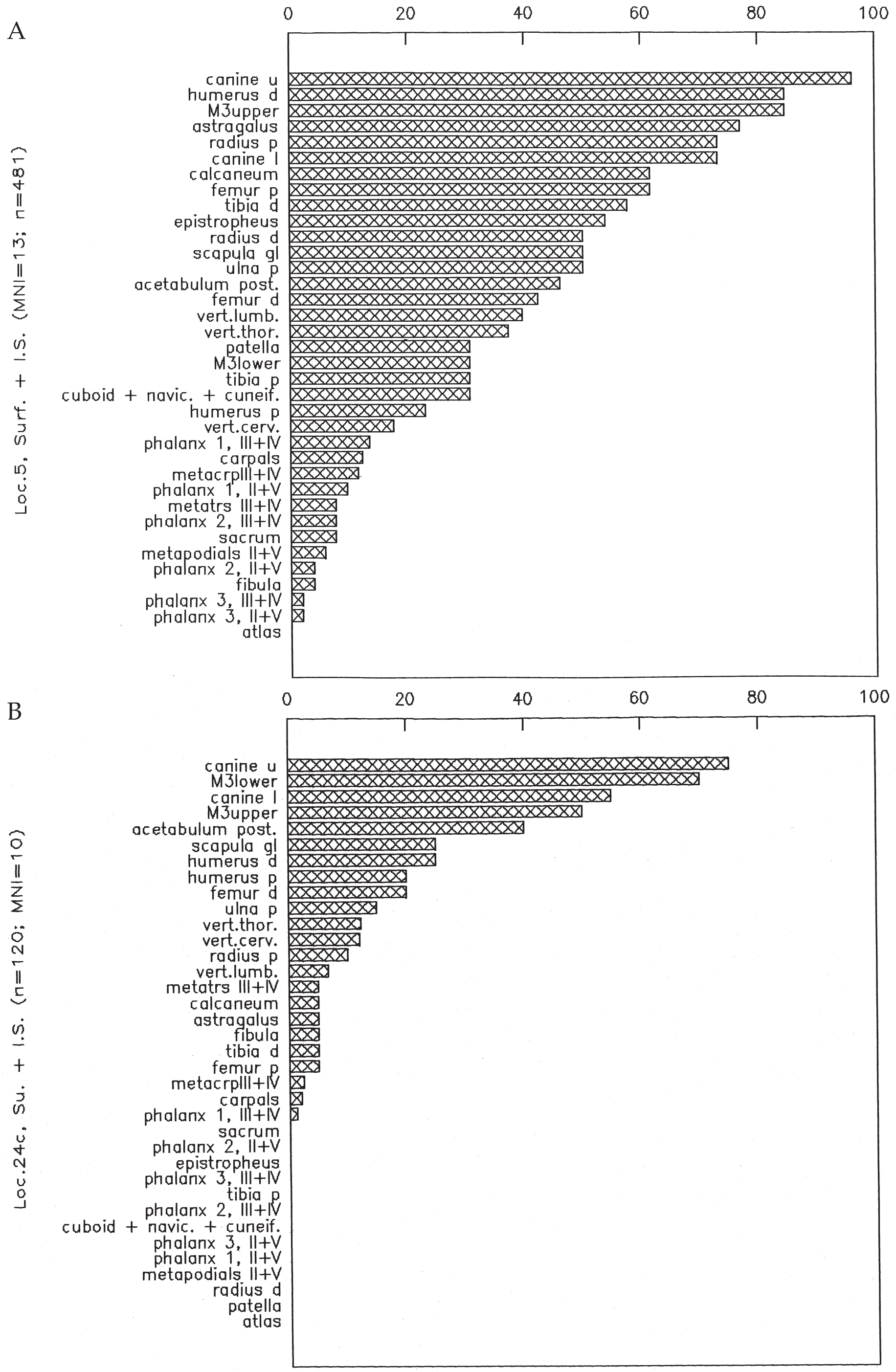
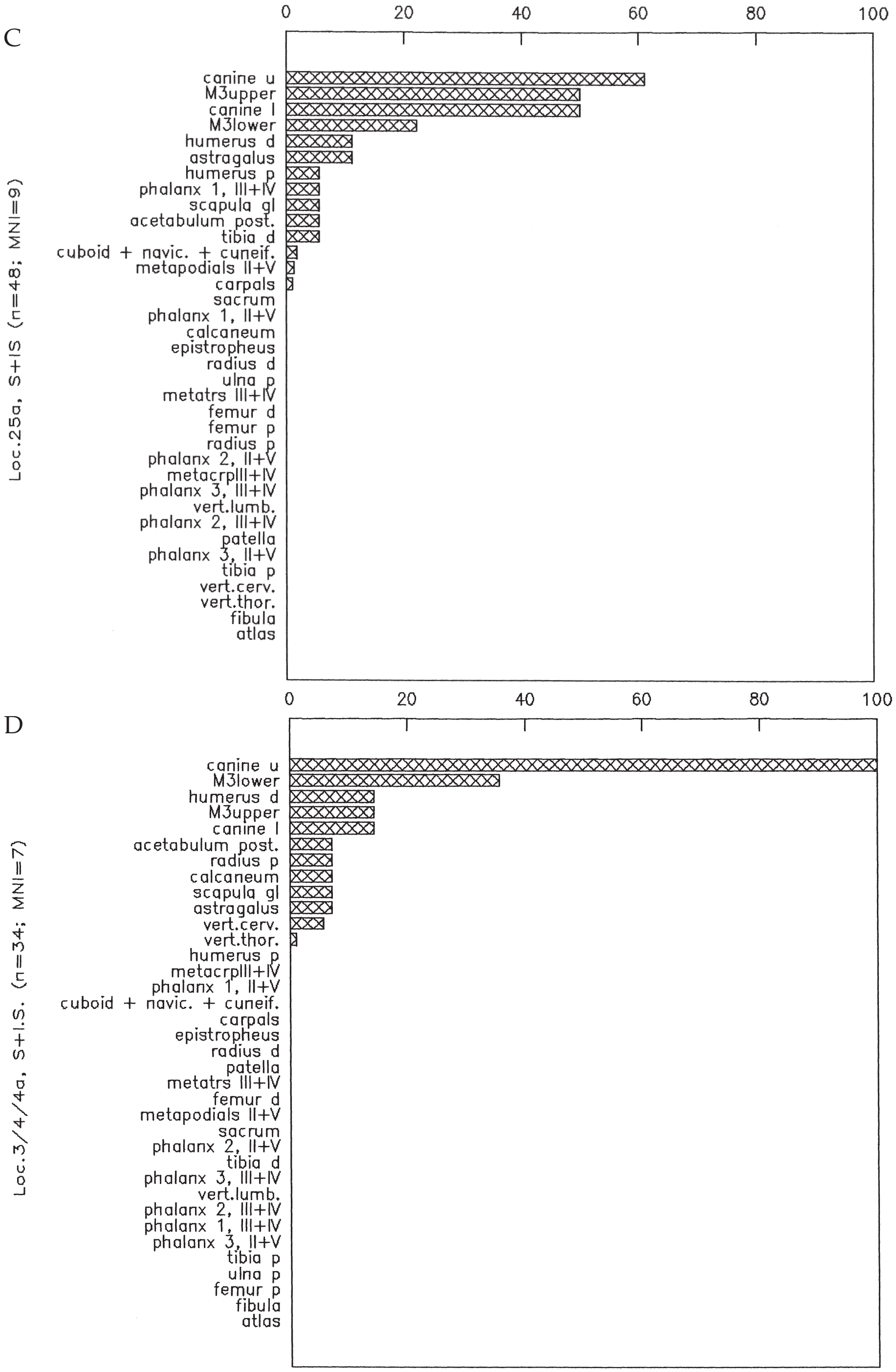


Fig. 47. Bone representation graph of skeletal elements of *Celebochoerus heekereni* obtained at FVL-5 (A), FVL-24c (B), FVL-25a (C) and FVL-3/4/4a (D).



Surface collected fossils and in situ collected fossils have been combined in order to obtain larger samples. For further explanation see text.

are strongly underrepresented. This is in accordance with the fact that here the fossils occur in high-energy, fluvial layers.

Bone preservation — Concerning the state of preservation of fossil *Celebochoerus* bones from FVL-5 and FVL-24c the following can be noted. A few in situ fragments of single bones, which could be fitted together, were found separated by a distance of 15 cm to 1 m. Complete long bones are rare and were only found in situ, though they were usually found broken in the sediment. There is one dextral tibia, one dextral radius of a submature individual, one dextral ulna, and two humeri, one dextral and one sinistral. Fragile bones such as skulls, vertebrae and ribs were found to be heavily fragmented in all cases. In situ skulls were completely squeezed and broken into small fragments closely concentrated in the sediment. Both the breakage of the complete long bones as well as the fragmentation of the skulls seem to be the result of compaction of the clay after burial. Other in situ specimens, such as costa fragments and vertebrae, were all found broken as well, with the missing pieces not in the direct surroundings. It thus seems that considerable fragmentation of the bones and the subsequent dispersal of their fragments took place prior to burial. Some long bones had an inclined or even vertical orientation in the clay. The long bones that were found fragmented showed either sharply fractured edges with right-angle offsets or helical edges. The bone surfaces generally appeared smooth without superficial cracks. However, in some cases superficial damage of bones was characterized by irregularly pitted surfaces, especially occurring in juvenile bones. This type of damage seems to be caused by postmortem dissolution. Of some bones the finely fractured terminations were found to be filled with caliche concretions. No clear signs of carnivore activity, such as isolated pits or heavily gnawed epiphyses, were found on the bones.

Discussion — The above-described features suggest that the skeletons were disarticulated before burial and that the major bone damage was caused by trampling and in addition by compaction of the clay after burial. The fossil-bearing horizon remained probably below the water table prior to final burial. Submergence of the death bodies or parts of them would have improved the decaying of the tendons that kept the bones together, which could explain the complete disarticulation of the skeletons. Submergence could also explain the selective removal of the smallest elements by wave action or weak currents and the absence of superficial damage due to desiccation and solar radiation. After burial compaction of the clayey matrix may have led to some breakage in addition. Especially the damage to the skulls seems largely related to compaction of the clay. Especially the frontal and parietal regions of the skulls contain large cavernous sinuses, and these parts are likely to collapse after increasing pressure due to burial and compaction of the clay. In addition, dissolution may have caused selective removal of bones, especially those of juvenile individuals.

Gifford & Behrensmeyer (1977) studied the bone assemblage remaining on an occupation site after people of the Dassanetch tribe had camped there for four days. The people butchered a great number of animals of different species in a dry riverbed on a substratum of sand. After the Dassanetch had left, Gifford & Behrensmeyer (1977) mapped all bones that were visible on the surface. After the rainy season they found that some of the smaller bones on the surface had been dispersed, while the remainder was buried. During the excavation they found many more bones than the ones originally mapped, all being of a small size (less than 2.5 cm or larger but very thin fragments). These small excavated bones were of the same species as those found in the surface sample but underrepresented in the surface sample. They were interpreted as being buried by trampling.

The original bone concentration at FVL-5 could not have been caused by hominid activity and must be due to other factors, e.g. starvation at a drinking place or preying by crocodiles. Even though FVL-5 has the least bone removal of the four sites considered here, selective loss of bones has been considerable. The bones that are most underrepresented are the smallest elements with relatively low densities, like phalanges, carpals, and metapodials, and those elements with low densities, such as vertebrae (Behrensmeyer, 1975). These bones can most easily be transported by watercurrents. The underrepresentation of small bones could have been caused by trampling processes in a similar way as at the Dassanetch site. Part of the smaller bones could have been trampled into the sediment, thus escaping removal by currents, whereas larger and denser elements were too heavy to be transported from the site. Only the small bones that were not trampled into the sediment could have been removed by weak currents.

There are no clear indications for carnivore activity at any of the sites mentioned above. Though no mammalian predators are recorded in the Walanae Fauna, the presence of crocodiles, represented by both isolated teeth and skeletal elements and dermal scutes, makes it likely that crocodiles influenced the composition of the bone assemblages. Crocodiles may have been responsible for the bone accumulation in the first place. These reptiles do not gnaw bones. They sometimes let their prey putrefy in the water for some days before they start dismembering and consuming it. They close their jaws around some part of the prey and rotate their body until lumps of meat get loose, which are swallowed entirely including the bones. Some of the dissolution features observed may have originated in the digestive system of these reptiles.

The bone assemblage at FVL-24c (Fig. 47B) indicates that here selective removal of bones has been more marked than at FVL-5. Though the total amount of *Celebochoerus* fossils included in the count was four times lower than at FVL-5, the MNI based on the amount of upper canines was still 10, versus 13 at FVL-5. Except for the absence of caliche concretions around fossils at FVL-24c, the fragmentation of bones appeared to be of a similar type as at FVL-5, the fracturing most likely being caused by a combination of trampling and compaction. Because chemical alterations of bone seems to have been less severe at FVL-24c (except for the elephantoid bones obtained from the yellow calcareous concretions = 4 in Fig. 43), it is assumed that the increased loss of postcranial elements, including the larger limb bones, has been caused by either more intense fracturing due to trampling or by increased removal by flowing water. As small elements like phalanges and carpals are almost entirely absent at FVL-24c, it is thought that stronger water currents were mainly responsible for the removal of bones here. For in the case of a higher degree of trampling one would expect more smaller bones to have been trampled into the sediment and thus escape removal by water currents, even though these were supposedly stronger than at FVL-5. The assumed stronger water currents at FVL-24c would be in accordance with the fact that sandy laminae are intercalated in the fossiliferous silty clay layer at FVL-24c, but not at FVL-5. These sandy streaks indicate a (periodical) higher hydrodynamic regime at FVL-24c than at FVL-5.

The bone assemblages of FVL-25a and the combined FVL-3/4/4a (Fig. 47C and 47D, respectively) underwent even more selective bone removal. Contrary to FVL-5 and FVL-24c, with the bone concentration occurring in fine-grained layers, FVL-25a and FVL-3/4/4a are both characterized by the fact that the bones originate from coarse-grained fluvial layers. Though most fossils were found on the surface at these sites, the bulk of the fossils must have originated from the fossiliferous coarse-grained fluvial layers at both places, because many had a coarse-grained matrix of the fossiliferous layers still attached. At FVL-25a only 3 out of 137 fossils were collected in situ from the sandstone layer, which was found laterally exposed over some 50 m. This indicates that the overall bone density in the fossiliferous sandstone layer is much lower than the clay of FVL-5 and FVL-24c.

From the diagrams of Fig. 47 it follows that elements with high density and great resistance against weathering, such as canines and teeth, have become relatively more concentrated at these fluvial sites than they are at FVL-5 and FVL-24c (note that the MNI is rather high whereas the total number of fossils is much lower than at FVL-5 and FVL-24c). The bones seem to have been transported and reworked prior to final deposition, and during this transport most of the weaker and lighter elements either disintegrated completely or were transported further downstream. The easily transportable vertebrae are completely (FVL-25a) or almost completely (FVL-3/4/4a) absent, while limb bones are also much more underrepresented or completely absent relative to dental elements, when compared with FVL-5 and FVL-24c, where currents are thought to have had less influence. At FVL-25a and FVL-3/4/4a fluvial transport seems to have been responsible for a concentration of those elements with the highest density and strength, which are dental elements.

In an experiment carried out by Behrensmeyer (1975), bones were buried beneath the water table near Lake Rudolf. After two years the bones were recovered again and appeared to be very fragile due to the loss of their organic contents. Because dental elements contain less organic material, they were found less fragile after burial and could therefore have a good reworking/ preservation potential. In contrast, reworking of the skeletal elements would certainly have led to complete disintegration. Reworking of buried bones and teeth by shifting and eroding channels may thus under certain circumstances lead to a concentration of dental elements in the river channel deposit. Such processes may account for the strong enrichment of dental elements at the fluvial sites FVL-25a and FVL-3/4/4a.

Conclusions

From the present study it may be concluded that the concept of the *Celebochoerus-Archidiskodon* Fauna of Hooijer (1954e) has to be rejected. Following the original concept of Hooijer, this Late Pliocene to Early Pleistocene fauna from South Sulawesi included elements, which are still extant in Sulawesi, such as *Anoa depressicornis* and *Sus celebensis*. However, it has been shown here that extant species are totally lacking in the upper reaches of the Walanae Formation. The suggestion made by Musser (1987) that the modern Sulawesi fauna is completely different from the fossil one, is now substantiated by stratigraphical data.

Instead, the faunal history appears more complex, and at least three successive terrestrial faunas can be identified now. These are from old to young: Walanae Fauna (Late Pliocene to Early Pleistocene and perhaps even extending into the Middle Pleistocene), Tanrung Fauna (Middle Pleistocene) and the sub-Recent to Recent Fauna (which may extend back as far as Late Pleistocene). The composition of the Walanae Fauna is fairly well known now by the large fossil assemblages obtained from various localities, which yield a consistent pattern. The most abundant element of the Walanae Fauna is the suid *Celebochoerus heekereni*. Through time this suid underwent a slow evolutionary change towards shorter legs and probably also smaller size. The fauna is further characterized by the presence of two pygmy elephantoids, *"Elephas" celebensis* and *Stegodon sompoensis*, and a giant tortoise, *Geochelone atlas*. The main predator in the Walanae Fauna is represented by a large crocodile, *Crocodylus* sp.[2].

The Tanrung Fauna, present in the Tanrung Formation, is still insufficiently known, but the data indicate that new immigrations of large-sized mainland elephantoids took place, again a *Stegodon* and an *Elephas*. These taxa probably replaced the dwarf elephantoids of the Walanae Fauna. However, the time period during which these replacements took place is not known, due to an hiatus in the rock sequence. The suid *Celebochoerus* probably continued in the Tanrung Fauna, but no indications for the continuation of *Geochelone* has been found so far.

Eventually, also *Celebochoerus* became extinct and was replaced by the unrelated suids *Sus celebensis* and *Babyrousa babyrussa* in the Subrecent to Recent Fauna, which supposedly entered South Sulawesi from Central Sulawesi. All elephantoids became extinct on South Sulawesi somewhere during the end of the Middle Pleistocene or Late Pleistocene.

Seen in the context of regional geology, it is most likely that the ancestors of the various taxa recognized in the fossil and (sub)Recent Faunas reached Sulawesi by at least crossing one sea barrier. During periods of low glacio-eustatic sea-level, the sea barriers must have been of a more limited extent than those isolating present-day Sulawesi. The minimum distance between west Sulawesi and the east coast of Borneo may have been reduced to c. 50 km during such periods of low sea-level. This distance is within the swimming capacity of modern elephants. Several shallow carbonate platforms south of the Makassar Basin may also have served as stepping stone islands during such episodes of low sea level.

The first arrival of humans on Sulawesi may have occurred much earlier than the end of the Late Pleistocene as hitherto thought. The gravel deposits associated with group 1 artefacts of Keates & Bartstra (1994), are possibly much older than Late Pleistocene. It has been argued that the gravels exposed in the surroundings of Beru are probably not related to a Walanae River terrace system, but instead belong to Subunit B of the Beru Member, which is the youngest exposed interval of the Walanae Formation in this area. Other coarse gravels associated with artefacts are thought to belong to an old alluvial fan system, which could develop after a compressive phase resulting in the uplift of the Puncakoro Block to the south. Based on compositional differences, these Alluvial Fan Gravels are supposedly younger than Subunit B of the Beru Member, and may be Middle or Late Pleistocene in age.

4. Sulawesi: description of the Elephantoidea remains

Introduction

Hooijer (1949) announced the presence of a dwarf elephantoid among the first fossils recovered by van Heekeren in the southwestern arm of the island Sulawesi, at the locality Sompo. Subsequently, collecting at several localities yielded more fossil material, which permitted Hooijer (1953a,c, 1954e, 1955b, 1972b) to establish the peculiarities of this species, which he named *Archidiskodon celebensis*. This species has a small size, the teeth being twice as small as those of *A. planifrons*, with which the molars bear great resemblance. It is further characterized by some primitive characters, such as the occasional presence of mandibular tusks and the development of premolars. In his revision of the Elephantidae, Maglio (1973) placed this species in the genus *Elephas*, which was followed by Hooijer (1974). The designation to the genus *Elephas* has been questioned more recently (Sondaar, 1984; Aziz, 1990; van den Bergh et al., 1992). In these papers the uncertain taxonomic position has been expressed by placing the generic name *Elephas* between quotationmarks, as will be done in the present work.

In addition to *"Elephas" celebensis*, the presence of *Stegodon* sp. among the fossils found in South Sulawesi was also announced by Hooijer (1953b). In his first announcement Hooijer still doubted whether the fragmentary material should be attributed to a pygmy *Stegodon* or to a normal-sized *Stegodon*. Later Hooijer (1964a) described additional material and concluded that all the *Stegodon* material from Sulawesi described so far belonged to a dwarf species, which he named *S. sompoensis*, after the locality Sompo. After the already mentioned collecting expedition on Flores, Timor and Sulawesi carried out in 1970, Hooijer (1972b) described more *Stegodon* material from Sulawesi. The new material included three molar fragments of supposedly large size from the localities Marale and Beru that Hooijer then ascribed to *S.* cf. *trigonocephalus*. In the same paper he reconsidered two molar fragments that had been determined as M3 fragments of *S. sompoensis* in 1964a, but which he now regarded as M1 fragments of the large-sized *S.* cf. *trigonocephalus*.

Fachroel Aziz of the GRDC at Bandung conducted fieldwork in South Sulawesi in 1985 and 1986, during which more fossil material was collected. Among this material were a fairly complete though damaged skull of *"Elephas" celebensis* from South Sulawesi. In 1989 dental and postcranial remains of a large-sized *Stegodon* from the island of Sangihe were recovered as wel (Aziz, 1990).

During the period from 1989 to 1993 field campaigns were conducted in Sulawesi by a joint team of the National Natural History Museum at Leiden (NNM), the Geological Research & Development Center at Bandung (GRDC) and the Institute of Earth Sciences at Utrecht (IESU), during which numerous elephantoid remains were collected. Most of these findings were surface collected, but also in situ fossils were excavated at various places. All these specimens are listed in Table 6. This material comprises 50 dental remains attributable to *"E." celebensis*, 11 dental remains and a skull attributable to *S. sompoensis*, 13 dental remains of *S.* cf. *sompoensis*, 57 postcranial remains of pygmy elephantoids, 5 dental remains attributable to *Stegodon* sp. B, 1 mandible with a molar fragment of *Stegodon* cf. sp. B, 9 dental remains of a *Stegodon* species, 9 postcranial elements of large-sized elephantoids, and finally, 1 molar fragment of a highly advanced *Elephas* species. Some of these findings have been discussed in two earlier papers (van den Bergh et al., 1992, 1994).

In 1993 the Lore Utara district in Central Sulawesi was visited, where elephant fossils reportedly had been discovered for the first time by local villagers (Bartstra & Hooijer, 1992; van den Bergh et al., 1994). Furthermore, a few isolated elephantoid fossils from South Sulawesi have been mentioned recently by Bartstra & Hooijer (1992) and Bartstra et al. (1994).

Chapter 4 will give a description of the recently discovered elephantoid material from Sulawesi and summarize the present data on the various taxa that can be recognized.

"Elephas" celebensis (Hooijer, 1949)

Archidiskodon celebensis nov. sp.; Hooijer, 1949: pl. VIII, figs. 1-3.
Archidiskodon celebensis Hooijer; Hooijer, 1953a: pl. XIX.
Archidiskodon celebensis Hooijer; Hooijer, 1953c: pl. VII, figs. 1-15.
Archidiskodon celebensis Hooijer; Hooijer, 1954e: pls. XX-XXII.
Archidiskodon celebensis Hooijer; Hooijer, 1955b: 89-92.
Archidiskodon celebensis Hooijer; Hooijer, 1972b: pl. 1; pl. 2, figs. 3-4.
Elephas celebensis (Hooijer); Maglio, 1973: 46-7.
Elephas celebensis (Hooijer); Hooijer, 1974: 92.
"Elephas" celebensis; Sondaar, 1984: 229.
"Elephas" celebensis; Aziz, 1990: 42-55, pl. III, figs. 1-4, pl. IV, figs. 1-3.
"Elephas" celebensis (Hooijer); van den Bergh et al., 1992: 31, fig. 5A
Elephas celebensis (Hooijer); Bartstra & Hooijer, 1992: 116, fig. 2.
"Elephas" celebensis (Hooijer); van den Bergh et al., 1996: 242, fig. 23.2a (below the figure erroneously indicated as *Stegodon sompoensis*).

Holotype — An incomplete, unworn, dextral posterior M^2 fragment (specimen A: Hooijer, 1949: pl. VIII, figs.1-2), kept at the NNM at Leiden.

Hypodigm — The paratype (specimen B: Hooijer, 1949: pl. VIII, fig. 3) is a dextral, posterior M^3 fragment. There are 9 premolar and milkmolar remains described by Hooijer (1953c: pl. VII), which are presently kept in the collection of Hans van Essen. Besides the type specimens there are around 40 identifiable molar remains kept at the NMNH and the GRDC, and two skulls (one fragmentary skull at the office of the Lembaga Purbakala at Jakarta, and a more complete one with a complete M^3 kept at the GRDC). The GRDC material, which is listed in Table 6, includes milkmolars, premolars and molars, mostly fragmentary. Furthermore, there are various tusk fragments and a dextral, incomplete humerus (GRDC LR-3707), which can be attributed to the present species.

Type locality — Sompo (also written as Sompe or Sompoh; 4°15′S, 120°00′E), Soppeng District, South Sulawesi Province, Indonesia.

Age and localities — Remains of this species have been found in the surroundings of the following villages, places and rivers: Sompo (FVL-25), Lepangeng (FVL-1), Sabbang Baru (FVL-26), Beru, Ciangkange (FVL-22, 23), Celeko (FVL-27), Calio, Lonrong, Sare Batue, Paroto, Palangiseng, Padali (all villages), Marale, Bulu Cepo (places) and in the surroundings of the Lakibong River. Except Lonrong and Padali, all these localities are situated in the Sengkang Anticline area east of the East Walanae Fault (Soppeng District, Southwest Sulawesi). Stratigraphically all the localities can be placed in the Beru Member, which constitutes the uppermost, terrestrial part of the Walanae Formation. The age of the Beru Member is Late Pliocene (lower boundary of the Beru Member dated at 2.5 Ma), presumably continuing into the Early Pleistocene and perhaps even early Middle Pleistocene for Subunit B of the Beru Member.

Original diagnosis — See Hooijer (1955b: 89).

Revised diagnosis — (modified after Hooijer, 1955b, and van den Bergh et al., 1992: 31) Cranium very short and high; fronto-parietal region very narrow between the temporal fossae, showing antero-posterior convexture; absence of dorsal parietal swellings; well developed, strongly flaring fronto-parietal crests; orbits strongly projecting with a thickened rounded edge; premaxillary tusksheats directed forward and downward, diverging and separated by a shallow, triangular interalveolar fossa; mandibles with prominent, downturned symphysis, occasionally provided with functional mandibular tusks (males?); lower tusks piriform in cross section, or with only one median longitudinal groove; upper tusks slightly curving and weakly laterally compressed; molar size around half the size of equivalents in *Elephas planifrons* Falconer & Cautley 1845; x10x or x11x lamellae on the M3; crown height equaling or slightly exceeding width; strong cement coverage; lamellae characteristicly possessing 4-6 digitations, of which the two median ones are prominent; digitations separated by shallow clefts; anterior and posterior median pillars prominent at two-third below the apex of the lamellae but rarely free at their apices; median pillars produce pronounced sinuses upon wear; upon further wear the enamel wear patterns or loops become sub-lozenge to sub-triangular in shape; interlamellar valleys usually narrower than the antero-posterior thickness of the lamellae and U- or V-shaped at their base; relatively thick enamel (2.0-3.7 mm in the M2/M3); enamel very weakly or not folded except some irregular folds at the position of the median pillars; enamel consists of a thicker inner layer and a thinner outer layer that comprises less then one third of the total enamel thickness; presence of functional premolars (P3 and P4) in the upper and lower jaw.

Differential diagnosis — *"Elephas" celebensis* has a similar small size as *Stegodon sompoensis*, with which it concurs in several localities. It differs from the pygmy stegodont in lacking 'Stufenbildung' at the worn enamel surfaces and the delicate enamel wrinkling seen in stegodont molars. *S. sompoensis* molars lack the median pillars and associated median sinuses seen in *"E." celebensis*. *S. sompoensis* has almost parallel oriented tusksockets, whereas those of *"E." celebensis* are flaring. The 'guilloches' pattern visible in cross sections of tusks of *S. sompoensis*, and of stegodonts in general, is rarely visible in *"E." celebensis* tusks, both upper and lower ones. Instead, cross sections of tusks of the latter mentioned species show a radiate fracture pattern. In addition, concentric incremental lines are usually developed in *"E." celebensis* tusks (lower and upper), while these have not been noticed in the *Stegodon* tusk material from Sulawesi. The braincase of *"E." celebensis* is relatively narrower between the temporal lines but comparatively broader between the postorbital processes or zygomatic processes of the frontals.

Description of the material

Molars — The 1985-1986 and 1989-1993 collections contain 33 jaws with molars, isolated molars and molar fragments. Of 23 specimens the rank of the molar(s) can be positively identified. In addition to the material already described by Hooijer (1949, 1953a,c, 1954e, 1972b), most dental elements are now known either by complete specimens or fragments, except for the dP_2. Locality information of the new specimens described below are given in Table 6 and in chapter 3. Summary measurements of the molars of *"Elephas" celebensis* are presented in Table 30.

dP_3: n = 1 (NNM: Hooijer, 1953c: 224, pl. VII, figs. 5-6) The isolated dP_3 described by Hooijer (1953c) is very worn. It has 6 lamellae and measures 32 mm by 20.5 mm. The LF amounts 17.8 and the ET is 0.9 mm. It has two roots diverging in antero-posterior direction.

P_3: n = 4 (GRDC S-3949, Lp-3196, Lp-3192. NNM: Hooijer, 1953c: 223, pl. VII, figs. 3-4) S-3949 (Pl. 3, figs. 1-2) is a dextral mandible fragment with a P_3 and the anterior fragment of a dP_4. The latter has x$3^1/_2$- lamellae preserved and a length of 33+ mm as far as preserved, against a width of 24.6 mm at the third lamella. The LF is 12.3 mm. This milkmolar was clearly larger than the dP_3 described by Hooijer (1953c: pl.VII, figs.5-6) and thus must represent a dP_4, which indicates that the premolar in front of it must be a P_3. The P_3 has x3x lamellae, all worn. The three digitations of the anterior halfridge are just abraded by wear, whereas the first and second lamellae show the development of completed enamel loops. The tiny wear patterns show anterior and posterior medial sinuses similar to those in molars. Of the third lamellae the digitations are again abraded into a single crest in which dentine is not yet exposed and median sinuses are not developed. The P_3 has a total length of 20.8 mm. It widens in posterior direction, though a weak constriction is visible between the first and second lamellae. The first lamella has a basal width of 12.4 mm. The second one is 14.9 mm wide while the maximum width of 15.2 mm occurs at the third lamella. The worn height measures 9.6+ mm. The LF is 20.8. The ET varies between 1.2 and 1.6 mm. A little cement is deposited between the lamellae. There is a diastema of several mm between the P_3 and the dP_4 behind it, and the P_3 lacks a posterior contact facet. Its well developed root is exposed over a vertical distance of 19 mm. Just below the crownbase it has a antero-posterior diameter of 18.5 mm against a maximum width of 12 mm posteriorly. Further down a constriction divides the root in an anterior and a posterior part, both parts still connected in the middle.

The isolated specimen believed by Hooijer (1953c) to represent a sinistral dP_2, is less worn. It measures 18.8 × 12.7 mm and corresponds in size and shape with specimen S-3949, both being oblong, slightly constricted in the middle at the base and widest posteriorly. Contrary to S-3949, the Hooijer specimen was isolated, which made it difficult to ascertain its rank. A dP_2 of *E. planifrons* erroneously figured by Falconer & Cautley (1846: pl. 14, figs. 10, 10a) as *E. hysudricus* (see Falconer 1868 II: 92), appears relatively wider than both P_3s of *"E." celebensis* here under consideration (heaving a L/W ratio of 1.33 versus 1.35-1.48 in the P_3 of *"E." celebensis*). Falconer & Cautley (1845: pl. 12, figs. 8, 8a and 9) also figured a mandible fragment of *E. planifrons* with a P_3 emerging from below the worn remnant of a dP_3. This one has an elongated rounded form, but shows no distinct ridge divisions (Falconer 1866, II: 93). It has about the same dimensions (c. 20 × 13 mm) as the P_3s of *"E." celebensis* and with a L/W ratio of about 1.5 it is more elongated than the dP_2 of *E. planifrons*. Compared to the other teeth of *E. planifrons* the P_3 is rather small considering the fact that milk-molars and molars of *E. planifrons* are all considerably larger in size as compared to equivalents in *"E." celebensis*. This, together with the fact that various *"E." celebensis* premolars were found worn and thus functional, could mean that the premolars were of relatively greater importance in this dwarfed species from Sulawesi.

Because the Hooijer specimen resembles closely the P_3 in mandible fragment S-3949, it is more likely that the Hooijer specimen also represents a P_3. The Hooijer specimen has no roots preserved but possesses a constricted pulp cavity.

In both juvenile mandibles Lp-3196 and Lp-3192 the only part that remains of the P_3s are the in longitudinal cross section '8' shaped, constricted roots. These roots measure 22.3 × 9.9 mm and 22.8 × 10 mm respectively, which would correspond with the dimensions of the other two P_3 specimens.

dP_4: n = 4 (GRDC Lp-3196, Lp-3192, S-3949. NNM: Hooijer, 1953c, p. 226, pl. VII, fig.m 8). The specimen determined as a fragmentary dP_4 by Hooijer (1953c) consists of -3- worn lamellae, with a maximum width of 22 mm. Lp-3196 is a sinistral mandibular ramus of a juvenile individual, with the anterior, broken, part of the M_1 still in the alveole and in front of it two broken teeth, of which only the roots remain. The outline of the root in front of the M_1 shows a keyhole pattern with a constriction anteriorly. The total length of the root is 51 mm, the width 18 mm. The length of this root is considerable larger than the dP_3 described by Hooijer (1953c), which suggests that the root is of a dP_4. Anteriorly of this dP_4 root there is a second, smaller root in front of the jaw. The crown is broken and the root, which shows an '8' shape and is double, is 22.3 mm long and 10 mm wide. This size appears to be much smaller than the dP_3, but corresponds with the size of the P_3 specimen S-3949.

Lp-3192 (Pl. 3, fig. 3) is a dextral mandibular ramus (of another individual as Lp-3196) in which the M_1 is more complete, but with two anterior teeth also broken at the roots. The largest root in the middle consists of an anterior hook and a larger posterior rootmass separated from each other and thus broken at a lower level than in Lp-3196. The total length from the anterior hook to the anterior surface of the M_1 amounts 55 mm, which must have been approximately the length of the dP_4. Anteriorly in the jaw a double '8'-shaped root, similar as in Lp-3196, is of the P_3. It is 22.8 mm long.

In the dextral mandible fragment, S-3949, the anterior part of the dP_4 remains (length as far as preserved = 33+ mm). The dP_4 has $x3^1/_2$- lamellae left, which are considerably worn to such an extent that the dentine of the anterior two lamellae has fused at the buccal side. The largest measurable width at lamella 3 amounts 24.6 mm. This lamella shows the characteristic loxodont wear pattern. Cement is only deposited between the lamellae but the flanks are free of cement. The LF is 12.3. The ET varies between 1.4 and 1.5 mm, the enamel being delicately wrinkled with 2-4 folds per cm and an amplitude of 0.5 mm or less.

P_4: n = 2 (GRDC 1307. NNM: Hooijer, 1953c: 227, pl. VII, figs. 12-13). Specimen 1307 (Pl. 3, figs. 4-5) is a fragment of the sinistral horizontal ramus of a mandible. The medial part of the ramus is broken away. In front a small unerupted tooth remains still in the alveole. Behind it is a portion of the root of a molar, which had erupted above the gingival border. The tooth in front thus represents a premolar and not a milkmolar. The root posteriorly of this premolar is broken along its midline so that only the lateral portion remains. It consists of an anterior hook and the anterior portion of a larger, posterior rootmass. The anterior hook is fractured through the pulpa cavity and half its transverse diameter from its buccal margin to the pulpa cavity is 11 mm, while the antero-posterior diameter measures 19 mm. The total transverse diameter of the hook can be estimated to at least 20 mm, but probably more. It could belong to an M_1. Further, the size of mandible 1307 must have been considerably larger than the juvenile mandibles S-3949 and Lp-3192, which are both mandibles in an ontogenetic stage characterized by the presence of an erupted P_3. The premolar in front of 1307 therefore can only be a P_4, also because of its larger size compared to the various P_3s in the collection. The P_4 has x3x unworn lamellae. It is 31 mm long and has an elongated oval shape. The anterior halflamella has two digitations and is 13 mm wide against a height of 13 mm. Its apex is inclined backward. The first lamella is estimated to have a width of 17e mm, though the exact width can not be measured because its buccal side is covered at the base. Its apex is broken so that the height and number of digitations can not be given. The enamel figure visible at this lamella is ovally shaped and has no median sinuses. The ET varies between 1.8 and 2.0 mm. The maximum width of 19e mm occurs at the third lamella, which has also the greatest crown height of 21 mm, giving an hypsodonty index of 110e. It bears four neatly aligned digitations. The fourth lamella is 18e mm wide and 20.5 mm high, and also bears four aligned digitations. The posterior halflamella consist of a single, transversely elongated conule, which is 8.5e mm wide and 16 mm high. The root is exposed on the lingual side. It is broken 15 mm below the crownbase and consists of an anterior and a posterior portion, which are still connected as far as preserved but marked by a transverse constriction. Its total length just below the crownbase is 26 mm. The width of the root at the broken end is 11 mm anteriorly versus 14 mm posteriorly. A posterior fragment of a P_4 of *E. planifrons* is figured by Falconer & Cautley (1845: pl. 12, figs. 10, 10a and 11). It is unworn and still in the alveole in front of a complete M_1. Of the P_4 there are -1x ridges preserved, with 4 digitations on the fully developed ridge. The width (c. 30 mm) is considerably larger than that of the P_4 of *"E." celebensis*.

Hooijer (1953c: pl. VII, figs. 12-13) considered an isolated tooth to represent a P_4. The plate formula is x3x. It has a similar morphology as compared to the P_3s, but is considerably larger, measuring 28.5 × 20.3 mm. It corresponds in size and shape with the P_4 in mandible 1307, but morphologically it differs slightly from the latter in having a median cleft splitting the anterior lamella. Nothing of such a median cleft is visible in the (apically broken) anterior lamella of specimen 1307. Nevertheless, this small difference is considered as a variation and the Hooijer specimen probably represents a P_4 as well. The ET varies between 1.6 and 1.8 mm, which is also similar as in 1307. The root is broken. An isolated and much worn premolar bought at Sangiran is figured by Hooijer (1982: pl. I, figs. 4-5) and determined as a P^4 of *E. planifrons*. It measures 41 × 27.5 mm and has x3x ridges, with the notion that an extra, aberrant incomplete ridge is inserted on the lingual side in between the second and third ridges. However, van den Bergh et al. (1992) are of the opinion that the occurrence of *E. planifrons* on Java is not sufficiently proven on dental and cranial remains other than the few premolars attributed to this species (see also below under P^3 and P^4) and that care should be taken in assigning these isolated specimens as specific premolars of *E. planifrons*.

M_1: n = 7 (GRDC S-2412, Lp-3196, Lp-3192, L2-2378, STL/010186-20. NNM: Hooijer, 1953a: 315, pl. XIX, upper right and lower left figures. Bartstra & Hooijer, 1992: 116, fig. 2). The dextral M_1 described by Hooijer (1953a: 315) originates from Sompe and is complete but half worn. It has x8x lamellae, is 85 mm long and has a maximum width of 31 mm. The hypsodonty index at the last, unworn lamella is 94. The LF is 11. It resembles closely a specimen figured more recently (Bartstra & Hooijer, 1992: fig. 2), which reportedly measures 80 × 30 mm and also bears x8x lamellae.

S-2412 is a sinistral unworn M_1 fragment consisting of $-^{1}/_{2}3-$ lamellae. Cement coverage is strong, leaving only the digitations free, of which there are 4 or 5. The anterior lamella has a width of 29.3 mm, the most posterior preserved one 31.4 mm. The maximum width might have been slightly larger, but clearly the width of S-2412 fits well with the complete M_1s mentioned above. The h/w index of the three lamellae varies between 126 and 132. The fragment is strongly curved which indicates that it is a lower molar fragment. Due to the curvature the lamellar frequency at the buccal side is considerably higher than lingually (11.8 versus 8.2). This gives a LF of 10. The ET, which can be measured at the broken anterior lamella, is 2.3 mm.

The dextral mandible Lp-3192 has a complete M_1 still in the alveole. The molar is partly exposed because the covering bone sheet has been largely broken away (Pl. 3, fig. 3). It has x8 lamellae, entirely uncovered by cement but already fused at their base. The antero-posterior length is 84 mm apically, while the maximum length at the crownbase is estimated at 94e mm. The lamellae have 5-7 digitations. Due to the lack of cement, the anterior and posterior medial pillars, which would give the anterior and posterior sinuses upon wear, can be distinguished in the lower two-third of the valleys between the lamellae. The largest width can not be exactly measured because the crownbase is covered by bone, but it is estimated at 30e mm. The maximum height is estimated at 32e mm, which gives an H/W index of c. 106e. The lamellar frequency on the occlusal surface is 9.4, on the lingual side 8.4, but it cannot be measured buccally. There is another juvenile mandible fragment, Lp-3196, with only an anterior, buccal portion of the M_1 preserved. This molar was not yet fully matured, and only the anterior three of the in total five partially preserved lamellae have fused at the base. The lamellar frequency along the broken midline of the molar amounts 11.1 at the base. The ET is 1.6-2.2 mm, but the enamel did probably not yet reach its full thickness.

Specimen L2-2378 is a sinistral, halfworn anterior M_1 fragment. The occlusal surface is slightly concave indicating that it is of the lower side. There are $x3^{1}/_{2}-$ lamellae preserved, which show the medial anterior and posterior sinuses in the enamel wear patterns. The width of the lamellae from the first to the third one measures 27.7 mm, 29.3 mm and 29.2 mm, successively, which is including some cement that covers the flanks. The LF amounts to 11.5. The ET varies between 2.3 and 2.8 mm, of which around 0.6 mm forms the outer enamel layer. The enamel is weakly folded with 0.5-3 folds per cm with an amplitude of less than 0.5 mm.

Finally, there is a posterior M_1 fragment with -5x worn lamellae, STL/010186-20. The largest width of 35.2 mm occurs at the most posterior lamella. Cement is again strongly developed. The LF is 9.7. The wear patterns are of the characteristic type, with the posterior medial sinus slightly weaker developed than the anterior one. The enamel is hardly folded, rather undulous to straight, contrary to the other M_1 specimens. The ET lies around 1.7 mm.

M_2: n = 3 (GRDC L1-2356, LR-2737. NNM: Hooijer, 1954e: 110, pl. XXI, fig. 1, pl. XXII, fig. 1) The best preserved M_2 specimen is described by Hooijer (1954e), still in the mandible. All lamellae except for the posterior halflamella are worn. In front the tooth is damaged, but the length can be estimated from the alveolar outline of the anterior hook. The specimen measures 115e × 38 mm. The plate formula is $(x^{1}/_{2})^{1}/_{2}8x$ and the LF equals 8.6. The ET varies between 2.3 and 2.7 mm and the enamel is hardly folded. The widths of the successive lamellae can be given as follows: posterior halflamella = 20(c) mm, I = 31.6(c) mm; II = 35(c) mm; III = 36(c) mm; IV = 38(c) mm; V = 37.5(c) mm; VI = 34.6 mm; VII = 33.5 mm. Lamella VIII is damaged lingually. As noted by Hooijer (1954e) the crown terminates rather abruptly behind, indicating that is does not represent an M_3. It is also too large for an M_1.

Specimen L1-2356 is an unworn posterior fragment consisting of -2x lamellae. The width of the penultimate lamella is 41e mm, the height 42 mm, which gives an h/w index of 102. The same measurements for the last lamella are 41.4 mm and 38.5 mm with an h/w index of 93. The ET is 3 mm, the outer enamel layer occupying less than one third of the total ET. There are 4 digitations on the posterior lamella.

LR-2737, a sinistral posterior M_2 fragment, has -3x lamellae preserved. It has a posterior contact facet and terminates abruptly, indicating that we deal with an M_2. In the most anterior lamella a complete enamel loop has been formed, showing a single anterior median sinus and a weaker, bifurcated posterior one. Of the posterior two lamellae the digitations, of which there are 5 to 6, are just abraded by wear. The largest width of 41.1 mm occurs at the penultimate lamella. The LF amounts 9.0 and the ET varies between 2.2 and 2.9 mm. The enamel is weakly folded with 0-2 folds per cm of less than 0.5 mm amplitude.

M_3: n = 8 (GRDC LR-3517, SCL/030186-41. NNM: Hooijer, 1953a: 312, pl. XIX, upper left and lower right figures; Hooijer, 1954e: 112, pl. XXI, fig. 4, pl. XXII, fig. 2; Hooijer, 1954e: 110, pl. XXI, fig. 2; Hooijer, 1954e: 110, pl. XXI, fig. 3; Hooijer, 1954e: 110, table 3; Hooijer, 1972b: 5, pl. 2, figs. 3-4) The specimen described by Hooijer in 1953a is a complete M_3 still in a sinistral jaw. A small, completely worn remnant of the M_2 is still in place in front. The M_3 has x11x lamellae and measures 166 × 42.2 mm. The anterior 6 lamellae are worn. As the molar is still embedded in the jaw not al the W measurements could be taken. The lingual side of the jaw had been removed however, so that the height measurements of the posterior, unworn lamellae can be given. The measurements are: anterior halflamella: W = 24 mm; 1: W = 38.5 mm; 2: W = 41.8 mm; 3: W = 42.2 mm; 4: W = 41e mm; 5: W = 41e mm; 6: H = 49e mm; 7: H = 47 mm; 8: H = 45 mm; 9: H = 41 mm; 10: H = 39 mm; 11: H = 31 mm; posterior halflamella: H = 26 mm. The LF is 7.1. The ET varies between 2.6 and 3.2 mm. The lamellae possess 4-5 digitations. Enamel folding is hardly developed, the EF lying between 0 and 1 folds per cm, with an amplitude of less than 0.5 mm. Of the jaw a large portion of the downturned symphysis is preserved, which happens to be edentulous.

Another sinistral mandible fragment described by Hooijer (1954e: pl. XXI, fig.4 and pl. XXII, fig. 2) possesses an alveole for tusks in the downturned symphysis. A posterior molar remnant, believed by Hooijer to represent an M_2, is present in the jaw. The plate formula can be given as $-(2^1/_2)^1/_24x$, but as the anterior root is missing at least, there must have been originally more than 7 lamellae. All remaining lamellae are worn except the posterior halflamella, which is completely covered by cementum. The mandibular ramus is broken at the level of this posterior halflamella. The anterior portion of the molar, including the anterior root, had been shed. The length as far as preserved, including a portion of the roots that remains in front, is 108+ mm. The W measurements of the successive lamellae are: posterior halflamella = 13(c) mm; I = 30(c) mm; II = 40.7(c) mm; III = 44.2(c) mm; IV = 48(c) mm. The LF amounts to 6.6. The ET varies between 3.0 and 3.5 mm. There are 0.5-1.5 folds per cm with an amplitude of up to 1 mm. Hooijer (1954e: 112) noted that there is a posterior contact facet, which made him conclude that the present specimen represented an M_2. However, reexamination of the specimen revealed that a posterior contact facet is not evident. The comparatively large size and associated low LF in combination with the fact that the molar is strongly tapering, makes it more likely that we are dealing with an M_3. The other specimens described by Hooijer are incomplete posterior M_3 fragments.

Specimen LR-3517 is a large, tapering posterior portion of a dextral M_3. It has -7x lamellae preserved, of which only the last one is unworn. Anterior and posterior medial sinuses are well developed in the halfworn lamellae IV and V, while the enamel wear pattern of the more worn anterior lamellae is lozenge shaped. The number of digitations on the last two lamellae amounts four. The length as far as preserved is 98 mm. The largest width of 42.5 mm is at lamella V. The LF is 7.3. The ET varies between 2.7 and 2.9 mm, with the outer layer occupying less than one third of the total ET. The enamel has 0 to 2 folds per cm with an amplitude of less than 0.5 mm.

Specimen SCL/030186-41 is an intermediate portion of lower molar with -4- unworn lamellae preserved. Though the fragment, which lacks the roots, is probably of the anterior region of the tooth and does not show any tapering, its large width of 53.1 mm suggests that it represents the last lower molar. The lamellae have 4 to 5 digitations and vary in height between 48.2 and 51.0 mm. The h/w indices vary between 95 in the two posterior lamellae and 97 in the most anterior one. Cement is only developed between the lamellae. The LF is 5.8.

dP^2: n = 1 (NNM: Hooijer, 1953c: 228, pl. VII, figs. 14-15) The isolated complete but worn specimen described by Hooijer (1953c) was taken to represent a P^3. However, this specimen differs from the P^3 specimen in the maxilla fragment No. GRDC-1344 in being wider and having a more rounded shape (21.8 × 19.0 mm) and in possessing x2x instead of x3x ridges. It has a posterior contact facet and rather thick enamel (ET = 1.5 mm). The root is broken, but from what is left of it an “8-shaped” outline can be deduced, suggesting that the root was double. The specimen figured by Hooijer probably represents a dP^2.

dP^3: n = 1 (NNM: Hooijer, 1953c: 224, pl. VII, fig. 7) The specimen figured by Hooijer (1953c) is a posterior fragment consisting of -3x lamellae. Hooijer thought it to represent a dP^4, but the relative small maximum width of 25.3 mm at the penultimate lamella in combination with a LF of 17.9, suggest that it represents a dP^3.

P^3: n = 3 (GRDC 1344; L-3985. NNM: Hooijer, 1953c: pl. VII, figs. 1-2). A dextral maxilla fragment, specimen 1344 (Pl. 3, figs. 6-7), has the double root of a milkmolar partly preserved. The size of the root is at least 35 mm long as far as preserved and more than 8 mm wide. It consists of an anterior hook and a larger posterior rootmass.

Its double-rooted morphology and dimensions correspond with a dP^4. In front of this root there is an alveole with in it a complete, unworn P^3, which had not yet erupted. This P^3 has a length of 20.3 mm and possesses x3x lamellae. The anterior halflamella has three digitations, the first, second and third lamella all possess four, whereas the posterior halflamella has two minute cusps. The shape of the tooth is ovaloid, with the widths and heights of the successive lamellae as follows: anterior halflamella = 8 × 11.3 mm; first lamella = 12.9 × 16.7 mm; second lamella = 15e × 15.4 mm; third lamella = 13e × 13.3 mm; posterior halflamella = 7e × 11.2 mm. The morphology of the first lamella is distinct from the two posterior ones. A median cleft splits it in two parts, each part bearing two digitations. Of the two digitations of the buccal part, the medial one is located posteriorly of the lateral one, whereas in the lingual part, also with two digitations, the medial one is placed anteriorly of the lateral one. In the two posterior lamellae on the other hand, all four digitations are aligned. Cement occurs between the lamellae.

In shape and morphology this P^3 matches exactly the isolated worn specimen figured by Hooijer (1953c: pl. VII, figs. 1-2), which was thought to represent a dextral dP^2. This specimen measures 19.9 × 13.9 mm, also with the largest width occurring at the posterior lamella and not at the middle one like in the lower P_3. The worn isolated specimen described by Hooijer (1953c) has an ET of c. 1.5 mm. The remains of the root show that it was constricted in the middle.

A third isolated, sinistral P^3 is represented by specimen L-3985. Again the morphology is the same, with x3x lamellae and a median cleft dissecting only the anterior lamella. This specimen is slightly smaller (18.8 × 14.2 mm) than the other two. The largest width occurs again at the lamella 2. Cement has filled the valleys. The buccal conelets of the anterior lamella are broken, so that the ET could be measured. This varies between 0.6 and 0.8 mm. The first lamella has the largest height of 10.1 mm (at the lingual portion), giving a h/w index of 85. The second and third lamellae are both 9.6 mm high, giving h/w indices of 68 and 76 respectively, which is lower than in the unworn specimen 1344. Further, the root of this specimen is largely preserved. It consists of a single root with a slightly constricted cross section, which is widest posteriorly.

A sinistral P^3 of *E. planifrons* is figured by Falconer & Cautley (1845: pl. 6, figs. 4-5). It occurs in a maxilla in front of a worn dP^4 but is itself only slightly abraded. Its shape is rather distinct from the P^3s of *"E." celebensis* in being much more rounded (L/W ratio of c. 1.1 versus 1.35-1.43 in *"E." celebensis*) and having the digitations huddled together in an irregular manner so that the division in x2x ridges is rather vague. Its size is almost twice as large (29.5 × 26.5 mm) as that of the *"E." celebensis* P^3s. A similar, but more worn specimen bought in Java and attributed to *E. planifrons*, is described by Hooijer (1982: pl. I, figs. 1-2). It has x2x irregular ridges, the posterior one divided by a strong median cleft, and measures 27.5 × 27 mm. This specimen seems too big for a dP^2 of *Stegodon trigonocephalus*, with L and W varying between 15-19 and 16-19 mm, respectively. As stated before, there is not much proof for the occurrence of *E. planifrons* on Java other than by the little known premolars, and care should be taken in assigning these isolated premolars to this species.

dP^4: n = 4 (GRDC 1342 and 1343 (pair of one individual), 890602-2. NNM: Hooijer, 1953c: 224, pl. VII, fig. 11) The dP^4 specimen described by Hooijer (1953c) constitutes a posterior fragment of -2x lamellae, with a width of 30.0 mm at the penultimate lamella and an ET varying between 1.3 and 1.4 mm.

A pair of complete dP^{4}s (Pl. 4, figs. 1-2) are represented by specimens 1342 (dextral) and 1343 (sinistral). They have a plate formula of x7x. All lamellae are worn to fully developed enamel loops with the exception of the most posterior one, of which the digitations are just abraded by wear. This lamella has 6 digitations. Only the anterior surfaces of the intermediate, halfworn lamellae have well developed medial sinuses, while posteriorly only weak bifurcated sinuses are developed. Cement is only developed between the lamellae. The lengths are 53 mm and 54 mm, respectively. The maximum width occurs in both specimens at the fifth plate (26 mm). The LF amounts to 14.4. The ET varies between 1.2 and 1.4 mm, with a very thin outer enamel layer. The enamel is delicately wrinkled with 2 to 4 folds per cm. The root is best preserved in 1343. Though the anterior hook is broken it can be seen that it supported the two anterior lamellae.

Specimen 890602-2 is an almost complete dextral dP^4, slightly damaged buccally at the anterior termination. Contrary to the foregoing specimens, it possesses only x6x lamellae. Of the last one the digitations, of which there are 7, are just abraded by wear. The penultimate lamella shows two enamel loops which are not yet connected: a larger lingual and a smaller buccal one. In the more anterior lamellae complete enamel loops have formed, though a conspicuous constriction is developed just buccally of the medial sinuses. The wearsurface is weakly convex. The dP^4 is 53 mm long. The first lamella is 22.6 mm wide. The width successively increases in posterior direction and the largest width of 27.7 mm occurs at the penultimate lamella. The LF is 12.8. The ET is c. 1.4 mm and the enamel is more coarsely folded than the paired specimens described above, with 1 to 2 folds per cm. The roots are threefold with the anterior hook supporting the 2 anterior lamellae. A smaller lingually developed root follows below the third lamella in front of the larger posterior rootmass.

P^4: n = 1 (NNM: Hooijer, 1953c: 227, pl. VII, figs. 9-10). A small isolated tooth with a round shape and x3x lamellae is considered as probably representing a P^4 by Hooijer (1953c). It is considerably larger (it measures 28.0 × 23.9 mm) than the upper P^{3}s described above, and could indeed represent a P^4. It has an ET ranging between 1.6 and 2.0 mm. An isolated upper premolar from Java was determined by von Koenigswald (1950: figs. 2a-b) as a P^3 of *Archidiskodon praeplanifrons*, a species considered to be slightly more primitive than *E. planifrons* from the Siwaliks. Its morphology resembles very much the *"E." celebensis* P^4 figured by Hooijer, but it has a larger size (37 × 35 mm). Hooijer (1953c: 227) thinks it more likely that the Javanese specimen represents a P^4 of *E. [A.] planifrons* because of its larger size than the P^3 figured by Falconer & Cautley (1845: pl. 6, figs. 4-6). However, also this interpretation remains uncertain unless the occurrence of *E. planifrons* on Java is proven by other dental or cranial remains (van den Bergh et al., 1992). The premolars from Java may represent a distinct primitive elephant, e.g. *"E." indonesicus* (Kretzoi).

M^1: n = 1 (NNM: Hooijer, 1954e: 109, pl. XX, figs. 4-5) The only M^1 fragment so far known is represented by the sinistral anterior fragment described by Hooijer (1954e). It has x6- lamellae preserved, of which the anterior three are worn. The maximum width is 33 mm, the h/w index of the last three lamellae lies around 118, and the LF is 10.9.

M^2: n = 6 (GRDC BC-2945, MTL/251285-1, SCL/030186-37. NNM: Hooijer, 1949: 206, pl. VIII, figs. 1-2 (= holotype specimen A); Hooijer, 1954e: 106, pl. XX, figs. 6, 8; Hooijer, 1954e: 107, pl. XX, figs. 2-3).

The holotype specimen A is an incomplete dextral M^2 with -$^1/_2$6x lamellae preserved, all unworn. The maximum width of 42 mm occurs at lamella III from behind. The LF is 7.3.

Aziz (1990: pl. IV, fig. 2) figured a complete sinistral M^2, which is specimen MTL/251285-1 mentioned above. This M^2 has x8 or x7x lamellae, all worn except the last one, which is c. 20% lower than the foregoing lamellae and could be considered as a halflamella. The anterior half-lamella is fused with the first lamella due to advanced wear. The anterior enamel surface is slightly damaged. The enamel wear patterns of lamellae 1 to 3, which are half worn, are lozenge shaped. Lamellae 4 to 6 are also expanded medially and possess strong medial sinuses anteriorly. These sinuses become wider with increasing wear (that is from lamella 6 to 4). The posterior sinuses are weaker developed and double or bifurcated. Lamella 7 has the digitations, of which there appeared to be 5, just abraded by wear. The slightly worn height of lamella 7 is 55+ mm. Lamella 8 or x is less high (h = 49 mm) and almost completely covered by cement. The occlusal wear surface is convex in antero-posterior direction but plane in transverse direction. The buccal half of the lamellae is slightly more worn than the lingual half. The maximum length is estimated at 136e mm. The first lamella has a width of 47 mm, the second 51 mm and from there it is increasing to the largest width of 58 mm at the seventh lamella. Cement is abundantly present covering the lingual flanks of the lamellae and most of the buccal flanks. The lamellar width measurements given above thus include some cement. The LF amounts to 6.4. The ET varies between 3.0 and 3.4 mm, with the outer enamel layer occupying less than one third of the total ET. The enamel is weakly folded with 0-2 folds per cm and amplitudes of 0.5 mm or less. A large portion of the root is preserved but covered by a thin sheet of maxillary bone laterally. The anterior hook supports x1$^1/_2$- lamellae.

SCL/0301186-37, a dextral M^2, is also complete and has a plate formula of x8x. It is smaller than the foregoing specimen, with a total length of 114 mm. Again the maximum width of 43 mm (including cement) occurs at the seventh lamella. Only the anterior four lamellae are worn to such an extend that complete enamel loops have formed, which have a similar pattern as in MTL/251285-1: the single anterior medial sinuses are stronger developed than the bifurcated posterior ones. The unworn posterior two lamellae have 6 digitations, of which the two medial ones are the largest. SCL/0301186-37 has a LF value of 8.2, which is higher than specimen MTL/251285-1 due to its smaller size and higher amount of lamellae. The ET varies between 2.0 and 2.3. A part of the root is preserved, which appears to consist of three parts: an anterior hook placed buccally, a second smaller lingual root and the large posterior rootmass. The anterior hook supports x1$^1/_2$- lamellae.

BC-2945 is a completely worn posterior M^2 remnant of the left side. It has a plate formula of -6x, but of the three anterior plates only the completely worn buccal half is preserved. The dentine of these lamellae was already fused along the medial axis. Due to lateral damage only the width of Lamella III and I can be given, which is 50 mm and 51 mm, respectively. The LF amounts to 7.6, and the ET varies between 2.9 mm and 3.1 mm.

M^3: n = 7 (GRDC: LUTL/151186-1 (in skull), SCL/030186-38, LCL/221086-1, 890522. NNM: Hooijer, 1949: 209-212, pl. VIII, fig. 3 (paratype specimen B); Hooijer, 1954e: 104, pl. XX, fig. 1. LPJ: Hooijer, 1972b: 2, pl. 1; pl. 2, fig. 1 (in skull)).

The paratype specimen described by Hooijer (1949) is of the dextral side and has -6x lamellae preserved, all worn except for the most posterior lamella and halflamella. The W measurements as given by Hooijer (1949: 210-211) are: I = 31 mm; II = 40 mm; III = 43 mm; IV = 48(c) mm; V = 49(c) mm; VI = 49(c) mm. The LF is 7.4, and the ET varies between 3 and 3.5 mm.

Hooijer (1954e) figures an incomplete posterior fragment of a sinistral M^3, having -4x lamellae preserved. The basal width of lamella IV amounts 42 mm. Later (Hooijer, 1972b) a partial skull is added with the sinistral M^3 complete. The complete M^3 in the skull has x11x lamellae and a total length of 160 mm. The largest width at lamella 6 reportedly amounts to 52 mm.

A more complete skull with the dextral M^3 complete is specimen LUTL/151186-1, which is figured by Aziz (1990: pl. III, figs. 1-4). The M^3 in the skull has x10x lamellae and a total length of 187 mm. The largest width of 56 mm occurs at lamella 7. All lamellae are worn. The LF is 5.7 and the ET varies between 2.2 and 3.5 mm. The skull is figured again in this paper (Pl. 5, figs. 1-2).

A dextral posterior M^3 fragment, specimen LCL/221086-1, is figured in van den Bergh et al. (1992: fig. 5A). It has -$^1/_4$7x lamellae preserved, of which the last two are unworn. The maximum width of 53 mm occurs at lamella VI from behind. The LF is 6.2 and the ET varies between 2.6 and 3.0 mm. Except for the complex medial sinuses, the enamel is unfolded in the lingual and buccal part of the enamel loops in this specimen. Both the anterior and posterior sinuses are bifurcated but asymmetrical upon slight wear (lamella V), becoming wider in a more advanced stage of wear (lamella VII). The posterior lamellae have 6 digitations. The h/w indices of the unworn lamellae II and III amounts 109.

Another posterior M^3 fragment is of the left side. In this specimen, SCL/030186-38, there are -$^1/_2$5x lamellae preserved. Lamella V is damaged laterally so that no width measurements can be taken. Lamella IV is 45 mm wide, the posterior ones becoming successively narrower as is characteristic for M^{3}s. Only lamella I and the posterior halflamella are unworn. Lamella IV and V are worn half down and show prominent single medial sinuses both anteriorly and posteriorly. In the less worn lamellae II and III the median sinuses are weaker developed. Lamella I has 4 digitations. The LF is 6.3. The ET varies between 3.4 and 3.7 mm, with the outer enamel layer occupying one fourth of the total ET. The enamel is very weakly folded, rather undulating, in the buccal and lingual portions of the enamel loops. In both last mentioned specimens the wear surface is convex in antero-posterior direction.

Specimen 890522 represents a small dextral posterior M^3 fragment with only -$^1/_4$2x worn lamellae preserved. The ET in this specimen varies between 3.2 and 3.7 mm, and again the enamel is hardly folded.

One posterior molar fragment (paratype specimen B: Hooijer, 1949: 209) was originally described and figured together with the holotype, both at that time thought to be either M^{2}s or M^{3}s. Later (Hooijer, 1954: 105) they are both regarded as M^{2}s. This seems true for the holotype specimen A, but specimen B is clearly tapering posteriorly and represents an M^3. Hooijer mentions that the LF of specimen B (LF = 7.5) is higher than the LF of the M^3 fragment (LF = 6) described in 1954 (Hooijer, 1954: p.104), and therefore specimen B is regarded as an M^2. However, as can be seen in Table 30, the size of the various elements varies considerably, and so does the LF. Specimen B consists of a worn dextral M^3, which has -$^1/_4$6x lamellae preserved. Both lamella V and VI are 49c mm wide, and this value seems to be close to the maximum width.

Molar fragments of uncertain rank: Besides the above mentioned molar remains there are a number of small molar fragments of which the rank could not be ascertained, but which could be positively ascribed to *"E." celebensis*. In these fragments the absence of scalloped enamel and the presence of a clear median sinus in the enamel wear patterns makes this determination possible. These fragments are listed in Table 6 as well.

Tusks

Lower tusks: n = 4 (GRDC: LCL/221086-24, BEUL/191086-6, 1364. NNM: Hooijer, 1954e: 116, pl. XXII, figs. 3-4) Hooijer (1954e) figured an 8 cm long portion of a lower incisive tusk of *"E." celebensis*, which is characterized by a vertically compressed cross section and a shallow median groove on the dorsal surface. The apex of the pulp cavity is just preserved in this specimen, and the dimensions at this level are 56 × 39 mm. The groove is 20 mm wide and 3 mm deep, and the cross section of the tusk appears kidney-shaped. A mandible with the alveole for a lower tusk in the downward protruding symphysis is also figured by Hooijer (1954e: 114, pl. XXII, fig. 2), though there are also a number of mandibles lacking this character. Hooijer (1954e) attributes the occasional presence of lower tusks to sexual dimorphism.

Recently more material of the lower tusks of *"E." celebensis* has been collected, which differs from the specimen described by Hooijer (1954e). Specimen LCL/221086-24 is a 17 cm long intermediate portion of a lower tusk, believed to be of the left side. Nothing of the pulpa cavity is preserved. The fragment is tapering distally. The cross section (Fig. 48) is distinct from the fragment described by Hooijer (1954e) in being pear-shaped or piriform instead of kidney-shaped. The incremental lines visible at the proximal broken end have the same shape as the cross-sectional outline, indicating that the grooved surface morphology is not due to secondary wear of the tusk. When seen in lateral view, the tusk is slightly curved upward. In dorsal view the medial border is very slightly convex, almost straight, while the lateral border is somewhat more concave. The transverse diameter proximally measures 44 mm, whilst at the most distally preserved end it is 31 mm. The vertical diameters proximally and distally are 30.5 and 22.5 mm, respectively. There is no enamel on the outer surface present.

The next fragment, specimen 1364, consists of a 7 cm long portion of a sinistral lower tusk, of which the ventral side is broken away. It is again slightly upward curved. The transverse diameter at the proximal end is 57 mm, while more distally the medial side is broken. On the dorsal side a clear concave longitudinal groove is preserved at the proximal end. This groove is situated laterally of the median axis of the tusk, similar as in tusk fragment LCL/221086-24. Likewise, the original cross section of fragment 1364 may have been piriform.

Another fragment (BEUL/191086-6), believed to be of the right side, is smaller and distinct in cross section compared with the foregoing two pieces. It is preserved over a length of 9 cm. The tusk is also curved upward and outward (the medial border being relatively more convex than in specimen LCL/221086-24), but its cross section has basically an oval shape, lacking clearly developed grooves except for a very weak and shallow one dorso-laterally. No pulpa cavity is included, and the transverse and vertical diameters are 36 × 25 mm at the broken proximal end and 30 × 22 mm respectively at the distal end. This specimen probably represents a more distal portion of the lower tusk as specimens LCL/221086-24, which may explain the distinct cross sectional morphology.

All lower tusk fragments bear no signs of wear on the preserved portions, leaving their functionality uncertain. However, the fact that tusks were not present in all mandibles (Hooijer, 1954e), suggests that females did not possess them or that at least not all individuals possessed them. Therefore their function for food gathering cannot have been very important.

More evidence for the occasional development of lower tusks can be found in the juvenile mandible Lp-3196, which is broken at the symphysis. An alveole with an oval cross section and a diameter of 8 mm is visible in the broken symphysal end.

Upper tusks: Before describing the maxillary tusk material attributable to *"E." celebensis*, some remarks must be made first concerning the criteria used to distinguish them from tusks of the other dwarf elephantoid present in the Walanae Fauna: *Stegodon sompoensis*. The distinction between *S.* cf. *sompoensis* and *"E." celebensis* tusk material can be made macroscopically, provided that the fragment is sufficiently large and/or weathered at the broken terminations. Adult upper tusks of *"E." celebensis* are slightly dorso-ventrally compressed giving an ovaloid cross-section, and are generally more curved when compared to *Stegodon* tusks. Unworn upper tusk fragments of the latter usually have an almost perfectly circular cross-section, though this character does not always make a distinction possible, especially in fragments where the ventro-lateral side is worn by use. More importantly, tusks of both species show a distinct micropattern of the tusk dentine in weathered cross-sections perpendicular to the length axis (Fig. 49). In cross-sections of *S.* cf. *sompoensis* tusks (and in tusks of *Stegodon* and most other advanced elephantoid taxa in general) the visible structure of the dentine shows the typical decussating pattern with curved parallel lines, starting obliquely from the outer surface, spiraling inwards, in two opposite directions. This leads to a pattern of minute lozenges with slightly curved borders, the so-called 'guilloches' pattern. In *"E." celebensis* tusks on the other hand, this 'guilloches' pattern is usually poorly visible on weathered cross-sectional surfaces, or not at all. Instead, a radiate fracture pattern can be better distinguished in most cases. This holds true for both upper and lower tusks, though the lower tusks are more strongly dorso-ventrally compressed and the fractures are developed perpendicular to the outer surface. The radiate fracture pattern may be related to a weaker or slightly distinct internal structure of the dentine. In addition, concentric incremental lines are usually developed in *"E." celebensis* tusks (lower and upper), whilst these have not been noticed in the *Stegodon* tusk material from Sulawesi.

The radiate cracking pattern in *"E." celebensis* tusks could be caused by specific diagenetic circumstances during fossilization, like the absorption and subsequent crystallization of salts in the dentine under marine or brackish water conditions. *"E."*

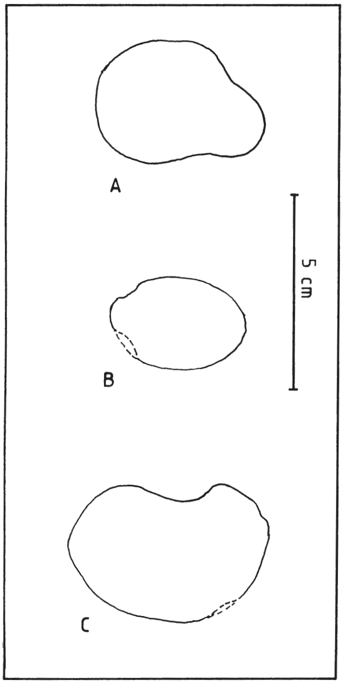


Fig. 48. Cross sections of lower tusks of *"Elephas" celebensis*. A: GRDC LCL-221086-24, sinistral. B: GRDC BEUL-191086-6, dextral. C: Specimen figured by Hooijer (1954e: pl. XXII, fig. 3.). All cross sections are taken on the most proximally preserved tusk surface. Of each tusk figured the upper side of the cross section represents the longitudinally concave side of the tusks.

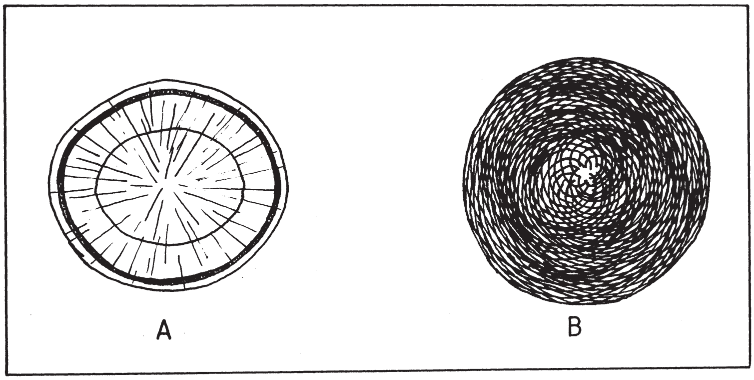


Fig. 49. Schematic representation of the macroscopically visible distinctive features visible in cross sections of tusks of *"Elephas" celebensis* (A) and *S. sompoensis* (B). In *"E." celebensis* the tusks are dorsoventrally compressed (ovaloid) whereas unworn sections of *S. sompoensis* tusks show a circular cross section. Concentric, dark-coloured, incremental lines were frequently observed in *"E." celebensis* tusks but not in those of *S. sompoensis*. The most distinctive feature however, concerns the 'guilloches' pattern, which is commonly developed in elephantoid tusks, but which is not visible in *"E." celebensis* tusks, and which was present in all tusk specimens attributable to *Stegodon*. Instead of the 'guilloches' pattern, the *"E." celebensis* tusks, both upper and lower ones, showed a radiate fracture pattern.

celebensis remains may have accumulated preferentially in estuarine environments and *S. sompoensis* tusks in fluviatile environments. The radiate cracking pattern observed in *"E." celebensis* tusks may have been due to specific environmental conditions. This could be for example the case at FVL-25a, where the fossiliferous layer directly overlies shallow marine layers. However, at other localities, like FVL-5 and FVL-3/4/4a, both tusk fragments with and without the radiate cracking pattern have been found. At FVL-5 no marine influences can be deduced for the vertebrate-bearing layer from the sedimentological or palaeontological context. The observed difference in cross-sectional tusk pattern between *"E." celebensis* and *Stegodon* tusks thus indeed seems related to a different dentine micromorphology, but this feature has not been further investigated during the present study. There remains to be mentioned another difference between the tusks of the two dwarf elephantoids from South Sulawesi. The upper tusks of *S.* cf. *sompoensis* tend to have a larger maximum diameter as compared to *"E." celebensis* tusks, though there is a considerable overlap (average max. diameter = 63 mm; range = 38-85 mm in *S. sompoensis* (n = 8) versus *"E." celebensis*: average max. diameter = 50 mm; range = 31.5-63 mm, n = 9). These measurements are based on isolated tusk fragments on which the maximum preserved diameter was measured. There is one juvenile *"E." celebensis* tusk fragment from FVL-5, with a diameter of only 19.1 mm (this fragment was not included in the average given above). The measurements for tusks of *S.* cf. *sompoensis* include two measurements taken on tusk sockets in adult skulls. One had a maximum diameter of 85 mm (specimen BC-3050) and the other a maximum diameter of 79 mm (premaxilla LIII-3036).

Deciduous upper tusk: n = 1 (GRDC: S-3951). Specimen S-3951 is a slightly curved tiny tusk with the apex of the conical pulpa cavity preserved proximally and distally worn into a rounded tip lacking enamel. The total length is 28 mm. The proximal transverse cross section is not perfectly circular but ovaloid. The largest diameter of 9.1 mm is that oriented perpendicular to the plane of strongest longitudinal curvature of the tusk. The smallest diameter of 7.5 mm runs parallel to this plane. The pulpa cavity has a diameter of 1 mm. The largest diameter/smallest diameter ratio (compression ratio) is 1.21.

Sikes (1971) mentions that the deciduous premaxillary incisors, or tushes, may reach a length of 5 cm in the African elephant. The tiny S-3951 probably also represents such a tush. Both the core dentine adjacent to the pulpa cavity and the superficial dentine layer are white, whereas the intermediate dentine is dark gray. A black concentric incremental line marks the transition between the white superficial layer and the dark gray intermediate layer. Unlike the permanent tusk material of *"E." celebensis*, no radiate fractures have developed in this deciduous tusk. With regard to this observation it is of notice that Sikes (1971) mentioned that the dentine of tushes differs from that of permanent tusks in lacking the diamond (= 'guilloches') pattern.

Permanent upper tusk: n = 6 (GRDC: 2252, 1341, 1328-1340, S-3952, LR-2759, 890602-3). Specimen S-3952 is a 10 cm long slightly curved tusk fragment lacking any sign of the pulpa cavity. The largest and smallest proximal diameters are 32 and 28 mm respectively, giving an l/s index of 1.14. An outer dentine layer is black (1-2 mm thick), while the dentine core is white. The radiate fracture pattern is only developed in the white core dentine but does not continue into the black outer dentine layer.

Specimen 2252 is a curved tusk portion of 6 cm long with an oval cross section in which the radiate fracture pattern is clearly developed. The largest diameter of 49 mm lies in the plane of the maximum curvature. The smallest diameter is 42.5 mm, which gives a compression ratio of 1.15. The fragment was found in situ as two halves that were split along the longitudinal plane tangential to the center. In the longitudinal cross section the distally converging incremental lines are visible, reminiscent of the successive positions of the wall of the pulpa cavity.

Specimen 1341 is a juvenile tusk fragment of 9.5 cm long. At the proximal end the pulpa cavity is included. The tusk is weakly curved with again the largest diameter oriented in the plane of the maximum curvature. The fragment is hardly thinning in distal direction. The proximal maximum and minimum diameters are 20.0 × 17.3 mm, while at the distal (broken) end they are 19.1 × 15.9 mm respectively. Thus, the proximal compression ratio amounts 1.16 versus a distal one of 1.20. In cross section again the radiate fracture pattern is developed except for a thin dentine surface layer.

LR-2759 is a 7 cm long portion of another juvenile tusk with a maximum diameter of 15 mm. It lacks wear or pulpa cavity, and therefore the original length of this tusk must have been considerably larger than 7 cm. The size seems too large for a tush. In cross section a black superficial dentine layer can be observed, which contrasts with the reddish core dentine. Again, only the core dentine shows the radiate cracking pattern.

No. 890602-3 is a 9 cm long tusk segment broken along the longitudinal axis. The remaining segment includes the center of the tusk and represents approximately one third of the originally cylindrical tusk. No pulpa cavity is preserved. The fragment is very weakly curved. Its diameter as far as preserved is 35 mm. The outer dentine layer has again a distinct, darker color than the white inner part of the segment. No ‘guilloches’ pattern can be observed, but instead radiate cracks are developed in the white inner dentine.

The last fragmentary tusk which will be described here was found on the surface broken in many smaller and larger fragments (specimens 1328-1340). Not all fragments fitted together but judging from the state of preservation they all belong to a single tusk. The largest fragment is broken longitudinally along the center. The diameter across this half is 52 mm. Nothing of the pulpa cavity is included. Again it shows the radiate fracture pattern in cross section, except for the outer layer. It also has several concentric incremental lines. Several smaller fragments must have formed part of the distal end of the tusk, as their outer surfaces are locally polished and showing striae. The largest of these worn fragments represents a tusk segment of 7 cm long. The outer surface as far as preserved is not round but consists of two almost flattened planes making an angle of 90 with each other and rounded at the corner where they meet. In cross section it can be observed that one of the outer surfaces, supposedly representing the ventral side of the tusk, cuts off incremental lines that run parallel to the surface perpendicular to it. It is on this supposedly ventral surface that striae are most prominently present. The striae are oriented mostly perpendicular to the longitudinal axis if the tusk. To a lesser degree striae are present which are oriented obliquely to the longitudinal axis, but none has an orientation parallel to it. Also other, smaller fragments are present with the striae perpendicular to the length axis of the tusk. This suggests that the tusks were used in some kind of transverse movement.

Mandibles — Various mandible fragments attributed to *"E." celebensis* have been described by Hooijer (1953a, 1954e). One of these is a mandible portion, which possessed a strongly developed and downturned symphysis with in it an alveole for a tusk. Three other mandibles appeared to have been tuskless. At present three more mandible fragments can be added, all belonging to juvenile individuals. They have already been mentioned in the sections describing the deciduous and premolars. Below only the recently collected material will be described.

n = 3 (GRDC: S-3949, Lp-3192, Lp-3196). A juvenile mandible fragment is represented by specimen S-3949 (Pl. 3, figs. 1-2). It is a dextral portion of the horizontal ramus lacking the symphysal region and broken in front of the ascending ramus. The ventral surface is broken away at the level of the mandibular canal. The fragment contains the P_3 and the anterior portion of the dP_4. The occlusal wear surfaces of the dP_4 and P_3 are on the same horizontal level, but the crownbase of the P_3 is much more elevated above the gingival border than that of the dP_4. Consequently, a large portion of the P_3 root is exposed, whereas that of the dP_4 is completely concealed by its alveole. The minimum dorso-ventral diameter of the mandibular ramus from the lateral alveolar rim of the dP_4 downward as far as the ramus is preserved, amounts to 40+ mm. The original dorso-ventral diameter at this level (measurement M5) is estimated to have been c. 50e mm. The transverse diameter at the most posteriorly preserved termination is 40 mm.

A larger mandible fragment is represented by specimen Lp-3196. It is a sinistral ramus fragment with the anterior part of an unerupted and not yet completed M_1 and the broken roots of the dP_4 and P_3. Judging from the molar progression it must have been in a slightly earlier ontogenetic stage as the foregoing specimen. The maximum preserved length is 175+ mm from the broken symphysis to the onset of the (broken) ascending coronoid process. Behind the root of the P_3 the medial side of the ramus is largely broken away, including the medial portion of the M_1. The mandible is rather slender and elongated at the front, and the preserved anterior portion of the ramus in front of the anterior alveolar border of the P_3 to the broken termination of the partial symphysis has a length of 60+ mm. This anterior portion points down with its ventral border making an angle of 160 with the posterior part of the horizontal ramus in lateral view. The minimum transverse diameter of the ramus in front of the anterior tooth (measurement M20) is 31.5 mm. The vertical height in front of the anterior tooth (measurement M5) can not be given because the dorsal border is damaged, but can be estimated to have been approximately 65e mm. In the broken surface of the anterior symphysis a cylindrical cavity with a diameter of 9 mm and a depth of 12 mm is present. The longitudinal axis of this cavity runs parallel with the longitudinal axis of the downturned anterior portion of the ramus, in a similar way as in the mandible described by Hooijer (1954e: 114), though in the latter one, which belonged to an adult individual, the relative and absolute dimensions of the cavity are much larger. Hooijer concluded that this cavity could not represent other than the alveole for a lower incisive or tusk, and likewise specimen Lp-3196 is thought to have been originally provided with a tusk.

Specimen Lp-3192 (Pl. 3, fig. 3) is a dextral mandible in a slightly more advanced ontogenetic stage than the foregoing specimen, as its entire M_1 is almost completed lacking only cement yet. Unfortunately, also in this specimen the P_3 and dP_4 are broken off at their roots. Though the anterior portion of the horizontal ramus is broken off more posteriorly in this specimen, just in front of the root of the P_3, its posterior portion is more complete than the foregoing specimen. It includes a large portion of the ascending ramus. The bony sheet covering the alveole of the M_1 is broken, but more anteriorly the medial side is largely intact. The total length as far as preserved is 202+ mm in the plane parallel to the ventral border of the horizontal ramus. The vertical height of the horizontal ramus just in front of the coronoid process (measurement M6) is 47 mm. The transverse diameter at the same level (measurement M18) is 54 mm. The inclined coronoid process expands rapidly in lateral direction. This is also the case in the adult mandibles described by Hooijer (1954e: pl. XXI, figs. 1, 4). The minimum transverse diameter in front of the anterior tooth (M20) is 33.3 mm. The ventral border at the transition between the horizontal and ascending ramii is rounded, lacking a well defined angle. The angle between the tangents of the ventral borders of the horizontal and ascending ramii is very wide, viz. 135. None of the adult mandibles described by Hooijer (1953a, 1954e) are sufficiently well preserved to measure this angle. A wide mandibular angle is not encountered anymore in the Pleistocene Elephantinae, but is still developed in the Stegodontidae and in the tusked mandibles of the earliest elephants, the stegotetrabelodonts (Maglio, 1973). It is generally considered a primitive character. However, a wide mandibular angle also occurs in the earlier ontogenetic stages of the more advanced brevirostrine Pleistocene and Recent elephants.

Skull — In 1986 Aziz found a fairly complete skull north of the Lakibong River at Tociapa (= FVL-7). The skull (GRDC LWTL/151186-1) was found in situ in a horizontal layer of pebbly sandstone pertaining to Subunit B of the Beru Member. The complete dextral M^3 present in the skull leaves no doubt that the skull belonged to *“Elephas” celebensis*. This is the second skull of *“E.” celebensis* known. The first one, in a much more fragmentary state, was described by Hooijer (1972b). Skull LWTL-151186-1 has been already figured by Aziz (1990: fig.7; pl. III, figs.1-4), and briefly described. A more detailed description will be given below.

Though the present skull is rather complete, it appears to be rather distorted (Pl. 5, figs. 1-2). The right side of the skull is better preserved than the left side. Both tusks are gone but the premaxillaries are preserved over almost their entire length, having only their antero-lateral margins damaged. The region of the external nares is distorted and broken, leaving the outline of the nasal opening unclear. The zygomatic process of the frontal is broken off on the left side. On the right it is largely preserved though fractured and distorted, with the postorbital or frontal crest eroded. The orbital on the same side is almost complete, but the jugal and zygomatic process of the squamosal are lacking. The right maxillary is intact including the M^3. The braincase is complete, though a lot of superficial damage of the left squamosal has occurred. The occipital is completely present, though its surface has collapsed largely on the pneumatic tissue, leaving little detail of the nuchal fossa visible. The left condyle is complete, the right one broken in half. The right glenoid fossa is intact and on the same side the pterygoid wing of the sphenoid is preserved. Auditive bullae and other delicate structures on the basicranium are gone or have been eroded and not much detail can be distinguished.

Most distortion of the skull appears to have taken place above the plane passing through the condyles and lacrymals. Compression directed approximately dorso-ventrally has caused the occipital surface to collapse and the temporal fossae and squamosals to become squeezed in the same direction. On both sides the temporal fossae have vertically oriented cracks with a small offset. Some folding also seems to have taken place parallel to these cracks. As a result of this deformation, the braincase has been displaced c. 3 cm to the right relatively to the antero-ventral part of the skull. The main offset runs through the nasal aperture and the nasal process of the premaxilla, with several larger and smaller fractures and cracks. Notwithstanding this deformation, it is possible to give the following characteristics:

1) Very short and high skull architecture and the basicranium almost vertically oriented (Pl. 5, fig. 2). The maxillaries are of intermediate height above the alveolar borders as compared to the mastodonts on the one side and the more advanced Elephantidae on the other side.

2) Relatively forward instead of downward pointing premaxillaries (Pl. 5, fig. 2), with distally diverging tusksockets (Pl. 5, fig. 1) and with a slightly upward curvature. The tusksockets are separated by a well developed but shallow, triangular fossa incisiva.

3) Robustly built, bulky and laterally projecting orbitals, which are rounded at their rim (Pl. 5, fig. 1). Posteriorly of the infraorbital foramen below the orbit, a relatively wide shelf for attachment of the masseter muscle is developed.

4) A relatively small external nasal aperture as compared to the large postorbital width at the frontals. Wide concave shelves separate the orbital edges from the nasal aperture.

5) Strongly backward converging frontal crests, which merge into well marked edges at the temporal fossae (Pl. 5, fig. 1). The frontal crest on the right side, which is superficially damaged, has a vertical orientation. This seems to be due to the compressional deformation of the skull and originally it may have been more inclined.

6) Frontoparietal region relatively narrow between the temporal fossae and weakly convex in antero-posterior and transverse direction; there are no parietal swellings developed (Pl. 5, fig. 1).

7) Wide but strongly backward inclined occiput. Although the occipital surface is rather damaged and to a certain degree collapsed over the pneumatic bone underlying it, the degree of pneumatization of the supraoccipital seems to have been limited. Due to the postdepositional collapse of the supraoccipital the transition between parietal and occipital plane is abrupt, formed by an overhanging and to a certain degree abraded bony protrusion. In occipital view the occipital condyles are strongly protruding in ventral direction.

8) Widely separated but short (in transverse direction) glenoid fossae. The glenoid fossa are strongly concave in transverse and convex in antero-posterior direction. On the right side of the skull the glenoid fossa is laterally bordered by a broken, but very strongly built zygomatic process of the squamosal. The surface of the glenoid fossa terminates abruptly posteriorly and is separated from the post-glenoid fossa by a weak ridge.

9) The post-tympanic processes of the squamosal and the ventral portion of the exoccipital are strongly tilted.

The size of skull LWTL/151186-1 is very similar to the *"E." celebensis* skull fragment described by Hooijer (1972b), as follows from the measurements presented in Table 16. Because *"E." celebensis* was considered as closely related to *E. planifrons*, the measurements of two *E. planifrons* skulls are also given in Table 16 for comparison. One of the measured *E. planifrons* skulls is in the collections of the BMNH (M-3060). It originates from the Pinjor horizon in the Siwalik Hills and was designated by Lydekker (1886, IV: 100) as lectotype. It is figured by Maglio (1973: pl. XII, fig. 1). Both M^3s are in situ, but only the sinistral one is worn. The width of the right M3 is 85 mm, which is at the lower boundary of the width range given by Maglio (1973: table 20: width range of the M^3 varies between 86 and 111 mm). This, and the relatively small overall dimensions of the skull, suggest that it belonged to a small, probably female individual. The other skull of this species is in the Collection Dubois of the NNM at Leiden (4963). It was collected by Dubois near Haripoor and described and figured by Hooijer (1955b: 96, pl. XII, figs. 1-2). It likewise represents a rather small individual of similar size as the lectotype and has the M^3s in wear. The *"E." celebensis* skull LWTL/151186-1 on the other hand, has an M^3 which is at the upper boundary of the size variation of this species. It therefore probably represents a male individual. The estimated values of measurements taken in antero-posterior direction on the dorsal side of the cranial vault (Lb, Lc) of this skull may be slightly underestimated because the nuchal crest is eroded.

The values of size measurements taken on *"E." celebensis* skull LWTL/151186-1, on the two *E. planifrons* skulls, and on two *Elephas maximus* skulls (one juvenile and one adult), have been converted into a log-ratio diagram (Fig.50). The *E. planifrons* lectotype skull has been selected as the reference specimen in this figure (corresponding with the x-axis). As follows from Fig. 50, the two *E. planifrons* skulls match very well in size, all measurements differing less than a factor 1.25 between the two skulls, except the antero-posterior diameter of the nasal aperture (measurement Ld), which is 1.46 times smaller in the Leiden specimen. The same figure also shows that many distances measured on the *"E." celebensis* skull are of comparable magnitude as in the *E. planifrons* skulls, especially those measured on the lateral side of the skull and the transverse distances on the skull base and occiput. Some of the measurements taken on the skull of the supposedly dwarfed *"E." celebensis* are even larger than in one or both of the *E. planifrons* skulls, e.g. the antero-posterior diameter of the tusk alveole (DAP tusk). Transverse and antero-posterior dimensions of the dorsal surface of the *"E." celebensis* skull on the other hand, are relatively smaller than in both *E. planifrons* skulls, differing with a factor more than 1.5x (measurments Lb, Lc, lb, lc, ld and lg). Also the foramen magnum (measurement ll) is rather small in the Sulawesi species, suggesting that the braincase is comparatively small.

The adult *E. maximus* skull is the largest of the various specimens represented in the same Fig. 50. The braincase and frontals are relatively narrow (relatively small lb and lc) and the premaxillaries are narrow (small ld), which is to be expected in a female individual with small tusks. Superficial bossing of the parietals, more strongly developed is the modern *E. maximus*, results also in relatively large Aa and Ad values. Compared to the adult *E. maximus*, the juvenile specimen has an extremely elongated forehead (large Lb, Lc) but is very narrow at the orbitals (small lc) and premaxillaries (small ld). The small premaxillaries seem to be correlated with the still under-

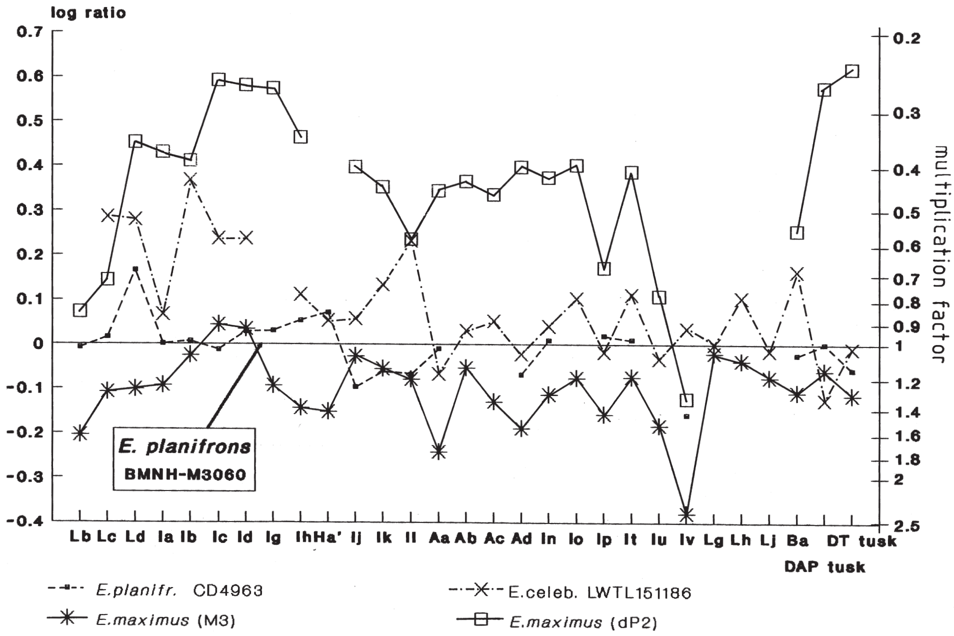


Fig. 50. Comparative log-ratio diagram for skull measurements (as defined in Fig. 7), taken on various elephantoid skulls (see also Fig. 21). The *Elephas planifrons* lectotype skull (BMNH/M3060) is the reference specimen (zero values). It represents an adult, presumably female individual with the sinistral M^3 in wear (the dextral one is not abraded, presumably due to malocclusion or some other pathogenic disorder). Skulls further measured are *"E." celebensis* skull GRDC/LWTL-151186-1 and *E. planifrons* skull NNM/CD-4963, which are both in a comparable dental wear stage as the *E. planifrons* lectotype specimen. Also plotted are the values for two *E. maximus* skulls, one juvenile with the dP^2 slightly abraded by wear (VFUU/AA-136; triangles) and one female adult from a Zoo, of ca. 40 years old, with the M^3s in wear (Coll. FVUU; lozenges).

developed tusks (small alveolar diameters). Both the adult and the juvenile *E. maximus* are characterized by a widely separated interalveolar crests (large lv), which is not the case in the other specimen examined.

Discussion

In an early paper Hooijer (1949) considered the dwarf elephant from Sulawesi, which he named *Archidiskodon celebensis*, to be a direct descendant from *Elephas [Archidiskodon] planifrons* Falconer & Cautley, 1846, the latter known from the Late Pliocene to Early Pleistocene of the Asiatic mainland, including the Middle East. This assumption was based on similarities in molar morphology between the two species. Later (Hooijer, 1953c) he discarded this view, after the discovery in South Sulawesi of real premolars and what seemed to be a mandibular tusk, in the same area where the first molars had been found. More convincing even were indications that one of the mandibles from the same area possessed a large alveole for the incisor (Hooijer, 1954e). He speculated on an independent origin for the Sulawesi dwarf elephant and considered the Elephantidae as a polyphyletic group derived from the Gomphotheridae. Maglio (1973), however, placed both *planifrons* and *celebensis* in the genus *Elephas*, holding the opinion that they were indeed closely related. At that time vestigial incisive germs had been found to occur in mandibles of *E. planifrons* (Maglio, 1970), and he (Maglio, 1973) considered the reappearance of functional lower tusks in *E. celebensis* to be a result of paedomorphosis. In the same paper he included several molar remains from Java in *E. celebensis*, notably an upper molar described originally as an M^1 of *E. planifrons* by van der Maarel (1932) and two molar fragments attributed by Hooijer (1954d) to a pygmy stegodont, *Stegodon hypsilophus*. Subsequently, Hooijer (1974) accepted the descendance of *E. celebensis* from *E. planifrons* but placed the Sulawesi and Java material in two different subspecies: *E. celebensis celebensis* and *E. celebensis hypsilophus*, respectively. Van den Bergh et al. (1992) contested the occurrence of *E. celebensis* on Java and postulated that there is neither enough proof to assume the presence of *E. planifrons* on that island.

The close relationship between *planifrons* and *celebensis* has been based mainly on the resemblance in molar morphology. Now that the skull of *celebensis* is better known we can reconsider the phylogenetic relationships. The high and short shape of skull LWTL/151186-1 is clearly that of an adult individual, not resembling the more elongated shape observed in juvenile individuals of the more advanced Elephantidae. A juvenile skull morphology could be expected in the case of paedomorphosis, but this seems not to be the case. Furthermore, the small width between the temporal fossae, the convexity of the frontoparietal region, the strong backward sloping occipital surface, and the narrow, rather crested temporal portion of the squamosals all seem to suggest that pneumatization of the braincase was rather limited and that it lacks the characteristic parietal swellings seen in *Elephas* and *Mammuthus* skulls or the more globular domed shape of *Loxodonta*. The limited pneumatization of the skull can either have been due to secondary reduction in the coarse of dwarfing, or it may be a primitive character directly inherited from its ancestor. Parietal swellings are already developed in *E. ekorensis*, the earliest (Late Pliocene) elephant known from Africa (Beden, 1979). It has been assumed that secondary loss of pneumatic tissue on the braincase in dwarfed elephants, such as in *E. falconeri* from Sicily, has been the result of dwarfing (Accordi & Palombo, 1971; Sondaar, 1977). The dwarf elephants from the Mediterranean islands, such as *E. falconeri* and *E. creticus*, have been related either to *Loxodonta* (Kuss, 1966), *Elephas antiquus* (Bate, 1907; Sondaar & Boekschoten, 1967; Ambrosetti, 1968; Maglio, 1973) or *Mammuthus meridionalis* (Kuss, 1973). Though the molars of *E. falconeri* most closely resemble those of *M. meridionalis*, as already noted by Bate (1907), the relationship with *E. antiquus* is most often advocated. This relationship, however, seems to be prompted more by the fact that fossils of *E. antiquus* have been found on several islands that have also yielded *E. falconeri* remains, rather than that it is based on morphological criteria. The globular skull shape of *E. falconeri*, lacking the strong pneumatization seen in *E. antiquus*, is usually explained as a response to the size reduction. It is argued that body size reduction leads to a decrease in weight, scaling to the third power. On the skull the surface area for attachment of the neck muscles, which scales to the second power, could therefore be greatly reduced (Accordi & Palombo, 1971; Sondaar, 1977). However, more recently the original view of Kuss (1973) is followed again by some authors (Lister & Bahn, 1994; Mol et al., 1996), stating that *E. falconeri* as well as some other dwarf elephants from the Mediterranean islands such as *Elephas creticus*, may have been derived from *Mammuthus meridionalis*. The latter hypothesis fits better with the morphological evidence, and also with absolute datings which have become available recently (Belluomini & Bada, 1985; Reese, 1996), showing the dwarfs *E. falconeri* and *E. creticus* to be older than the *E. antiquus* remains on the same islands. The lack of parietal swellings in *E. falconeri* should thus have been inherited from *M. meridionalis* according to this model, and there would be no evidence to support the view that dwarfing leads to a loss of skull pneumatization. Following this way of reasoning the lack of such swellings in *celebensis* is thus most likely also a plesiomorphic character inherited from its ancestor and not due to size reduction.

The skulls of *E. planifrons* show some degree of parietal and occipital expansion, resulting in a midsagittal depression or concavity of the forehead, though a weak one, bordered by weakly convex parietal swellings. Such concavity is lacking in *celebensis* all together. Apart from this difference, there are some close similarities in skull morphology between *celebensis* and *E. planifrons*. One is the relatively small nasal aperture compared to the wide postorbital width. The shape of the nasal aperture is very characteristic in *E. planifrons*, with its anterior margin showing a midsagittal forward protrusion. Unfortunately, the exact shape of the nasal aperture cannot be precisely reconstructed in the *celebensis* skull due to postmortem damage, though it is clear that its overall size was relatively small. The relatively small size of the nasal aperture is not shared with other species of *Elephas*, such as *E. ekorensis*, *E. recki*, *E. hysudricus*, or *E. hysudrindicus*.

Other characters shared by *celebensis* and *E. planifrons*, apart from the similar molar morphology and the presence of premolars as already pointed out by Hooijer (1949, 1953c), are the very thick and bulky lacrymal processes and infraorbital margins, and the associated strongly developed facial crests and long infraorbital foramini.

Characters that seem to be derived in *celebensis* are the widely laterally protruding zygomatic processes of the squamosals. The squamosals are strongly compressed antero-posteriorly and the postglenoid fossae are deep and strongly inclined towards the occipital plane in *celebensis*. Characters shared by *celebensis* and the genus *Loxodonta* are the lateral and upward curvature of the tusk sockets (though this feature also occurs in some elephants such as *E. namadicus*), the anteriorly inclined occiput and the antero-posteriorly convex forehead.

Clearly a plesiomorphic character in *celebensis* is the small width of the braincase between the temporal fossae (measurement lb). Particularly in this character the Sulawesi dwarf appears more primitive than the *E. planifrons* lectotype and the skull in the NNM. Also the occasional retainment of functional tusks in some of the *celebensis* mandibles suggests a more primitive ancestor than *E. planifrons*, contrary to the view of Maglio (1973), who advocated that the reappearance of lower tusks should be attributed to paedomorphosis. The only elephantid genera known to have possessed functional lower tusks are *Primelephas* Maglio, 1970 and *Stegotetrabelodon* Petrocchi, 1941. Maglio (1970; 1973) and Maglio & Ricca (1978) considered the genus *Stegotetrabelodon* to be a primitive member of the Elephantidae, a view proposed earlier by Aguirre (1969) and later followed by Coppens et al.(1978), Tassy (1986) and Kalb & Mebrate (1993). *Stegotetrabelodon* is exclusively known from Africa, although Tobien (1978) and Tobien et al.(1988) attribute some fragmentary molar remains from the

Pliocene of Europe and Asia to this genus. They place *Stegotetrabelodon* amongst the bunodont longorostrine mastodonts, though they agree that this mastodont group is nearer than all other mastodonts to the source of the elephants, an opinion which is shared by Beden (1979). Molars of *Stegotetrabelodon* still have a strongly developed median cleft, which is greatly reduced or lacking in *Primelephas* (Maglio, 1970). The latter genus is usually included in the subfamily Elephantinae together with the other elephant genera *Loxodonta*, *Mammuthus* and *Elephas*. The strong development of median pillars in *celebensis* is shared with *Primelephas* and with the earliest varieties of *Elephas planifrons* (e.g. see Hooijer, 1955a; 1958). In the total number of lamellae and hypsodonty index *celebensis* more closely resembles *E. planifrons* than *Primelephas*. However, increase of the amount of ridges and hypsodonty have evolved independently in various elephantoid lineages, and may have evolved independently in *celebensis* as well.

The dwarf elephant from Sulawesi may have diverged considerably from its colonizing ancestor, hampering the assessment of its phylogenetic position. The skull and dental morphology clearly indicate that it should be included in the true elephants. The adult skull of *celebensis* has no juvenile proportions, suggesting that no paedomorphosis has occurred, as was suggested by Maglio (1973) to explain the occasional retainment of lower tusks in *celebensis*. Descendance from the earliest representants of *E. planifrons* in Asia is still the most likely possibility. Spatial and temporal data would support this relationship. The oldest occurrence of *celebensis* on South Sulawesi can be dated at about 2.5 Ma. It occurs at the very base of the lowermost fluviatile layers of the Walanae Formation. However, *celebensis* was probably present on Sulawesi already earlier. *E. planifrons* has its latest occurrence in the Siwaliks at around 2.7 Ma, when it is replaced by *E. hysudricus*. It was already present at least some 3.3 Ma ago on the Indian subcontinent (Hussain et al., 1992). The earliest stage of *E. planifrons*, alluded to as *Archidiskodon* cf. *planifrons* by Hooijer (1958), may be represented by the Late Pliocene fauna from Bethlehem, which amongst others includes *Hipparion*. Measurements on molars from this locality in the Middle East are close to the lower limit of the range of variation of *E. planifrons*, have the lowest HI index (74-100), and still strongly developed median pillars. According to Maglio (1973) the Bethlehem specimens represent the earliest occurrence of *Elephas* outside Africa. Though a mandible from Bethlehem does not possess lower tusks (Hooijer, 1958), it cannot be excluded that one of the earliest populations of *E. planifrons*, in which the presence of lower tusks could have been restricted to male individuals only, ended up in Sulawesi after this taxon had left Africa.

Alternatively, a close relationship between the Sulawesi specimens and *Primelephas* can not be excluded. However, the latter genus has never been reported from outside Africa. Until skull material of *Primelephas* will become available, it seems appropriate to place the generic name of *Elephas* between quotation marks, to express the uncertain generic affinity of *"Elephas" celebensis*.

Van der Maarel (1932) described an upper molar from Ci Pangglosoran near Bumiayu on Java as an M^1 of *E. planifrons*. Kretzoi (1950) made it the type specimen of a new species, *Stegoloxodon indonesicus*, whereas Maglio (1973) considered it an M^2 of *E. celebensis*. Van den Bergh et al.(1992) demonstrated that independently from whether the molar is considered an M^1 or M^2, it differs markedly in size from *E. plani-*

frons and most likely represents an M_2 of a dwarfed member of the Elephantinae, but that the molar differed from *"E." celebensis*. Now that more material of the latter species from Sulawesi is available for comparison, the Ci Pangglosoran molar does appear to fall within the size range of variation of the M^2 of the Sulawesi elephant, though its LF (6.2) is slightly below the range observed in the M^2 of *"E." celebensis* and its ET (varying between 1.9 and 2.6 mm) corresponding with the lower limit of variation of the Sulawesi species (Table 30). As both islands were separated throughout the Plio-Pleistocene (see chapter 3), a common ancestry for both dwarfs (early stock of *E. planifrons*?) is the most likely possibility.

Stegodon sompoensis Hooijer, 1964

Archidiskodon celebensis nov. sp., Hooijer, 1949: pl. IX, figs. 1, 5 specimens C & D.
Stegodon sp.; Hooijer, 1953b: pl. V, figs. 1-5.
Stegodon sompoensis nov. sp.; Hooijer, 1964a: pl. 1, figs. 1-6.
Stegodon sompoensis Hooijer; Hooijer, 1972: pl. 3, figs. 1-3.
Stegodon cf. *trigonocephalus* Martin; Hooijer, 1972: 11 (referring to two molar portions described in 1953b as *Stegodon* sp.).
Stegodon sompoensis Hooijer; Aziz, 1990: 60-61.
Stegodon sp. A cf. *trigonocephalus* Martin; Aziz, 1990: 62, specimens 13/3, 20/1 and 20/2; pl. V, figs. 1-2.
Stegodon sompoensis Hooijer; van den Bergh et al., 1996: 242, fig. 23.2b.

Holotype — A very worn and incomplete dP^3 or dP^4 kept at the NNM (Hooijer, 1964a: pl. 1, figs. 1-2).

Hypodigm — There are around 20 molar remains kept at the NNM and the GRDC which can be attributed with certainty to this pygmy species. There are two nicely preserved sinistral mandibular ramii, one kept at the MPC in South Sulawesi and one at the GRDC. A complete skull only lacking dentition is kept in the GRDC collection. Various less well preserved cranial portions are in the MPC and GRDC collections.

Type locality — The type specimen reportedly (Hooijer, 1964a) originates from the surroundings of the village Sompo (also written as Sompe or Sompoh; 4°15′S, 120°00′E). Its derivation from the main fossil-bearing layer east of Sompoh, from which van Heekeren collected most of his material (FVL-25a in this thesis) is uncertain, however.

Age and localities — Further remains with certainty attributable to this species have been found in the surroundings of the following places as reported by Hooijer (1949, 1953b, 1964a, 1972b): Calio (FVL-20?), Celeko (FVL-27), Marale (FVL-18?), and Beru. The following localities have yielded remains of this species during our own research: Lonrong (FVL-24c), Batua Sange (FVL-9), Padali (FVL-30), Alupang (1 km east of FVL-17), Marale (FVL-15, FVL-16 and FVL-17), Bulu Cepo (FVL-10, FVL-11, FVL-12), Bulu Barere (FVL-28), Palangiseng (FVL-2), and the Lakibong River valley (FVL-5, FVL-6). Apart from the localities Lonrong, Padali, Bulu Barere, and FVL-11 near Bulu Cepo, all these localities are located in the structural block named here the Lakibong Triangle, west of the Bulu Cepo Fault. All localities are situated in the Soppeng District, Southwest Sulawesi, except for Bulu Barere, which lies in the Bone District. Stratigraphically all the localities can be placed in the Beru Member, which constitutes the uppermost, terrestrial part of the Walanae Formation. The age of the Beru

Member is Late Pliocene (lower boundary of the Beru Member at 2.5 Ma), presumably continuing into the Early Pleistocene and perhaps even early Middle Pleistocene for Subunit B of the Beru Member.

Original diagnosis — See Hooijer, 1964a: 43.

Revised diagnosis — A small-sized *Stegodon* species with molars (M1-M3) between one-half to two-thirds smaller than in *Stegodon trigonocephalus* from Java. Eight or nine ridges in the upper, and ten ridges in the lower M3. Ridges lower than wide (h/w indices ranging from 59 to 85), lacking median pillars and median clefts. Ridges showing 4-10 digitations, usually with 4 digitations larger than the others and separated by shallow clefts of about equal size, except in milkmolars, where deeper median clefts may be developed. Two principal median digitations usually widening towards the crownbase, leading to weakly developed double expansions in the enamel wear patterns, especially anteriorly. Enamel very thick, up to 5 mm in the M3, decreasing in thickness towards the crownbase. Scalloped, double-layered enamel, with both layers of about equal thickness, showing 'Stufenbildung' upon wear. Wrinkling becomes more delicate towards the crownbase. Adult skull resembling that of *S. trigonocephalus*, but of inferior size. Tusk sockets directed forward and downward, subparallel, and separated by a deep and wide interalveolar fossa.

Differential diagnosis — See differential diagnosis of *"Elephas" celebensis*.

Description of the material

Molars — Besides an almost complete skull, the 1985-1986 and 1989-1993 GRDC collections contains 14 jaws with molars, isolated molars and molar fragments, of which the rank could be ascertained. In addition, there is a mandible and two skull fragments with molar fragments present in the MPC. Locality information of the new specimens described below are given in Table 6, summary measurements of the molars are listed in Table 33.

dP$_4$: n = 1 (GRDC: LR-2703) Specimen LR-2703 is a posterior fragment of a sinistral milkmolar consisting of -$^{1}/_{2}$3x ridges, all worn. The ridges are wedge shaped, separated by valleys which are narrower than the ridges but open, U-shaped at their base. Vertical grooves developed in the enamel surfaces on both lateral sides of the ridges are characteristic for milkmolars. The weakly concave occlusal surface indicates that we deal with a lower milkmolar. As the ridges are more closely spaced along the left side, it must be a sinistral milkmolar. The width of ridge I is 35 mm, that of ridge II 40 mm, whereas that of ridges III and IV cannot be measured because they are damaged. All ridges except the posterior halfridge show single enamel loops, which are constricted along the median axis of the tooth and curved backwards. Ridges II and III show an anterior expansion on both sides of the median constriction. The ET varies between 2.2 and 2.6 mm. The enamel is double layered, with the outer layer slightly thicker than the inner one. It is folded into delicate wrinkles with 4 to 6 folds per cm, including the enamel of the median expansions. The folding is most prominent at the inner enamel layer. The LF amounts to 8.5. From what is preserved of the present specimen, it can be seen that it is not markedly tapering in anterior direction, suggesting that we deal with a dP$_4$ and not a dP$_3$. The molar is about 13% narrower than the smallest dP$_4$s of *S. trigonocephalus* from Java (W in the latter ranging between 46 and 53 mm).

M_2: n = 3 (GRDC: BC-2990. MPC: C3/2/79. NNH: Hooijer, 1972b: pl. 3, fig. 2) The specimen described by Hooijer (1972b) has -7x worn ridges preserved. It has a concave occlusal surface and is strongly curved to the left, indicating that it is a lower molar of the left side. Hooijer thought 2 ridges to be missing, but examination of the preserved anterior root indicates that at most 1 ridge and possibly an anterior halfridge are missing. The length as far as preserved is 105+ mm. The posterior end is not tapering and there are no vertical grooves on the lateral and medial sides of the ridges present, leaving only the possibility of an M_1 or M_2 open. Largest width of 46 mm occurs at ridge III-V, which is similar as in the M_3 described in the same paper (Hooijer, 1972b: pl. 3, fig. 1). Ridge IV and the more anterior ridges show single enamel loops. Ridge V shows double median expansions. Enamel is double layered with an ET of between 2.9 and 3.2 mm and wrinkled with 4 to 5 folds per cm. The LF is 7.7 (8 reported by Hooijer, 1972b: 9), which is slightly higher than the LF of the complete M_3 attributed to *S. sompoensis* in the same paper (LF = 7.2). The width is 18% smaller than in the smallest M_1 of *S. trigonocephalus* (56-64 mm) and its ET is thinner (2.9-3.7 mm in the M_1 of the Javanese species), indicating that we are dealing with a dwarfed species. The similar width and LF as in the M_3 of *S. sompoensis* strongly suggest that we are dealing with an M_2. If this is correct, than its width is 32% smaller than in the smallest M_2s of *S. trigonocephalus* (W = 68-80 mm).

Specimen BC-2990 is a sinistral mandible fragment with the worn posterior part of an M_2 and the unworn and uncompleted but damaged M_3 still in the alveole. Only the last ridge (I) and a posterior halfridge of the M_2 are intact. Ridge II has the anterior lingual portion of the enamel broken, and in front of it the lingual portion of ridge III is preserved. The mandible is broken at that level. The posterior halfridge is unworn, has 6 digitations and is 38 mm wide. Ridge I has a w of 55(c) mm, and bears 7 worn digitations of about equal size and of which the dentine is visible but not yet interconnected. Ridge II has a w of 57(c) mm and is slightly more worn with the dentine of the central digitations connected. Its worn height is 31 mm. Cement fills the valleys and covers the flanks of the ridges completely. The lamellar frequency at the buccal side is 7.4, that of the lingual side may have been slightly lower due to the lateral curvature of lower molars. The scalloped enamel is rather thick (ET = 3.6-4.2 mm). It is double layered, showing the 'Stufenbildung' characteristic for *Stegodon* molars.

A comparable posterior fragment of an M_2 remains in a sinistral mandibular ramus with behind it the erupted but unworn M_3, present in the collection of the MPC. There remain $-^{1}/_{2}1$x ridges of the M_2, in front of it the mandible is broken. Ridge I has a basal width of 44.5 mm. It is worn into a single enamel loop lacking median expansions. The ET varies between 3.0 and 3.6 mm. The scalloped enamel is double layered with 4 to 5 folds per cm and showing 'Stufenbildung'.

M_3: n = 9 (GRDC: 890522, MUTL/171186-1, MUTL/171186-2, BC-2946, CMTL/271285-1, BC-2990. MPC: C3/2/79. NNH: Hooijer, 1953b: pl. V, figs. 1-2; Hooijer, 1972b: pl. 3, fig. 1) The M_3 figured by Hooijer (1972b) remains the only complete specimen recorded so far. It carries x10x ridges and has a total length of 140e mm. The maximum width of 45 mm occurs at ridge 5. Ridges 5 and 6 have an unworn height of 38 mm, the height gradually decreasing in the more posterior ridges. h/w indices of the ridges 5 to 7 vary between 78 and 85. The LF is 7.2 and the

ET varies between 2.7 and 3.2 mm (measured on a cast present in the NNM).

Mandible C3/2/79 (Pl. 6, figs. 1-2) has the M_3 partly erupted but only ridge 1 is abraded by wear. There are x7- ridges visible over a length of 96 mm, the posterior part of the molar being concealed in the alveole. Only of the anterior two ridges the basal width can be estimated, the more posterior ones having their bases largely covered in the mandible. The width of ridge 1 and 2 is around 48e mm. The first ridge is divided in two portions by a median cleft, but this cleft is not developed in the more posterior ridges. Only the digitations, of which there are 7 or 8, are free of cement. The lamellar frequency measured at the apices of the ridges amounts to 7.1. At the crownbase it must have been slightly lower due to the upward curvature generally observed in lower molars. The proportions of this molar are only slightly larger than the M_3 figured by Hooijer (1972b), but much too small for an M_2 of *S. trigonocephalus*.

Another sinistral mandibular ramus with M_3, specimen CMTL/271285-1, has been figured previously by Aziz (1990: pl. V, figs. 1-2). The molar is fully erupted and carries $-^1/_2 8$x ridges, all worn except the posterior halfridge, which is completely covered by cement. The flanks of the posterior three ridges are also covered with cement. The anterior margin has already been worn out, but from what is left of the anterior hook, an original number of 9 ridges can be deduced. The length as far as preserved is 160+ mm. The original length can be estimated at around 175e mm. The molar tapers in posterior direction, which indicates that an M_3 is concerned. The maximum W of 62 mm occurs at ridge VI. The posterior ridge has four abraded digitations. In ridge II the dentine is visible but not interconnected. In ridge III the dentine of the central digitations is connected while ridges IV-VIII consist of single enamel loops. In ridge V and VI there are weak double dilatations developed in the enamel loops, both anteriorly and posteriorly. The scalloped enamel is double-layered, showing 'Stufenbildung', and the ET varies between 2.8 and 3.2 mm. The LF amounts to 5.8. The size of this M_3 is considerably larger than the M_3 described by Hooijer (1972b) but lies far below the size range of the M_3 in *S. trigonocephalus* (L = 266-304 mm, W = 81-98 mm). It is therefore interpreted as an M_3 of *S. sompoensis* on the upper limit of variation.

A right (MUTL/171186-1) and left (MUTL/171186) mandibular ramus fragment of a single individual, both with the anterior portion of an M_3, were only briefly mentioned by Aziz (1990: 62) under *Stegodon* sp. A cf. *trigonocephalus*. The dextral M_3 (Pl. 4, figs. 5-6) is the most complete one, carrying (x1)$7^1/_2$- ridges. The anterior margin is damaged but the outline of the root shows that x1- ridge must have been present here. The ramus is completely broken off through the middle of ridge 9, which has a basal width of 51 mm and an unworn height of 40 mm, giving an h/w index of 79. The number of ridges missing may be $-^1/_2 1$ to $-^1/_2 3$. The preserved length from the anterior border of the root to the broken posterior end is 135+ mm. The largest width of 55 mm occurs at ridge 4, which is worn into a single enamel loop with weak double median expansions. Ridges 7 to 9 are unworn, with only the digitations, 7-9 in number, left free from cement. The molar is strongly curved laterally, with a basal lamellar frequency of 5.7 at the lingual and 7.5 at the buccal side, giving a LF of 6.6. The ET is c. 2.5 mm, the enamel is double layered with the outer layer occupying approximately one third of the total ET. The scalloped enamel is regularly wrinkled with 1-3 folds per cm and an amplitude between 1.5 and 2 mm.

Specimen 890522 is a posterior fragment of a dextral M_3 with $-^1/_2 3$x ridges. The last ridge, bearing 5 digitations, and the posterior halfridge, consisting of a single digitation, are unworn. Of ridge II (4 digitations) and III (6 or 7 digitations) the digitations are abraded. Ridge IV seemed to have had a single enamel loop, but is broken transversely in half. The w of the successive ridges is: posterior halfridge = 17 mm, I = 39(c) mm, II = 48(c) mm and III = 52(c) mm. The enamel is very thick (ET varying between 3.9 and 4.2 mm), double layered, with 'Stufenbildung' visible at the occlusal wear surface of ridge IV. The enamel of ridge IV is regularly wrinkled with 2 to 4 folds per cm and an amplitude between 0.5 mm and 1 mm. No median sinus is developed in the enamel loop. The worn height of ridge III is 40+ mm, which gives a h/w index of more than 83+. As the tooth tapers strongly towards the back, this rather high h/w index may not be characteristic for *S. sompoensis*. The labial side of the tooth is worn down more than the lingual side.

A more worn posterior M_3 fragment of the right side is specimen BC-2946. It has -$^1/_2$4- ridges preserved, all worn down to their base. A small posterior halfridge is broken away. The w of the successive ridges is: I = 34 mm, II = 41 mm, III = 47 mm and IV = 49e mm. The lateral sides of the enamel loops are curved in posterior direction. The occlusal surface is concave both in longitudinal and transverse direction. The LF is 6.5 and the ET is c. 3.8 mm. There are 3-5 enamel folds per cm with an amplitude of 0.5-1 mm. 'Stufenbildung' is well developed. An anomalous conule blocks the valley on the buccal side between ridges II and III.

The fragmentary M_3 in mandible fragment BC-2990 was already mentioned briefly under the M_2. It had not yet erupted and was still under formation when the animal died, the three preserved posterior ridges not yet connected at their base. The lateral (buccal) surface of the tooth is completely enclosed in the alveole, while the medial (lingual) side is exposed, but broken in longitudinal direction behind ridge 4, so that no width measurements can be given. The height of ridges 4 to 6 is c. 42 mm as far as they are formed. The ridges carry 7-8 digitations. The lamellar frequency measured at the apices of the anterior ridges amounts to 6.6, but the basal lamellar frequency must be slightly lower because the ridges are converging slightly apically. The enamel consists of two layers of equal thickness (ET = 3.3-3.9 mm).

An anterior M_3 fragment was figured by Hooijer (1953b: pl. V, figs. 1-2) as an anterior portion of a lower left molar and was attributed to *Stegodon* sp. In the original paper Hooijer expressed his suspicion of this molar to be an M_3 of a pygmy *Stegodon*. Later, when Hooijer (1964a) described the holotype of *Stegodon sompoensis*, he included the anterior M_3 fragment described earlier (Hooijer, 1953b) in this pygmy species as well. After the finding of some large-sized molar fragments he changed his opinion and placed it under *Stegodon* cf. *trigonocephalus*, stating (Hooijer, 1972b: 11) that the specimen falls within the ranges of the M_1 *S. trigonocephalus*. The specimen under consideration has x5- worn ridges preserved, of which the fifth one is just abraded by wear. There is another fragment consisting of -2- unworn ridges (Hooijer, 1953b: pl. V, figs. 3-4), which based on size and fossilization probably belongs to the same molar, as was also noticed by Hooijer. The larger anterior portion is damaged on the lingual side at the base, so that width measurements cannot be given exactly for all the ridges. The w of the successive ridges is as follows: 1 = 47e mm; 2 = 51 mm; 3 = 53.8 mm; 4 = 60e mm; 5 = 59e mm. The smaller fragment has two ridges with widths of 59.5 mm and 58e mm. The anterior of the two ridges is damaged apically, but the posterior one has an unworn height of 38e mm, giving an h/w index of 66. The LF of the two fragments is 6.0 and 5.4, respectively, the lower LF caused by the stronger lateral curvature of the smallest fragment as compared to the anterior portion. The ET of the two fragments varies between 3.7 and 4.3 mm and between 3.7 and 4.1 mm, respectively. In the unworn posterior fragment the anterior ridge is damaged apically, but the posterior ridge has 6 digitations, of which four are clearly larger than the remaining two. There are several characters that speak against an M_1 of *S. trigonocephalus* and in favour of an M_3 of *S. sompoensis*: 1) the enamel is rather thick for an M_1 (ET varies between 2.9 and 3.7 mm in the M_1 of *S. trigonocephalus* and between 2.5 and 4.2 mm in the other M_3 fragments attributed here to *S. sompoensis*); 2) the low number of digitations corresponds better with *S. sompoensis* molars than with *S. trigonocephalus*; 3) the strong lateral curvature of the molar fits better with an M_3 than with an M_1; 4) The maximum width and the LF fall within the ranges observed in the M_3 of *S. sompoensis*. Taking these considerations into account this specimen is here attributed to *S. sompoensis*.

It follows that the M_3 of *S. sompoensis* has a size of between 23% and 47% smaller than the smallest M_3 from Java that has been attributed to *S. trigonocephalus*.

dP^2: n = 1 (GRDC: PT-3111) This worn out and fragmentary milkmolar is probably of the left side. The lingual side is broken. The buccal side runs straight forward but turns obliquely inwards halfway, merging into the narrower anterior border of the tooth. Very delicately wrinkled enamel borders the posterior side of the tooth and the posterior half of the buccal side. In front the enamel has been completely worn away. In the center a double enamel rim marks the boundary between two ridges worn down to their base. The ET is 1.0 mm and the wrinkles in the enamel have a frequency of 10 per cm with an amplitude of less than 0.4 mm. The length is 11.8 mm, but may have been slightly longer originally due to the loss of the anterior enamel margin. The width is 10.4 mm as far as preserved posteriorly. Only a small part of the posterior root is preserved.

dP^3: n = 2 (GRDC: BEUL/251285-1. NNH: Hooijer, 1964a: pl. I, figs. 1-2 (holotype)).

The type specimen was figured by Hooijer as a dextral dP^4 of *Stegodon sompoensis*, though the possibility of an M^1 was left open. The specimen is worn down to the root along the buccal side, where the dentine of successive lamellae has coalesced. It has -4x ridges preserved over a length of 39+ mm. Ridge IV is supported by the anteromedial root as well as by a small posterior part of the anterior hook. Therefore probably only one or two ridges are missing in front, giving a ridge formula of (x1)4x or (x2)4x, as already stated by Hooijer (1964a). The posterior halfridge is damaged buccally so that the width cannot be given. Ridge I is 28e mm wide, ridge II is 27.5e mm wide, ridge III and ridge IV are both 26e mm wide, though the original width of these ridges may have been slightly larger because the enamel along the buccal border is worn away down to the root. The LF of the tooth is 14.6. The enamel has an ET varying between 1.1 and 1.5 mm and is wrinkled with 2 to 5 folds per cm. The preserved lingual flanks of the ridges show well developed vertical grooves, characteristic for milkmolars but usually absent in the M1-M3 series. Hooijer (1964a: 39) states that the "determination of the present tooth as a DM^3 is out of the question, for a DM^3 narrows distinctly from back to front over three ridges, whereas in the Sompoh molar [=

the tooth under consideration] these ridges are of uniform width." It must be noted however, that because the tooth is very worn buccally, the original outline of the tooth cannot be assessed well. Furthermore, the tooth does taper slightly in anterior direction, not less so than for example in the complete dP^3 of *S. trigonocephalus* figured by Hooijer elsewhere (Hooijer, 1955b: pl. II, fig. 4). The w measurements of this dP^3 are as follows: posterior halfridge = 23 mm; I = 36.0 mm; II = 39.1 mm; III = 36.8 mm; IV = 33.5 mm; V = 30.9 mm; VI = 32.3 mm. From back to front the width increases first to ridge II and than starts to decrease. If only the four posterior ridges would have been preserved, like in the type specimen of *S. sompoensis*, tapering would be less well developed. Furthermore, the maximum width of the *S. sompoensis* type specimen does correspond with the width of another dP^3 fragment from the Walanae Formation (BEUL/251285-1: W = 29.0 mm), but is considerably smaller than a complete dP^4 attributable to this species (PA-3730: W = 41.4 mm). These observations corroborate the supposition that the *S. sompoensis* type specimen represents a dP^3 and not a dP^4 or M^1 as was originally put forward by Hooijer (1964a).

Specimen BEUL/251285-1 is likewise incomplete in front, consisting of -3x ridges, all worn except the posterior halfridge. The length as far as preserved is 30+ mm. The posterior halfridge bears 7 tiny digitations of equal size and is 20.5 mm wide. The largest width of 29.0 mm is at the posterior ridge I. Ridge II has a width of 28.3 mm, ridge III is 25.3 mm wide. The tooth tapers strongly from the back to front, but the lateral borders start flaring again at ridge III, marking the characteristic constriction of a dP^3. In *Stegodon* dP^3s there are only one or two ridges in front of the constriction, so that we can estimate the original number of ridges as 4 or 5. The tooth is of the left side. The occlusal surface is weakly convex. The wear pattern of ridge I consists of two enamel loops, a buccal one half as large as the lingual one. In ridge II a median cleft separates the bipartite wear pattern, while in ridge III a single enamel loop with three constrictions is developed. The LF is 11.8. The enamel is wrinkled with 3-5 folds per cm with an amplitude of up to 1 mm. The ET is c. 1.6 mm. The widths of this dP^3 and that of the holotype are around 15% smaller than the smallest width observed amongst the dP^3s of *S. trigonocephalus* from Java (ranging between 34 and 45 mm) and can therefore be safely attributed to *S. sompoensis*.

dP^4: n = 1 (GRDC: PA-3730) This is a perfectly preserved complete specimen in which only the anterior two ridges are worn (Pl. 6, figs. 3-4). It carries x7x ridges and is of the right side. The posterior halfridge consists of only two small digitations, and the ridge in front of it is considerably narrower and lower than the fully developed ridges further in front of the tooth, so that the plate formula could be better given as x6xx. The tooth is 79 mm long. Its LF is 8.6. The successive widths of the ridges from front to back are: x = 29.9 mm; 1 = 33.6 mm; 2 = 37.3 mm; 3 = 38.7 mm; 4 = 39.9 mm; 5 = 41.4 mm; 6 = 35.9 mm; x = 22.5 mm; x = 7.2 mm. Of the unworn ridges posteriorly of ridge 2 also the height can be given: 3 = 23.6 mm; 4 = 26.7 mm; 5 = 25.6 mm; 6 = 25.1 mm; x = 21.5 mm; x = 6.9 mm. The h/w indices thus vary between 61 and 70. The anterior halfridge is widening towards the buccal side. A small abraded isolated digitation marks the lingual termination of this halfridge, bordered on the median side by an isolated digitation of which the dentine is visible. In the remaining buccal portion of this halfridge a single enamel loop has formed. The enamel wear pattern of ridge 1 is divided by a median cleft, which is developed in all other ridges as well. Because cement is only weakly developed, the median cleft can be well distinguished in all ridges. A median cleft occurs more frequently in *Stegodon* milkmolars than in true molars (compare the *Stegodon* milkmolars from Ngandong described elsewhere in this thesis). The lingual half of ridge 1 is worn into a single enamel loop, whereas the buccal half is further divided by a weaker cleft. The wear pattern of ridge 2 is made up of 4 isolated dentine islands, all marked by a single constriction. The occlusal surface of the combined anterior x2- ridges is convex in antero-posterior direction and strongly inclined relative to the vertical axis of the ridges, indicating that we are dealing with an upper milkmolar. In the unworn posterior ridges there are 8-10 digitations, but 4 are clearly predominating, a character reminiscent of the stegolophodont ancestry. The scalloped enamel has an ET varying between 1.5 and 2.4, showing 'Stufenbildung' and delicate wrinkling with 4 to 5 folds per cm and an amplitude between 0.5 and 1.5 mm. The vertical grooves on the flanks of the ridges indicate that the tooth is a milkmolar, and its shape, weakly tapering in anterior direction without a transverse constriction in front, leaves only the possibility of an dP^4 open. The size of the tooth is more than 10% smaller than the smallest dP^{4}s of *S. trigonocephalus* from Java (L = 90-108 mm; W = 48-57 mm), so that it can be safely attributed to *S. sompoensis*.

M^2: n = 2 (GRDC: 890521. NNM: Hooijer, 1972b: pl. 3, fig. 3) Specimen 890521 is a fragmentary upper molar of the left side and has $-^{1}/_{2}6$ ridges preserved. Of the most anteriorly preserved ridge only the buccal half remains. The posterior rootmass closes below this buccal half and the antero-medial root must have been situated below the broken lingual half of this root. Probably one more ridge is missing in front at the place where the anterior hook is missing. This gives a ridge formula of $(x1^{1}/_{2})^{1}/_{2}6$. A pushmark of the succeeding molar is developed on the posterior ridge. The posterior two ridges are unworn. The last one is damaged on the buccal side, but ridge II can be seen to possess 7 digitations. Ridge III from behind has its 8 digitations abraded, and of ridge IV the buccal 4 digitations are worn open showing circular dentine circles (there are 9 digitations in total). Of ridge V the buccal half is broken at the apex. On the lingual half of this ridge there are two elongated dentine islands separated by a cleft. Ridge VI shows a single enamel loop with a median expansion on the anterior side. The occlusal wear surface is convex antero-posteriorly. The w measurements of the successive ridges are from back to front: I = ?; II = 50e mm; III = 52.5 mm; IV = 53.2 mm; V = 53.7 mm; VI = ?. Ridge II has an unworn height of 29.3 mm, ridge III 37.8 mm, giving h/w indices of 59e and 72 respectively. The enamel has an ET varying between 2.2 and 2.9 mm and is weakly folded with 1 to 2 folds per cm and an amplitude of c. 1 mm. The scalloped enamel is double-layered showing clear 'Stufenbildung' at the wear surface. The LF is 7.8 and the length as far as preserved 99+ mm. If indeed one ridge is missing in front, than the original length may have been around 115e mm.

Hooijer (1972b: 9, pl. 3, fig. 3) mentioned a palate with the posterior parts of two M^{2}s and an anterior part of the M^{3}s in alveolo. The right M^2 in this palate is the most complete one and has $-^{1}/_{2}5$x worn ridges left. The maximum width of 48 mm occurs at the fourth ridge from behind. The LF lies between 7.5 and 8.

M^3: n = 6 (GRDC 890603-1; BC-3050; L2-2370. MPC C1/23/6-9-86:246; C3/27-A/251286. NNM: Hooijer, 1953b: pl. V, fig. 5) There are no complete M^{3}s of *S. sompoensis* in any of the collections. Skull fragment (C1/23/6-9-86:246) has the root and the anterior part of the left M^3 intact but strongly worn. The posterior ridges are broken but still showing the basal enamel outline. In front of the M^3 there is still a small remnant of the M^2 visible, which is completely worn down to the root. The M^3 is tapering in posterior direction and the alveole behind it is filled with spongeous bone, clearly indicating that the tooth in use represents an M^3. The total length is 132 mm, but as the anterior ridge is worn out completely to the root, the original length may have been slightly larger (140e mm). Due to the heavy wear, dentine of the anterior ridges has coalesced and it can not be seen if an anterior halfridge has been present originally. The widths of the successive ridges from front to back can be given as: 1 = 47.5e mm; 2 = 57e mm; 3 = 61.2 mm; 4 = 61.0 mm; 5 = 60.2 mm; 6 = ?; 7 = 56e mm; 8 = 45.5e mm; 9 = 40e mm; x = 35e mm. The LF is 6.6 and the double-layered enamel has an ET varying between 3.4 and 3.7 mm. The length of this M^3 is 42% smaller, the width 29% smaller than the lowest values of the ranges observed in the M^3 of *S. trigonocephalus* from Java.

A second skull fragment in the MPC (C3/27-A/251286) has both M^3s broken at the roots. In the sinistral specimen the enamel of the 2 posterior ridges is preserved at the crownbase and of the posterior halfridge 8 intact digitations can still be distinguished. The widths of the posterior ridges can be given as follows: x = 27.2 mm; I = 37e mm; II = 50e mm; III = 54 mm. The strong tapering indicates that the molar represents an M^3. Anteriorly only the broken surface of the roots remain. The anterior hook and the antero-medial root as well as the posterior rootmass can be clearly distinguished. The length from the posterior halfridge to the anterior border of the hook amounts to 113 mm, so that the original length of the M^3 may be estimated at 125e mm, slightly shorter than the foregoing specimen. From the outline of the roots a ridge formula of (5)3x can be deduced.

Specimen 890603-1 is a tapering posterior M^3 fragment. Three ridges are intact behind plus the posterior halfridge. Of ridge IV from behind the lingual half is broken whereas of ridge V only the posterior buccal part is preserved. The posterior ridge and halfridge are unworn and completely covered by cementum. Of ridge II and III the apices are abraded, while the preserved half of ridge IV shows 5 circular dentine figures. The preserved part of ridge V shows a continuous wear pattern with very thick, wrinkled enamel. There are 2 to 3 folds per cm with an amplitude of 1-2 mm. ‘Stufenbildung’ is well developed. The ET varies between 3.8 and 4.3 mm. The w measurements of the complete ridges are as follows: posterior halfridge = 23(c) mm; I = 34.4(c) mm; II = 41.6(c) mm; III = 46.0(c) mm. The abraded height of ridge II is 30.4 mm, so that the h/w index must have been larger than 73. The occlusal wear surface is weakly convex both antero-posteriorly and transversely, so that this molar must be of the upper side. The LF is 7.7.

Another posterior M^3 fragment with convex occlusal surface is specimen L2-2370. It has -4x ridges preserved, all worn except the posterior halfridge. The widths of the successive ridges are from back to front: x = 30.8 mm; I = 38.8 mm; II = 45.0 mm; III = 48.8 mm; IV = 50.4 mm. The LF is 6.6. The enamel is very thick (ET varies between 3.5 and 4.2 mm), double layered showing the characteristic ‘Stufenbildung’ at the wear surface, and is delicately wrinkled with 3 to 5 folds per cm and an amplitude of between 0.5 and 1.4 mm. The single enamel loops of the two anterior ridges show weak double median expansions at the anterior border.

Of *Stegodon sompoensis* skull BC-3050 the dentition is broken, but the outline of the roots of both M^3s is still visible (Pl. 7, fig. 1). Both roots consist of a large single mass and is bordered anteriorly by steeply dipping maxillary bone covering the anterior termination of the alveoles. Nothing of an antero-medial root nor anterior hook is visible and these may have been resorbed already in the process of dental progress. From the transverse constrictions of the posterior rootmass the presence of at least 8 ridges can be deduced. If only the anterior roots have been resorbed, there may have been at most two more ridges present originally. The length of the dextral rootmass is 127 mm, that of the sinistral one 120 mm, with a maximum width of 49 mm and 51 mm respectively. The roots are tapering in posterior direction and posteriorly bordered by a thick bony rim. The pterygoidal wings are broken and the empty alveoles behind it are filled with matrix. The size of the roots, their tapering, the relatively high number of ridges and lack of succeeding molars in the alveoles are all indications that the broken rootmasses are of the M^3s.

Hooijer (1953b: pl. V, fig. 5) figured a posterior part of a dextral upper molar as *Stegodon* sp. Like the lower molar described in the same paper and referred to previously, this upper molar is successively (Hooijer, 1964a) determined as an M3 of *S. sompoensis* and later (Hooijer, 1972b) as an M1 of *Stegodon* cf. *trigonocephalus*. The upper molar fragment is clearly tapering in posterior direction and can be safely identified as an M^3 (w measurements of the successive ridges are: posterior halfridge = 44 mm; I = 54.7(c) mm; II = 58.4(c) mm; III = 62.2(c) mm; IV = 63.4(c) mm). The maximum width at the lacking anterior part must have been c. 65e mm, which is much too small for an M^3 of *S. trigonocephalus* (W of M^3 ranges from 86 to 113 mm). The estimated maximum width is 3 mm larger than in the widest lower M_3 ascribed here to *S. sompoensis*, and 4 mm wider than the largest upper M^3 of the same species. Because upper *Stegodon* teeth are generally a little wider than their lower counterparts, it is safe to attribute this posterior M^3 fragment to *S. sompoensis*.

Mandible — One of the best preserved mandibles of *S. sompoensis* is specimen MPC C3/2/79 (Pl. 6, figs. 1-2), of which the posterior M_2 fragment and the M_3 have already been described. It is of the left side. The ascending ramus including the condyle is largely intact, though the entire margin of the coronoid process is largely gone. The horizontal ramus is broken halfway. Hard sandstone matrix still covers the pterygoid fossa and parts of the horizontal ramus. The dental stage indicates that this mandible belonged to an adult individual. The M_2 is worn to the last ridge, and the M_3 is in a beginning stage of wear, having the digitations of the two anterior ridges abraded. This dental stage corresponds with stage M2 C in the dental age classification of Beden (1979), or with dental age group XIX according to Laws' (1965) scale, both elaborated for the African elephant, *Loxodonta africana*.

The mandible is characterized by a high and slenderly built ascending ramus. In lateral view the ventral margin of the ascending ramus appears rounded without a clear angle. The horizontal ramus is transversely thickened at the level of the onset of the ascending ramus. A wide concave shelf is located buccally of the erupted M_3. The ramus is rather low, especially at the transition between horizontal and vertical ramus on the medial side. A low horizontal ramus is characteristic for *Stegodon* mandibles as contrary to those of the Elephantidae. The mandibular foramen is situated a considerable distance below the condyle (measurement M8 = 125 mm), unlike in the mandible of *S. sondaari*, where it is placed just below the condyle. Measurements of C3/2/79 and other *S. sompoensis* mandible fragments are given in Table 14.

A second sinistral mandibular ramus of an older individual is specimen CMTL/271285-1. The posterior border of the M_3 has just erupted and the dental wear corresponds with stage M3 C′ of Beden (1979) or stage XXVI of Laws (1965). The horizontal ramus is broken at the symphysis and lacks the symphysal rostrum. The ascending ramus is broken just below the mandibular foramen. In this specimen the lower portion of the coronoid process is intact, including the lower part of the tuberosities for the masseter temporalis, but the superior border or sigmoidal incision is broken. The ventral surface of the ascending ramus is superficially damaged. The size of this mandible is only slightly larger than the foregoing specimen (Table 14). Its morphology is also similar, with a very thick horizontal ramus at the onset of the ascending ramus and a very low horizontal ramus. The ventral border of the ascending ramus is round and lacks a clear angle at the transition from horizontal to ascending ramus, contrary to adult mandibles of the Elephantidae. On the lateral side there are two mental foramini below the anterior part of the molar and at a distance of 20 mm from each other. The superior part of the interalveolar crest is preserved and runs forward and downward, and not straight downward as in the mandible of *S. sondaari* from Flores. The remaining mandibular fragments attributable to *S. sompoensis*, specimens BC-2990, MUTL/171186-1 and MUTL/171181, are much damaged and do not provide further information except that their size is similar to the other two more complete mandibles (Table 14). The wear progress of fragment BC-2990 is in stage M2 A of Beden (1979) (= stage XVII of Laws, 1965), and therefore represents the youngest of the 4 individuals represented by mandibular material. Specimens MUTL/171186-1 and -2 are dextral and sinistral ramus fragments of a single individual and can be related to wear stage M2/M3 C of Beden (1979) with half of the ridges of the M_3 in wear (= stage XXII of Laws, 1965).

The *S. sompoensis* mandibles are clearly smaller than *S. trigonocephalus* mandibles with a comparable dental wear stage, but their overall morphology is similar. They differ however, from the pygmy *Stegodon sondaari* sp. nov. mandible from Flores (which will be described further on in this thesis) in 1) having the mandibular foramen placed at a lower position, 2) in the relatively narrower occlusal surface (measurement M25) as compared to the total width of the horizontal ramus (measurement M18), 3) in the more forward protruding symphysis (measurement M21), and 4) in having a less robust horizontal ramus in front of the molars (measurement M20). These differences are easily noticed in the log-ratio diagram of Fig. 51. As compared to *"E." celebensis* mandibles the Sulawesi dwarf stegodont lacks the downward protruding rostrum of the symphysis (which in some cases is even provided with mandibular tusks) and has a lower horizontal ramus.

Skull — There are three skulls of *S. sompoensis* available for study now, two of them at the MPC in SW Sulawesi (specimens C1/23/6-9-86:246 and C3/27-A/251286) and one at the GRDC in Bandung (BC-3050). The latter mentioned specimen is the most complete one, and besides had been fully preparated. Both specimens in the MPC are still over large parts covered with a hard pebbly sandstone matrix and could

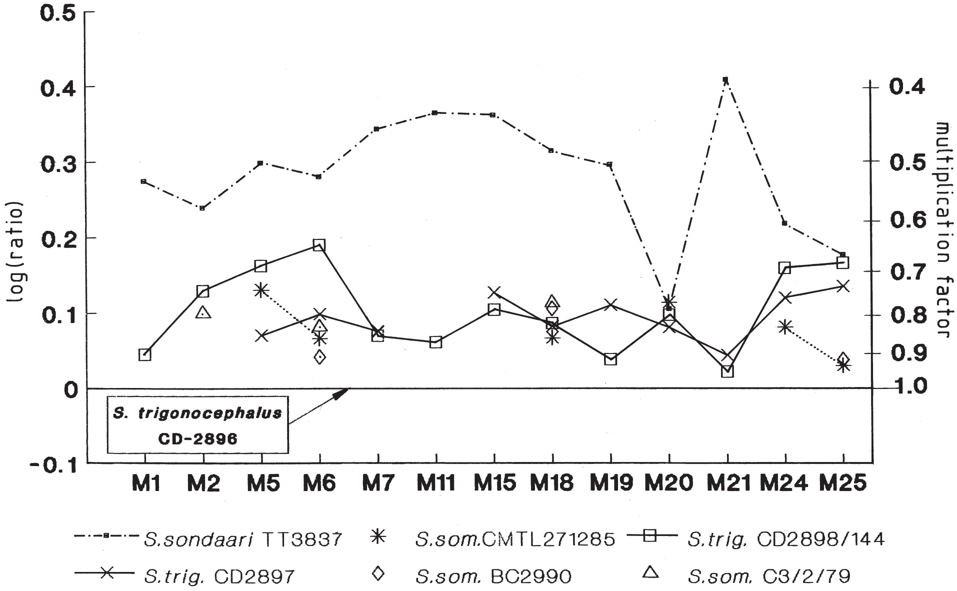


Fig. 51. Comparative log-ratio diagram of mandible measurements taken on *Stegodon sompoensis* mandibles MPC C3/2/79, GRDC CMTL/271285-1 and BC-2990, the holotype mandible of *S. sondaari* from Flores (GRDC TT-3837) and *S. trigonocephalus trigonocephalus* mandibles CD-2898/144 and CD-2897 from Trinil, Java. The reference mandible is *S. t. trigonocephalus* mandible CD-2896 (Trinil), in which the anterior 2 ridges of the M_3 are worn (adult individual). Dental wear stages of the other mandibles are: TT-3837 = 2 ridges of M_2 worn (subadult); C3/2/79 = 2 ridges of M_3 worn (adult); CMTL/271285-1 = 9 ridges of M_3 worn (adult); CD-2898/144 = 0 ridges of M_1 worn (juvenile); CD-2897 = 3 ridges of M_1 worn (juvenile); BC-2990 = 8 ridges of M_2 worn (adult).

not be studied in detail. At the GRDC is also a well preserved premaxillary with the sinistral orbital attached (L-III-3036).

Skull BC-3050 (Pl. 7, figs. 1-4) The braincase of skull BC-3050 is intact. The parts which are broken are: both molars, both zygomatic arches, the nasal processes, the superior portion of the premaxillaries in front of the orbits, both the pterygoid wings of the sphenoid, both bullae, and most of the sinistral squamosal including the left glenoid fossa. The upper margin of the left orbit is damaged, but at the right side only the tip of the zygomatic process of the frontal is broken. The skull is not distorted. All sutures are fully fused and can not be distinguished anymore. As argued before under the section describing the upper teeth, the broken teeth of which the roots remain in the alveoles must be the M^3s, so that the skull can safely be attributed to a fullgrown individual.

One of the diagnostic features of the Stegodontidae are their "roof-shaped" molar ridges. Though the molar structure in stegodonts resembles that of the earliest true elephants, the stegodonts lack accessory columns behind the ridges, which are prominently present in the earliest elephants (Maglio, 1970). These earliest elephants are further characterized by the presence of mandibular tusks and premolars, which have never been found in stegodonts. However, considering skull architecture the Stegodontidae have paralleled the Elephantidae in developing high and short skulls. As skull BC-3050 lacks the dentition, we need to look at other diagnostic criteria for identification.

Measurements of skull BC-3050 are given in Table 17. The skull is approximately of equal size as the *"E." celebensis* skull LWTL/151186-1 (compare with Table 16), but of a very distinct shape. The most striking difference is:

1) The comparatively large width of the frontoparietal region between the temporal fossae in specimen BC-3050 (Pl. 7, fig. 4), unlike the narrow braincase encountered in *"E." celebensis* (compare with Pl. 5, fig. 1 and measurements lb in the log-ratio diagram of Fig. 52). The forehead of BC-3050 is also relatively wider than in the early Stegodontidae *S. bombifrons* and *S. zdanski*. On the other hand, the advanced *S. ganesa* and *S. trigonocephalus* have relatively wider braincases.

Skull BC-3050 is further characterized by the following features:

2) The high position of the infraorbital foramini on the maxilla. The zygomatic process of the maxilla lacks a well developed facial crest (Pl. 7, fig. 2). The axis of the infraorbital foramini slopes upward in posterior direction and their lateral walls stand steeply.

3) What is left of the premaxilla, shows that the tusk sockets were almost parallel oriented and separated by a deep fossa incisiva (Pl. 7, fig. 4), strongly contrasting to the situation in *"E." celebensis* and in most Elephantidae, which have distally diverging tusk sockets and usually a shallow fossa incisiva. The deep interalveolar fossa in BC-3050 is narrow and only weakly widening distally (measurements lw & lx). The tusk sockets point forward and make an obtuse angle with the frontoparietal plane (Pl. 7, fig. 2).

4) The frontoparietal region is weakly convex, almost flat, in antero-posterior direction and convex in transverse direction. The forehead merges more gradually into the plane of the premaxillaries than is the case in the *"E." celebensis* skull, though in the latter much of the strongly sigmoidal dorsal skull profile seems to be shaped by postmortem deformation. The temporal lines form a clear ridge separating the temporal fossae from the forehead (Pl. 7, fig. 4), and the transverse cross-section over the temporal contractions has a rectangular shape. On the posterior side the nuchal line forms a weakly developed ridge separating the parietal and occipital planes.

5) A relatively high and short skull architecture (Pl. 7, fig. 2). The basicranium and forehead are steeply sloping, though less so than in *"E." celebensis*. The maxillaries are elevated as in *"E." celebensis* and in most Stegodontidae, but appear somewhat lower than in *S. ganesa* and in the more advanced Elephantidae.

6) The position of the orbits is high above the occlusal surface (Pl. 7, fig. 2). The postorbital process is directed laterally and not protruding anteriorly and the dorso-anterior orbital rim runs parallel to the sagittal plane of the skull and does not converge in anterior direction (Pl. 7, fig. 4), like in *"E." celebensis*. The dorso-anterior margin of the orbit is formed by a sharp edge, unlike the bulky and rounded orbit developed in *"E." celebensis* and *E. planifrons*.

7) The crista orbitotemporalis slopes downward and backward and encloses a teardrop-shaped intraorbital depression together with the crista orbitalis ventralis (Pl. 7, fig. 2). Such an intraorbital depression is only encountered in two stegodonts, viz. *S. ganesa* and *S. trigonocephalus* (Saegusa, 1987, 1995).

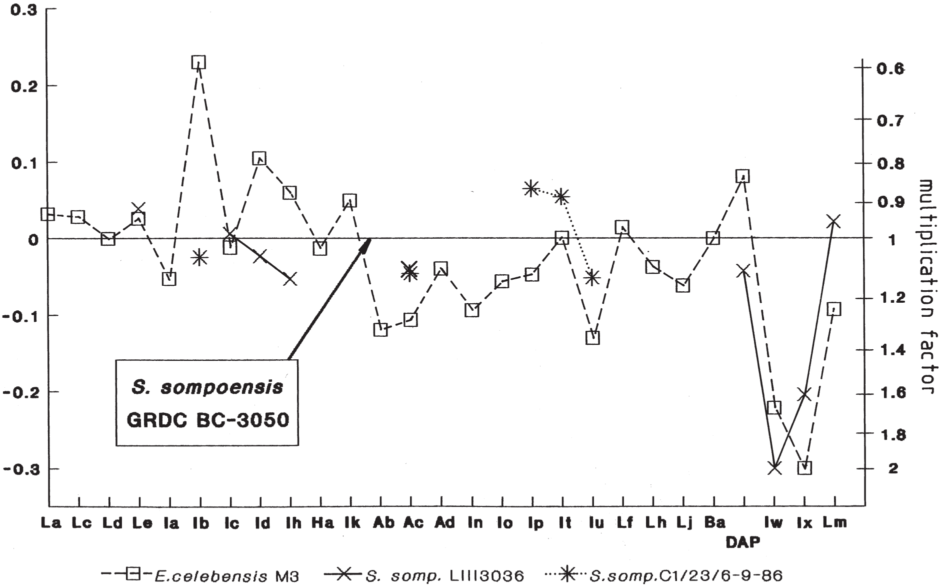


Fig. 52. Comparative log ratio diagram of skull measurements taken on *"Elephas" celebensis* skull GRDC LWTL-151186-1 (M^{3}s are worn in this skull) and the three skulls attributed here to *Stegodon sompoensis*. The reference specimen is *S. sompoensis* skull GRDC BC-3050, with both M^{3}s in function. The other two more fragmentary *S. sompoensis* skulls are GRDC LIII-3036 (dental wear stage not known) and MPC C1/23/6-9-86 (M^{3}s in wear).

8) Besides the infraorbital foramini there is a supraorbital foramen medially of each processus lacrimale (Pl. 7, fig. 4). The presence of supraorbital foramini is a plesiomorphic character, which is lost in the Elephantidae (Tassy, 1982; Tassy & Shoshani, 1988), but which is still retained in the Stegodontidae (Aziz, 1990). The supraorbital foramini present in skull BC-3050 and premaxilla L-III-3036 are placed in the center of a small depression and have a diameter of 15 mm.

9) The external nasal aperture is large and laterally sharply delineated without a stepwise hollowing of the processus nasalis of the premaxilla (Pl. 7, fig. 4). The perinasal area of the forehead is flat posteriorly of the nasal aperture.

10) The lower part of the occipital plane is wide and low and has an almost vertical orientation (Pl. 7, fig. 3). The fossa for the insertion of the nuchal ligaments is deep and wide. The upper rim of the occipital above this fossa is more strongly inclined forward and rather merging into the plane of the parietals, only separated of them by the weakly developed crest of the nuchal line. The angle between frontoparietal plane and occipital plane lies around 90 .

11) The fossa mandibularis, preserved only on the dextral side, is rather slenderly built as compared to *"E." celebensis*. It is weakly concave in transverse direction, contrasting to the strongly concave glenoid fossa in *"E." celebensis*. The zygomatic process of the squamosal is broken, but judging from its basal outline seems less heavy built as in *"E." celebensis*. Posteriorly, the glenoid fossa merges into the deep postglenoid fossa without a crested boundary (Pl. 7, fig. 1), which is present in *"E." celebensis*.

GRDC L-III-3036 (Pl. 6, fig. 5) This cranial fragment consists of the premaxilla, the anterior sheets of both maxillae and a large portion of the sinistral orbit, including the pyramidal process and the postorbital process. The tusk sockets are slightly damaged disto-laterally on each side, but the fossa incisiva is intact and also the alveolar border of the premaxilla is preserved at the median axis. Proximally the premaxilla is preserved up to the inferior border of the nasal aperture but on the left side also the lateral border of the nasal aperture is partly preserved, making it possible to measure the transverse diameter of it (measurement lh). L-III-3036 has similar dimensions as skull BC-3050 (Table 17). Like skull BC-3050, the present specimen is also characterized by a deep interalveolar fossa, which is however, almost two times wider than in the skull (Fig. 52), even though the premaxillary transverse diameter just in front of the orbitals (measurement ld) is only 1.5 cm larger. Contrary to *"E." celebensis*, and in common with BC-3050, the fossa incisiva is only weakly widening distally, and the widths between the lateral borders of the tusksockets (measurements ld, le and lf) are even decreasing in distal direction, so that the tusks must have been almost parallel oriented. Other characters in common with BC-3050 are the absence of a facial crest and the retention of supraorbital foramini. Of the crista orbitotemporalis and the crista orbitalis ventralis only the dorsal portions are preserved but it is not clear if a intraorbital depression was originally present at the point where both crests converged.

MPC C1/23/6-9-86:246 and C3/27-A/251286 Specimen C1/23/6-9-86:246 consists of the left portion of a braincase and both the maxillae. However, the dorsal and occipital surfaces are broken and the premaxilla is lacking. Both orbits are lacking. Besides the severe damage, the cranial fragment is largely covered with hard matrix. In Table 17 only a few measurements could be given, which indicate that this skull belonged to a slightly larger individual than BC-3050. The remnants of the M^3s allow to ascribe this skull to *S. sompoensis*. Like skull BC-3050 it is characterized by a relatively wide forehead between the temporal fossae (compare measurement lb in Fig. 52). Skull C3/27-A/251286, also with molar remnants indicative of *S. sompoensis*, is even more fragmentary and needs thorough cleaning. It will not be treated here.

Discussion

The high skull architecture and the wide forehead indicate that we are dealing with an advanced member of the Elephantoidea. Reduction of the facial crest (character 2) is a derived feature diagnostic for the Stegodontidae (Saegusa, 1987). In the Elephantidae a well developed facial crest is developed and the infraorbital foramen has a more horizontal orientation. The presence of (sub)parallel oriented tusk sockets and a deep fossa incisiva (character 3) are derived characters encountered in most *Stegodon* species. In *"E." celebensis*, *E. planifrons* and most Pleistocene Elephantidae, the interalveolar fossa is shallow and usually more strongly widening distally in conjunction with the diverging tusk sockets. The occurrence of a teardrop-shaped intraorbital depression (character 7) is a unique feature only encountered in certain stegodonts (Saegusa, 1987). The flat to slightly convex frontoparietal plane (character 4) and the retention of supraorbital foramini in the adult skull (character 8) are plesiomorphic characters shared with *"E." celebensis*. A convex forehead is present in both Stegodontidae and early Elephantidae. Due to the strong inflation of the parietal-occipital region in the more advanced Elephantidae, the longitudinal profile of the forehead becomes concave, except in *Loxodonta*, which possesses a globular braincase (Maglio, 1973; Beden, 1989). Amongst the stegodonts only *S. orientalis* is known to have developed parietal swellings independently, resulting in a concave forehead instead of the generally slightly convex forehead encountered in stegodonts (Saegusa, 1993). Characters 4 and 8 are retained in the stegodonts but lost in the more advanced species of *Mammuthus* and *Elephas* (Beden, 1979; Tassy, 1982). Thus, the combination of characters 2, 3, 4, 7 and 8 allows to refer skull BC-3050 to *Stegodon*, despite the lack of a diagnostic dentition. The small size of this skull fits well with the small stegodont molars and mandible fragments found in the same strata, and which are here attributed to *Stegodon sompoensis*. Also the relatively low number of molar ridges (9 or 10), which can be deduced from the outline of the roots still present in the maxilla, correspond well with the number of ridges in M3s of *S. sompoensis* (Table 33). Therefore, skull BC-3050 can be safely attributed to *Stegodon sompoensis*. Characters 2, 3 and 8 could also be ascertained in specimen L-III-3036 and therefore this premaxilla is also ascribed to *S. sompoensis*.

A high cranial vault (character 5) developed independently both in the Stegodontidae and in the Elephantidae (Saegusa, 1987). A wide forehead between the temporal contractions (character 1) is lacking in the more primitive stegodont species like *S. bombifrons*, *S. zdanski* and *S. aurorae*, but also in the primitive Elephantidae such as *"E." celebensis*. As already noted before, in *"E." celebensis* the value of measurement lb is much smaller whereas la and lc are larger than in skull BC-3050 (Fig. 52). In the more progressive forms of *Stegodon*, like *S. ganesa*, *S. orientalis* and *S. trigonocephalus*, the braincase has become more inflated. Comparison of the minimum width at the temporal contractions (measurement lb), the maximum width of the braincase at the occipital (measurement la) and the width at the postorbital processes (measurement lc) of skull BC-3050 and those of several *S. trigonocephalus* skulls in different ontogenetic stages can be made with the log-ratio diagram of Fig. 53. In this figure skull BC-3050 is plotted as the reference specimen. In the adult *S. trigonocephalus* skulls all la, lc, and in particular lb values are larger than in the pygmy *S. sompoensis* skull (Fig. 53). In the juvenile type skull of *S. trigonocephalus*, which has the anterior 4 ridges of the M^1 worn, lc is particularly small compared to la and lb, resulting in a triangular morphology of the frontals, which lead Martin (1884) to give the species its name. In fullgrown skulls attributed to *S. trigonocephalus* by Hooijer (1955b) the width at the postorbital processes has increased relatively compared to la and lb, thus weakening the triangular outline of the braincase slightly (Fig. 53). It also appears from Fig. 53 that in *S. sompoensis* skull BC-3050 the inflation of the braincase between the temporal fossae has proceeded slightly less than in *S. trigonocephalus*.

The laterally projecting orbits (character 6) is a condition in which *S. sompoensis* resembles *S. ganesa*, *S. pinjorensis* and *S. trigonocephalus*. In the other stegodonts and in the Elephantidae the postorbital processes and the dorso-anterior portion of the orbit are projecting more forward.

A character uniquely shared with *S. trigonocephalus* and *S. ganesa* is the presence of a teardrop shaped intraorbital depression between the crista orbitotemporalis and the crista orbitalis ventralis (character 7). In the morphology of the external nasal aperture, however, *S. sompoensis* resembles more *S. insignis*. According to Tassy (1994) in derived Elephantoidea the widened nasal aperture is laterally bordered by a hol-

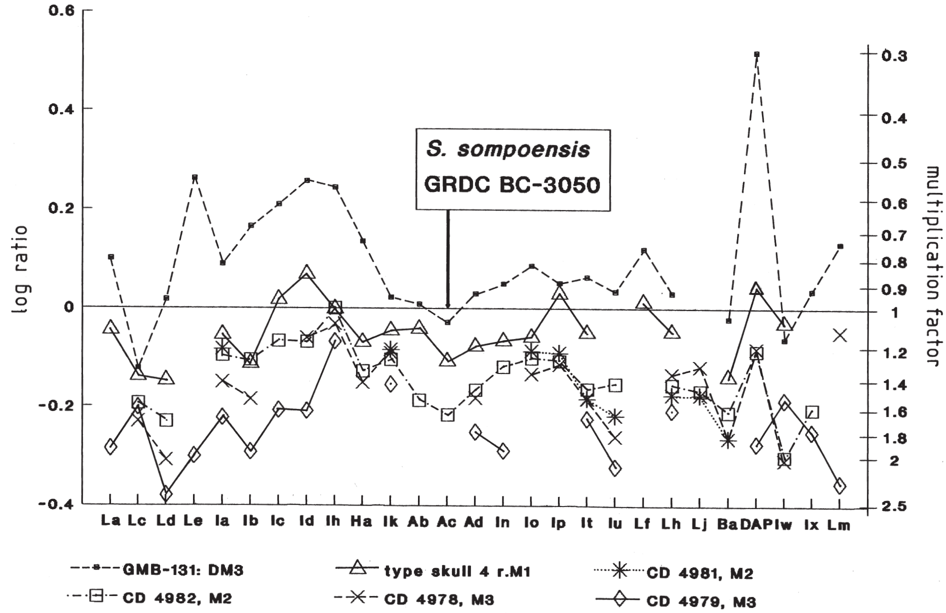


Fig. 53. Comparative log ratio diagram of skull measurements taken on *Stegodon sompoensis* skull GRDC BC-3050 (= reference specimen) and several *S. trigonocephalus* skulls in various ontogenetic stages. The dental wear stages of the various *S. trigonocephalus* skulls are: GRDC/GMB-131 = all ridges dP^3 worn; NNM holotype skull = 4 ridges M^1 worn; CD-4981 = 3 ridges M^3 worn; CD-4982 = 2 ridges M^3 worn; CD-4978 = 8 ridges M^3 worn; CD-4979 = ? ridges M^3 worn.

lowed processus nasalis of the premaxilla (as seen in *Choerolophodon*). In more derived taxa this hollowed premaxillary nasal process attains a step-like shape (amebelodontids and gomphotheres), a character also developed in *S. bombifrons* (Saegusa, 1995). In several stegodont species the processus nasalis premaxillae becomes reduced and three different derived morphologies can be distinguished (Saegusa, 1995): in *S. zdanski* and *S. aurorae* the hollowed area of the processus nasalis premaxillae are reduced into a faint, narrow groove. In addition, these two species share the unique development of a epifrontalonasal fossa above the nasal opening. In the second group of stegodonts the lateral border of the external nasal aperture is rounded and cannot be clearly delineated, a character state seen in *S. orientalis*, *S. pinjorensis*, *S. ganesa* and *S. trigonocephalus*. In *S. insignis*, on the contrary, the lateral border of the nasal aperture is sharply delineated, and it is with this morphotype that *S. sompoensis* shares the most resemblance. In the forward inclination of the upper portion of the occiput (character 10) *S. sompoensis* seems to be intermediate between the extreme forward bent upper occiput as encountered in *S. insignis* and the more vertical oriented upper occiput encountered in *S. ganesa* and *S. trigonocephalus*.

In an earlier publication (van den Bergh et al., 1996) it was stated that the amount of molar ridges in the broken M3s of skull BC-3050 probably has been 8 as deduced from the alveolar outline. However, during a reexamination of this specimen it was found that the anterior hook and the antero-medial root had already been resorbed and is not preserved in the broken rootmass. Thus, the original number of ridges was probably larger, 9 or 10. In two other skull fragments with the fragmentary remnants of the M^3s, which were examined recently (C1/23/6-9-86:246 and C3/27-A/251286), a total number of 9 ridges can be deduced. In the lower M_3s the total number of ridges is 9 or 10 (Hooijer, 1972b; this thesis). In *S. trigonocephalus*, *S. ganesa*, and *S. insignis* there are 10 or 11 ridges in the upper M^3 and 11 to 13 ridges in the lower M_3. *S. orientalis* has 11 to 12 ridges in the upper and 12 in the lower M3, whereas *S. aurorae* has 11 to 13 ridges in the upper and 12 to 13 ridges in the lower M3 (Taruno, 1991). High ridge numbers are also encountered in *Stegodon florensis*, with 12 ridges in the upper and 14 in the lower M3 (Hooijer, 1972a; this thesis), and *S. pinjorensis*, with 14 ridges in the upper M^3 (Osborn, 1942). At least in *S. aurorae*, the number of ridges seems to have increased independently from the other SE Asian stegodonts, because this species descended from *S. zdanski* with which is shares the unique development of a epifrontonasal fossa (Saegusa, 1995). *S. zdanski* still has a very low ridge formula (6-7 ridges in the upper and 7-8 ridges in the lower M3).

Based on skull morphology, it seems that *S. sompoensis* is most closely affiliated with the stegodonts from SE Asia and the Siwaliks (*S. trigonocephalus* and the *S. insignis* groups of Saegusa, 1987, 1996). It has no close affinity with the northern species *S. zdanski* and *S. aurorae*. *S. sompoensis* is probably most closely related to *S. ganesa*, with which it shares the derived feature of a teardrop shaped intraorbital depression. With *S. insignis* it shares the derived feature of a sharply delineated nasal aperture, but not the reduction of the frontals. In the cladogram presented by Saegusa (1995: fig. 1), *S. insignis* represents the sister group of the *S. trigonocephalus* group stegodonts, including *S. ganesa*. *S. sompoensis* may represent an early offshoot from the *S. ganesa* mainland stock. This would also be in accordance with the age and geographical distribution of both species. The oldest occurrence on Java of *S. trigonocephalus*, is at c. 1.2 Ma, whereas *S. sompoensis* appears on SW Sulawesi much earlier, around 2.5 Ma. This suggests that *S. sompoensis* could not have been derived from the Javanese stegodont.

Stegodon cf. *sompoensis* Hooijer, 1964

Description of the material

Molar remains — There are a number of molar fragments in the various collections, which do belong to *Stegodon*, but of which the rank can not determined. Most of these *Stegodon* molar fragments have morphological characters and size measurements, which fall within or just outside the ranges of variation encountered in *Stegodon sompoensis* molars as given in Table 33. Those are here attributed to *Stegodon* cf. *sompoensis* and are listed as such in Table 6. Because there is proof for the occurrence of a large-sized *Stegodon* species in South Sulawesi, though not in the lower part of the Beru Member, the fragmentary molars of uncertain rank here ascribed to *S.* cf. *sompoensis* will be treated in more detail below.

LR-2736 is an isolated, unworn, ridge of a *Stegodon* molar. The basal part is broken at one side but the width can be estimated at 50e mm. The height is c. 35e mm, giving an h/w index of 70e. The enamel is double-layered with an ET ranging between 4.4 and 4.9 mm. There are 6 digitations, 4 larger and 2 smaller ones, and there are no median pillars developed. Though the ET is larger than in any of the identifiable *S.*

sompoensis molars, the small size in combination with the thick enamel and low number of digitations allows to attribute this specimen to *S.* cf. *sompoensis*.

ABTL-161186-1 is a worn molar fragment consisting of -$^1/_2$2- ridges. It is of the lower side as the occlusal wear surface is concave. The largest width at the base is 61.5 mm in the posterior ridge. Its digitations are worn into nine isolated dentine islands. Two longitudinal clefts divide the enamel loop into a large median portion and two smaller lateral portions. This tripartite pattern is repeated in the slightly further worn ridge in front of it, though here the dentine is interconnected into three figures, with the larger median one slightly expanded as compared to the lateral ones. There is abundant cement between the ridges. The LF is 5.8 and the double-layered enamel has an ET varying between 3.5 and 3.9 mm. 'Stufenbildung' is developed at the occlusal surface of the enamel, which is wrinkled with 4 to 5 folds per cm and an amplitude up to 2 mm. There are no vertical grooves on the lateral sides of the ridges, indicating that this fragment does not represent a milkmolar. The molar fragment falls within the range of the M_3 of *S. sompoensis*.

One upper left *Stegodon* molar is represented by two fragments (BC-2957: anterior portion and BC-2959: posterior portion), which do not fit. The anterior fragment consists of x2- ridges, the posterior one, which is still covered by some hard pebbly sandstone matrix, has -$^1/_2$3$^1/_2$- ridges preserved. The ridges of the anterior fragment are worn except for the anterior halfridge. The width of ridge 1 is 42 mm. Its digitations are worn to such a degree that 6 rounded dentine islands are connected. The largest basal width of 49.5 mm occurs at the anterior complete ridge of the posterior fragment. The widths of the ridges behind it are 49 mm, 46.5 mm and 40e mm. The apex of the posterior fragment is largely concealed by matrix, but the posterior two ridges are unworn and have a height of 36e and 29e mm, giving h/w indices of 77e and 73e. The crownbase is slightly convex in apical direction and the molar is not strongly curved in lateral direction, indicating that the molar is of the upper side. There are no vertical grooves on the lateral sides of the ridges. The LF is 7.6 and the double-layered enamel has an ET varying between 3.6 and 3.8 mm. The measurements correspond with the size values of the M^2 or M^3 of *S. sompoensis*, and the fragments are therefore attributed to *Stegodon* cf. *sompoensis*.

A tiny posterior milkmolar fragment (GRDC 1637) has -$^1/_2$2 ridges worn down to the root. The dentine of the posterior two ridges has coalesced. Three small isolated conelets are separated from the main wear pattern, two on the right side (buccal or lingual?) and one on the left side. The one on the left side corresponds with an indentation of the enamel wear pattern, and indicates that its position coincides with the valley between ridges I and II. The wear surface is plane and the roots are broken of completely. The basal width is 18.9 mm for the posterior ridge and 18.7 mm for the penultimate ridge. The small difference between the width of the two ridges suggests that we are dealing with a lower milkmolar, but it is impossible to attribute this fragment to the right or left side. The LF amounts 20.8. The enamel is very thin (ET = 0.9-1.1 mm) and wrinkled with 5-6 folds per cm and an amplitude of less than 0.5 mm. The delicate wrinkling is suggestive of *Stegodon*. The basal width is smaller than in the dP^3 of *S. sompoensis* (Table 33), and the fragment can be best attributed to a dP2 of *Stegodon* cf. *sompoensis*.

Tusks — There are five tusk fragments from various localities, which based on their "guilloche" cross-sectional pattern can be distinguished from *"E." celebensis* tusks and which can be attributed to *Stegodon*. If the maximum diameter of these *Stegodon* tusk fragments did not exceed 85 mm (which is the diameter of the tusk alveoles in the adult *S. sompoensis* skull BC-3050) these tusk fragments have been attributed to *Stegodon* cf. *sompoensis* in Table 6. An exception is made for three tusk fragments with a smaller diameter than 85 mm, which were found associated with juvenile dentitions attributed in this thesis to *Stegodon* sp. B (specimens TA-3714, TA-3715 and PS-1/6). *Stegodon* tusk fragments larger than 85 mm in diameter are listed as large-sized *Stegodon* species in Table 6.

Stegodon sp. B

Stegodon spec. B cf. *trigonocephalus*; Aziz, 1990: 64, pl. VI, figs. 1-3.
Large-sized *Stegodon* spec.; van den Bergh et al., 1992: 37.
Stegodon spec. B; van den Bergh et al., 1994: 33-35.
Stegodon cf. *trigonocephalus*; Bartstra et al., 1994: 13, fig. 4.
Large-sized *Stegodon*; van den Bergh et al., 1996: 241.

Hypodigm — There is a well preserved upper dentition most likely consisting of a sinistral dP^4 remnant and a largely unworn M^1 (GRDC TA-3711; Pl. 8, fig. 1) and the associated dextral dP^4 remnant and M^1 (GRDC TA-3712; Pl. 8, fig. 2. This dentition was found associated with two opposite tusk fragments (GRDC TA-3714 and TA-3715). The fossils were found in situ in the Tanrung Formation at FVL-29 (4°18'S; 120°04'E) on the south bank of the Tanrung River, Bone District, South Sulawesi. There is a second more fragmentary upper dentition, probably representing a dextral M^1 remnant (GRDC PS1/1) and incomplete anterior dextral M^2 fragment (GRDC PS1/2) and an anterior M^2 fragment (GRDC PS1/3). Of the same individual there is also an associated tusk, a dextral astragalus, two mandible fragments a phalanx and a number of smaller bone fragments. These remains originate from the Pintareng Formation on the small island of Sangihe (Province of North Sulawesi). In addition, there is a sinistral mandibular ramus fragment with the posterior portion of an M_3 (GRDC TA-3723), originating from the Tanrung Formation. All these specimens are all housed in the GRDC collection.

The Tanrung Formation unconformably overlies the Upper Pliocene to Lower Pleistocene Walanae Formation and presumably has a Middle Pleistocene age. The age of the Pintareng Formation is considered Pleistocene (Samodra, 1989).

History

The material attributed here to *Stegodon* sp. B originates from two localities. One of these is situated along a small river near Pintareng village on the island Sangihe (Province of North Sulawesi). Sangihe island is located halfway between the northernmost extension of Sulawesi and the Philippine island of Mindanao. The fossils were discovered by local villagers and brought to the residence of the village chief, Mr Habibi. In 1989 a geologist of the GRDC, Mr H. Samodra, carried out a field survey at Sangihe island and obtained information concerning the fossil findings. Later that year Dr F. Aziz, vertebrate paleontologist at the GRDC, together with Professor

Tatsuo Shibasaki of the JICA, went to Sangihe to inspect the locality and collect the fossils. All the fossils from Pintareng are presently housed at the GRDC in Bandung and are believed to belong to a single individual. Aziz (1990) briefly described the Sangihe fossils and attributed them to *Stegodon* species B cf. *trigonocephalus*. Van den Bergh et al. (1992) attributed the specimens to *Stegodon* sp. B. The Sangihe dental elements will be described for the first time in more detail below, and the present study shows that the molars are significantly distinct from the Javanese stegodont.

Other dental remains here attributed to *Stegodon* sp. B originate from the Tanrung Formation, which crops out along the Tanrung River (Bone District, Prov. of South Sulawesi). Fossils were first recovered by our team from this deposit in 1990. Subsequent collecting in 1991, 1992 and 1993 yielded more elephantoid material, both dental and postcranial elements, all attributable to large- to medium-sized individuals, whereas true pygmy elephantoid remains have not yet been found in this unit. The molar and postcranial remains were briefly mentioned by van den Bergh et al. (1992, 1996) as belonging to a large-sized *Stegodon*.

Bartstra et al. (1994: fig. 4) figured a molar fragment from the collection of the MPC, reportedly originating from Tanrung (MPC TRG 12.01.91). The fragment consists of the two unworn posterior ridges of a *Stegodon* molar and was determined as the portion of a lower molar of *Stegodon* cf. *trigonocephalus*. Most probably, this fragment fits to the incomplete dextral M^1 (GRDC TA-3711) which will be described below and in which the posterior two ridges are missing. TRG-12.01.92 presents a mirror image of the posterior two ridges of the complete sinistral M^1 (GRDC TA-3712) of the same individual, and also the size measurements given by Bartstra et al. (1994: 13) match exactly our own measurements taken on TA-3712. The upper *Stegodon* dentition TA-3711/3712 was found by our team on 12 October 1991, in situ in a layer pertaining to the Tanrung Formation. We were guided that day by M. Anwar Akib of the MPC, who took the missing molar fragment and subsequently registered it in the collection of the MPC. On this occasion the numbers indicating the month (october) of the collecting date were presumably erroneously recorded. It is felt important to make these statements because Bartstra et al. (1994) suggest in their paper that the locality Tanrung is just another locality pertaining to the Beru Member of the Walanae Formation. However, as discussed in chapter 3 the fossiliferous unit cropping out along the Tanrung River forms a distinct stratigraphic unit (Tanrung Formation), lithologically distinct from the Beru Member sediments and unconformably overlying the Walanae Formation. The age of the Tanrung Formation is estimated to be Middle Pleistocene.

The dental material from Tanrung and Sangihe are very similar in morphology and characteristics, but can be distinguished from *S. sompoensis* and *S. t. trigonocephalus*. The *Stegodon* is here tentatively named *Stegodon* sp. B. The Tanrung dentition, which is more complete, will be described first below.

Description of the material

Upper dentition from the Tanrung Formation — The upper dentition of a single *Stegodon* individual was found in situ in the upper part of the Tanrung Formation. The dentition comprises two succeeding molars of the dextral side (GRDC TA-3712: Pl. 8, fig. 2) and the opposite equivalents of the sinistral side (GRDC TA-3711: Pl. 8, fig. 1).

Two broken, proximal tusk fragments, one of the dextral and one of the sinistral side (GRDC TA-3714 and TA-3715), were found at the same spot and belong to the same individual. Some poorly preserved remnants of the maxilla are attached to the dextral dentition. The two anterior molars are completely worn and the anterior portions were already shed during life. The dextral one is preserved over a slightly longer longitudinal distance, including a large portion of the roots. Apart of its less advanced wear, it constitutes a mirror image of its sinistral counterpart. Of the posterior pair of molars only the anterior two ridges are abraded by wear. The sinistral one (TA-3711) is intact, but two posterior ridges of the dextral specimen are broken. As already mentioned, this missing portion is the fragment figured by Bartstra et al. (1994, fig. 4). For convenience only the more complete dextral anterior molar (TA-3712) and the complete sinistral posterior molar (TA-3711) will be described in detail below.

The worn dextral molar (TA-3712) is preserved over a longitudinal length of 90+ mm. It bears -$^{1}/_{2}$5x ridges (Pl. 8, fig. 2). Of the anterior two and a half worn ridges the dentine has coalesced along the median axis of the crown. Of the most anterior one and a half preserved ridges also the lateral enamel borders have disappeared due to excessive wear. The remaining posterior ridges exhibit single enamel loops, except for the posterior half-ridge, of which the digitations are abraded. The wear surface is convex antero-posteriorly. The buccal side of the molar is worn down slightly more than the lingual side. Abundant cement covers the flanks of the ridges and is deposited between the ridges. The posterior half-ridge is broken on the buccal side. On the lingual side 5 abraded digitations can be distinguished. The maximum width (W) occurs at ridge II and amounts to 65.3c mm. The widths of the individual ridges are given in Table 34. The LF of the molar is 6.2. The enamel is rather thin, with an ET varying between 2.2 and 3.1 mm. It is regularly folded showing a scalloped pattern, with 2-5 folds per cm and an amplitude of 0.5-1 mm. Each ridge is supported by a slightly backwards curved root, but nothing of the anterior hook and antero-medial root remains, indicating that the molar originally possessed at least one or two more ridges at the front. The sinistral counterpart is slightly more worn, but matches the just described dextral molar in all aspects.

The succeeding pair of molars constitute mirror images apart from the fact that the dextral one lacks the two posterior ridges. The complete sinistral molar (TA-3711) has a total length of 155 mm and bears x8 ridges. The anterior halfridge is only developed on the buccal side, but is largely concealed by cementum. Cementum coverage is strong, leaving only the digitations free in the unworn posterior ridges. The anterior ridge is divided by a median cleft into a lingual and a buccal part (Pl. 8, fig. 1), both parts being curved backwards at the lateral and median ends. The buccal part is slightly more worn than the lingual part and the dentine is interconnected in the wear pattern. The median termination of the buccal part shows a prominently backward protruding dilatation, which would be equivalent with a median posterior pillar. The lingual part of the anterior ridge is straighter, and the dentine of the various digitations is not yet connected completely. Of the second ridge the digitations, of which there are nine, are slightly abraded, not yet exposing the dentine. This ridge is also divided in two parts by a well marked median cleft, which is developed a little lingually of the median axis of the molar. The third unworn ridge seems also to be divided by a median cleft at the same position as in the second one, but it is concealed by cementum. The total number of digitations of the third ridge cannot be given because cementum conceals some of them. This is also the case in the remaining ridges, except for ridge 5, where the cementum is largely broken away, revealing the presence of again 9 digitations. A cleft is also visible in this ridge, this time at a median position. This median cleft is apparently less deep than in the anterior ridges. The basal widths and heights of the successive ridges are given in Table 34. The maximum width (W) is 68.5c mm and occurs at ridge 5. The maximum height (H) is 48.5 mm and occurs at ridge 6. The h/w indices vary between 63e and 71. The molar has a rectangular shape and is not tapering posteriorly. The LF amounts 5.8 and the ET varies between 3.0 and 3.6 mm. The scalloped, double-layered enamel shows 'Stufenbildung' at the occlusal surface. In the anterior ridge there are 2-4 folds per cm with an amplitude between 0.5 and 1.5 mm. The root is largely broken but a small portion of the anterior hook and the antero-medial root is preserved, together supporting x2-ridges.

The associated two tusk fragments are weakly curved laterally. Both are proximal fragments, including a large portion of the pulpa cavity. They are broken distally approximately at the level of the former alveolar rim, and presumably they were still inside the premaxilla of the skull prior to burial. As follows from the poorly preserved and heavily dissolved maxillary fragments attached to the dentition, the skull or skull fragment has been probably disintegrated after burial and only the molars and broken tusks have resisted dissolution. The largest of the tusk fragments (TA-3714), supposedly of the left side, is preserved over a straight length of 254 mm measured at the convex side. The convex surface projects 15 mm above the straight line connecting both terminations of the convex side. The transverse diameter measured at the proximal end and perpendicular to the plane of curvature amounts 63.5 mm, that of the pulpa cavity 32.5 mm. The vertical diameter at this position cannot be taken as the dorsal surface is broken. The conical pulpa cavity extends to the broken distal end of the tusk fragment, where its diameter is 7 mm. The total tusk diameter at that level amounts to 57 mm. The opposite fragment (TA-3715) is a little shorter (226 mm as far as preserved) and of a more distal position. Its proximal diameter is 61 mm transversely and 59.5 mm dorso-ventrally. The diameter at the distal end is 51 mm transversely and 47 mm dorso-ventrally.

Comparison — The unworn posterior molars from this upper dentition are certainly not M^3s because of their rectangular shape. For comparison the reasonably well known upper molar series of *Stegodon trigonocephalus trigonocephalus* will be used. Normally, *S. t. trigonocephalus* M^2s have their maximum width (W) at a position anteriorly of the two most posterior ridges I and II. In contrast, dP^4s have their maximum width (W) coinciding with the most posterior or penultimate ridge (ridge I or II), whereas the width in successively more anterior ridges decreases steadily. M^1s, apart from having a W intermediate between that of the dP^4 and M^2, usually also have their W concurring with ridge II or III, at an intermediate position as compared to dP^4s and M^2s. This is graphically shown in Fig. 54A, in which the widths of successive ridges of various *S. t. trigonocephalus* dP^4s, M^1s and a characteristic M^2 are plotted. In the same figure the successive widths for TA-3711 (unworn posterior Tanrung molar) and TA-3712 (worn anterior Tanrung molar) are also plotted. TA-3711 has a rather rectangular shape with the maximum width (W) coinciding with either ridge

III, IV or V (as a thin layer of cementum covers the flanks of ridges I-VII in this molar, it is not possible to see which enamel ridge actually is the widest one). The shape of its ridge-width graph suggests that TA-3711 represents an M^2, though its size corresponds better with M^1s of *S. t. trigonocephalus*. If we assume that TA-3711 is a rather small M^2, than TA-3712 from the same maxilla would thus represent an M^1. As shown in the same Fig. 54A, TA-3712 indeed corresponds well with the M^1 of *S. t. trigonocephalus*, both in absolute size and shape of its (partial) ridge-width graph. Its maximum width lies clearly above the width range observed in the dP^4s of *S. t. trigonocephalus* (see also Table 31 and Fig. 55).

However, there are several points of difference that do not agree with the *S. t. trigonocephalus* M^1-M^2 sequence. First of all, the posterior molar (TA-3711) has a ridge formula (x8) which is one ridge less than that of the M^2 of *S. t. trigonocephalus*, which has x9x ridges (Besides 2 complete M^2 from Trinil, Hooijer (1955b) describes 3 more complete M^2s from other localities, all bearing 9 ridges and attributed to *S. trigonocephalus*).

Secondly, the size of the posterior Tanrung molar (TA-3711) is much smaller than the M^2s of *S. t. trigonocephalus*. Its total length (L) is only 155 mm, which is considerably shorter than the range of L values for the M^2 observed in *S. t. trigonocephalus* (L ranging between 191 and 221 mm, n = 5: see Hooijer, 1955b, table 14; this table includes specimens described by Janensch (1911) and specimens from other localities than Trinil and Kedung Brubus). Associated with this relatively small length is the relatively high LF value of 5.9, higher than in any of the *S. t. trigonocephalus* M^2s. The size differences between TA-3711 and *S. t. trigonocephalus* M^2s are graphically shown in Fig. 55, which represents a scatterdiagram of L versus W measurements of all complete molars attributable to *S. t. trigonocephalus* from Java. TA-3711 is clearly of intermediate size between the characteristic M^1s and M^2s of the Java species, though there are 2 molars from Java corresponding in size with TA-3711. One is the posterior molar of an upper dentition in a palate from Grobogan (specimen CD-3818/3822). This molar was determined by Hooijer (1955b) as an M^1, and the molar remnant in front of it as a dP^4. We will come back to this aberrant specimen from Java later on. The other is an isolated upper molar originating from the Ngandong terrace fill, here attributed to an M^1 of *Stegodon trigonocephalus ngandongensis*, a subspecies younger in age and with a more advanced plate formula than *S. t. trigonocephalus*.

Thirdly, a marked difference between the Tanrung dental succession and that of the M^1-M^2 succession in *S. t. trigonocephalus*, consists of the fact that the W values of both successive Tanrung molars are very similar, whereas the M^1-M^2 succession of *S. t. trigonocephalus* shows a marked increase in W values, without overlap (Table 31). The increase in maximum width (W) between the anterior and posterior molars of the Tanrung individual is very low, only 6.8%. In two *S. t. trigonocephalus* maxillas with M^1s and M^2s both present (CD-143 and CD-12811), the increase in maximum width between these successive molars amounts to 19% and 30%, respectively. Though these two values are considerably higher than in the Tanrung dentition, they are not of much significance if we don't know what kind of variation we might expect. Unfortunately, there are no other maxillas with both M^1 and M^2 and in which the W of both these succeeding molars could be measured. In order to obtain some idea of the W increase between M^1s and M^2s of *S. t. trigonocephalus*, the average W of all M^1s (complete and fragmentary specimen in which the W value could be measured) was calculated (average W = 65.3 mm, n = 7). This was also done for the M^2s (average W = 85.2, n = 11). The increase between these average values amounts to 30.5%, again considerably higher than in the Tanrung maxilla. Even if the increase in W between the widest M^1 (W = 68 mm) and the narrowest M^2 (W = 76 mm) is taken, we still come out at a value of 12% increase, two times the value of the Tanrung maxilla.

It can be concluded that the Tanrung dentition really appears to be quite distinct from the M^1-M^2 succession in *S. t. trigonocephalus*. Slight increases in width between the M^1s and M^2s comparable to the 6.8% encountered in the Tanrung dentition can be encountered in dwarfed stegodonts such as *S. sondaari* sp. nov. (see chapter 6). In an upper dentition belonging to an adult individual of *S. sondaari* (GRDC TT-4030/4031/4035/4037), the maximum width between of the M^1s and M^2s shows a 0.4%-2.9% increase only. Body growth, including growth of the mandible, appears to have stopped at an earlier ontogenetic stage in these dwarfs than is the case in large-sized elephants. In the dwarfed *S. sondaari* the last two molars do not show a marked increase in width compared to their preceding molars (Fig. 71). However, the Tanrung molars certainly did not belong to a fully dwarfed individual, because their size is comparatively large, larger than homologue molars of *Stegodon sompoensis* for instance (compare Table 33; note that even the W values of the M^3s in *S. sompoensis* are still lower than in the posterior Tanrung molars). Their attribution to *S. sompoensis* can therefore also be discarded.

Seen in the light of the considerations given above, it is assumed possible that the successive molars of the Tanrung dentition represent rather large dP^4s and M^1s as compared to homologue molars in *S. t. trigonocephalus*. Such a determination is also in accordance with the relatively small diameter of the tusks that are associated with this upper dentition (maximum diameter is 57 mm at level of the conical tip of the pulpa cavity). The tusks are even smaller in diameter than the tusk alveoles in the *S. trigonocephalus* holotype specimen (antero-posterior diameter of the alveole at the distal end of the premaxilla = 70e mm, estimated from the 1:6 scaled figure presented by Martin, 1887: pl. II, fig. 1). Originally the molars in the *S. trigonocephalus* type skull were erroneously attributed by Martin (1887) as the second and third “premolars”, but Hooijer (1955b) demonstrated convincingly that the worn anterior molars are dP^4s and the slightly worn posterior molars M^1s. If the Tanrung molars were considered as dP^4s and M^1s, the dentition would be in the same dental wear stage as the *S. trigonocephalus* holotype skull. The small size of the tusks associated with the Tanrung maxilla would thus be in accordance with the juvenile state of the individual. The possibility that the present individual pertained to a small-tusked *Stegodon* species is

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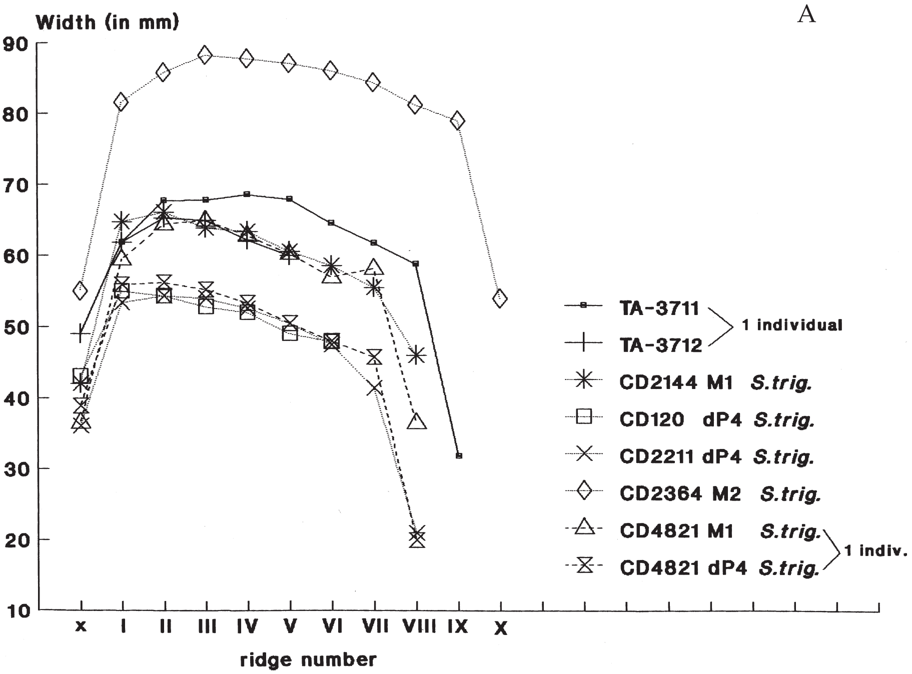
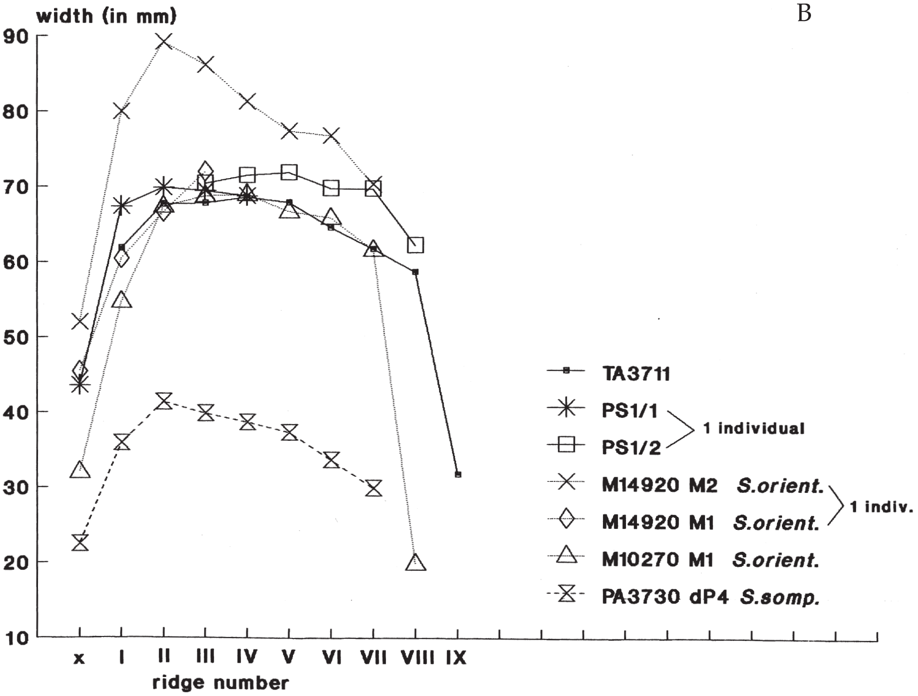
Fig. 54. Ridge-width graphs of various *Stegodon* intermediate upper molars. A: The widths of successive ridges are shown (counted from back to front) of the dextral, worn anterior molar (TA-3712) and sinistral, unworn posterior molar (TA-3711) of a single individual of *Stegodon* sp. B, originating from the Tanrung Formation, South Sulawesi. The ridge widths of various *S. t. trigonocephalus* dP^4s, M^1s and an M^2 are also shown for comparison. B: The widths of successive ridges are shown of the dextral, worn anterior molar (PS1/1) and the dextral, slightly worn posterior molar (PS1/2) of a single individual (attributed here to *Stegodon* sp. B) from Sangihe island. For comparison are also shown the ridge widths of specimen TA-3711, of three *S. orientalis* intermediate upper molars and one *S. sompoensis* dP^4.


A
Width (in mm)
90
80
70
60
50
40
30
20
10
x
I
II
III
IV
V
VI
VII
VIII
IX
X
ridge number
TA-3711
TA-3712
1 individual
CD2144 M1 S.trig.
CD120 dP4 S.trig.
CD2211 dP4 S.trig.
CD2364 M2 S.trig.
CD4821 M1 S.trig.
CD4821 dP4 S.trig.
1 indiv.


B
width (in mm)
90
80
70
60
50
40
30
20
10
x
I
II
III
IV
V
VI
VII
VIII
IX
ridge number
TA3711
PS1/1
PS1/2
1 individual
M14920 M2 S.orient.
M14920 M1 S.orient.
1 indiv.
M10270 M1 S.orient.
PA3730 dP4 S.somp.

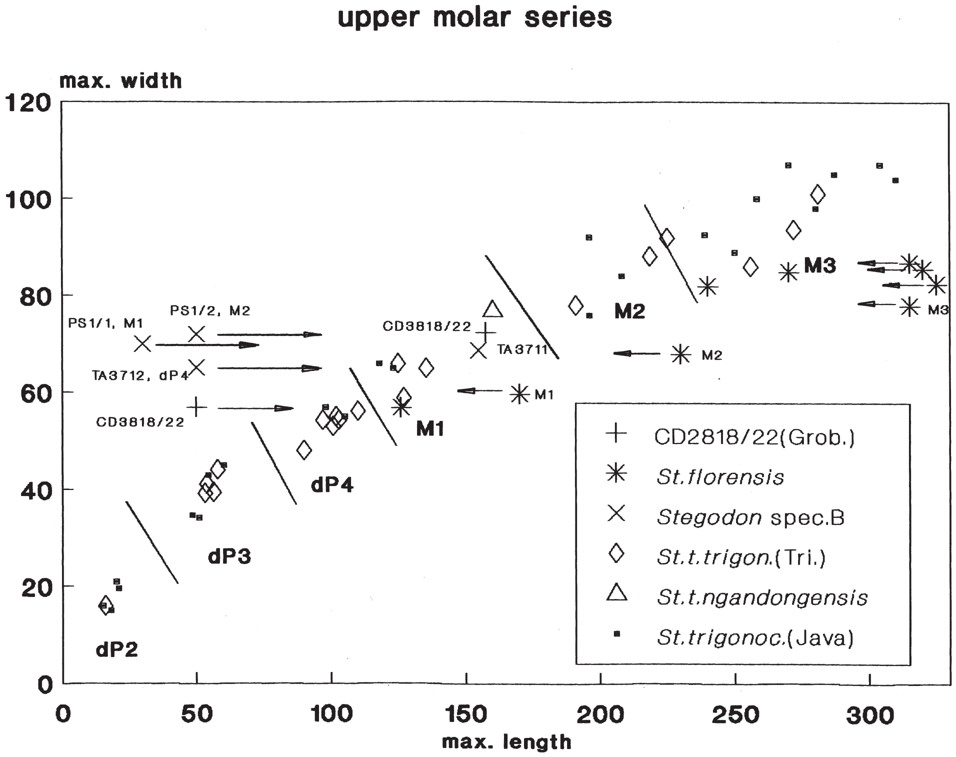


Fig. 55. Scatterdiagram of L versus W (in mm) of two upper *Stegodon* sp. B molars (TA-3711 and TA-3712) from the Tanrung Formation, South Sulawesi, and all complete upper molars from Java attributable to *S. trigonocephalus*. The Java sample includes the molars in the Dubois Collection described by Hooijer (1955b) and in the Selenka Collection described by Janensch (1911; measurements are from this publication) and additional material in the GRDC collection from the loc. Ngandong. Molars originating from the loc. Trinil are marked with distinct symbols (lozenges) as those from other localities (small black squares). Though the molars originate from different localities, 6 distinct groups can be distinguished, representing the 6 successive upper molars (only for the M^2 and M^3 there is some overlap in W, but these two elements could be easily separated on morphological grounds). Note that molars from Trinil tend to be slightly smaller on average than those from other localities. The L/W plots of the dextral, worn anterior molar (TA-3712; note that of this incomplete specimen only the W could be measured and that the L measurement indicated represents the length as far as preserved) and the sinistral, unworn posterior molar (TA-3711), representing a single individual of *Stegodon* sp. B. Specimen CD-3818/3822, an upper molar from Grobogan determined by Hooijer (1955b) as a large M^1 of *S. trigonocephalus*, falls outside the scatter for the remaining M^{1}s attributed to that species, but has dimensions close to those of specimen TA-3711. Molars PS1/1 and PS1/2 are from Sangihe island and belong to a single individual.

unlikely, because several large-sized tusk fragments with diameters of up to 12 cm have been found also in the Tanrung Formation.

Considering the Tanrung upper dentition as dP^{4}s and M^{1}s, we can again compare the maximum width (W) increase of equivalent molars in other stegodonts species. The W increase between dP^{4}s and M^{1}s in three individuals attributed to *S. t. trigonocephalus*, including the type specimen, is again considerably higher than in the Tanrung dentition, varying between 16% and 30%. The average W increase calculated from the average W measurements of isolated dP^4s and M^1s is 21.4% (average W of dP^4s = 53.8 mm, n = 11; average W of M^1s as given above), which is again a significantly larger increase than the 6.8% of the Tanrung dentition. Besides, the maximum width (W) of the worn anterior molars lies above the range observed in the dP^4 of *S. t. trigonocephalus* (compare with Table 31). As already mentioned above, there is 1 upper molar in the Dubois Collection which matches the posterior Tanrung molars in size. This specimen is a palate with an anterior worn molar remnant and a complete posterior molar (CD-3818/3822; measurements are shown in Fig. 55) originating from the locality Grobogan. The succeeding molars in this palate were attributed by Hooijer (1955b) to a dP^4 and a rather large M^1 of *S. trigonocephalus*. Unlike the M^1 of *S. t. trigonocephalus*, the complete Grobogan molar carries x8x ridges instead of x7x. The height of the unworn ridge 4 is 45e mm, giving a hypsodonty index of 67e. As can be seen in Fig. 55, the Grobogan specimen falls considerably outside the scatter for the remaining M^1s attributed to *S. t. trigonocephalus*, but is much smaller than the M^2s of that same species. The W of the completely worn out molar remnant in front of it (57e mm) falls just below the upper limit of the range of variation of the W of dP^4s attributable to *S. t. trigonocephalus*. The W increase in the successive Grobogan molars amounts to 26%, comparable to that in *S. t. trigonocephalus*. CD-3818/3822 could represent a dP^4-M^1 succession of a relatively large but yet unknown *Stegodon* species or subspecies (perhaps *S. t. ngandongensis*), or less likely, an M^1-M^2 succession of a size-reduced *Stegodon* form. However, the relatively large W increase between the successive Grobogan molars does not support the latter interpretation, and neither do they belong to the same species as the Tanrung molars. Unfortunately, the locality Grobogan can not be correlated with the biostratigraphical scheme for Java used in this thesis and which is shown in Fig. 24. The M^1 of *S. t. ngandongensis* (GRDC K-363) is slightly larger than the posterior Tanrung molar and has likewise (x)8x ridges. As follows from the description of *S. t. ngandongensis* lower milk molars from the Ngandong terrace fill (chapter 2), the ridge formula is more advanced than in *S. t. trigonocephalus*, which corroborates the interpretation of K-363 as an M^1. Other true molars of *S. t. ngandongensis* have not been described so far, hampering further comparison.

From the arguments presented above it may be concluded that the Tanrung dentition can not be attributed to *S. t. trigonocephalus* nor to *S. sompoensis*. Unfortunately there are not many other *Stegodon* species in which the dental size variation of intermediate molars is sufficiently well known. Apart from *S. t. trigonocephalus* and the pygmy *S. sondaari* sp. nov. from Flores, only of *S. orientalis* an almost complete sequence of complete upper and lower molars is known. *S. orientalis* material has been described by Colbert & Hooijer (1953). The material was collected between 1921-1926 by Walter Granger of the American Museum of Natural History. The fossils originated from the limestone fissures paralleling the Yangtze River in the Chinese Province of Sichuan. Colbert & Hooijer (1953) only treated the material housed in the AMNH, but a small part of the *S. orientalis* molars from the Granger Collection have ended up in the British Museum of Natural History. The latter material has been examined as part of this study, but for the AMNH material the data given by Colbert & Hooijer (1953) were used. I agree upon with the statements of these authors, that the distinction between *S. orientalis* Owen and *S. orientalis grangeri* Osborn cannot be appreciably demonstrated, and the material from the Granger collection will further be referred to as *S. orientalis*. The possibility that the *S. orientalis* material covers a relatively long time range during which subspecific differentiation may have taken place is not excluded here. For instance, there may have been an increase in ridge formula through time. Such an increase in ridge formula was shown to have occurred in the case of *S. trigonocephalus* in chapter 2. This enabled the distinction of three successive subspecies. However, as no stratigraphic control exists for the *S. orientalis* Sichuan sample, a similar subspecific distinction is at present impossible for *S. orientalis*. Pei (1987) attributed a primitive *Stegodon* sample from Liucheng cave in the Guangxi Province to *S. preorientalis*. According to Saegusa (1996) the fragmentary holotype of *S. preorientalis* cannot be distinguished from *S. orientalis*, but he agreed that the primitive Liucheng sample is specifically distinct from *S. orientalis* and named it tentatively *Stegodon* sp. B.

The lengths and widths of the successive upper molars of *S. orientalis* from Sichuan are plotted in Fig. 56 together with the Tanrung molars. The *S. orientalis* measurements are largely based on the values given by Colbert & Hooijer (1953), except for the measurements of an M^1 given by Hopwood (1935) and the measurements of two complete specimens in the BMNH (M-10270, a dextral M^1, and M-14920, a sinistral maxilla with the M^2 and the posterior portion of the M^1). The size of the posterior Tanrung molar TA-3711 matches perfectly with the (only) complete M^1 of *S. orientalis*, whereas the width of the anterior molar remnant (TA-3712) falls within the range observed in the dP^4 of *S. orientalis* (see also Fig. 54B). No measurements of dP^4-M^1 successions of single individuals can be given, but the increase in average W between dP^4s and M^1s in *S. orientalis* comes out at 16.9%, which is 4% lower than in *S. t. trigonocephalus* but still 10% greater than in the Tanrung dentition. For the M^1-M^2 succession of *S. orientalis* the increase in average W values is, like in *S. t. trigonocephalus*, greater than for the dP^4-M^1 succession, amounting to 25.8%. Though the size of the Tanrung molars corresponds better with those of the dP^4-M^1 succession of *S. orientalis* than with that of *S. t. trigonocephalus*, there are some differences with *S. orientalis* besides the less marked W increase between the anterior and posterior molar. First, there is the larger number of ridges in TA-3711 as compared to the M^1 of *S. orientalis* (x8 versus x6x/x7x). Secondly, the Tanrung molars have larger h/w indices, which fall outside the range observed in upper molars of *S. orientalis* (compare Table 32). In the Tanrung molars the h/w indices of individual ridges vary between 63e and 71. Colbert & Hooijer (1953) only give the unworn heights of the penultimate ridges, which may not correspond with the maximum heights in all cases. When using their height values together with the maximum widths, H/W indices varying between 44 and 58 are obtained for the upper molars, with an average of 50.2 (n = 16). Using the same method for calculation of the H/W index of an M^2 from Sichuan in the BMNH (M-14920), a value of 46 is obtained, which is inside the range as given by Colbert & Hooijer (1953). Using the same method in the TA-3711 molar an H/W index of 67 is obtained. The Tanrung molar appears thus clearly more hypsodont than the Sichuan material. Further qualitative differences with *S. orientalis* are that the Tanrung molars have a more strongly developed cementum coverage, and that the molar ridges have a more convex transverse profile over the digitations. It can be concluded that the Tanrung upper dentition cannot be attributed to *S. orientalis* either.

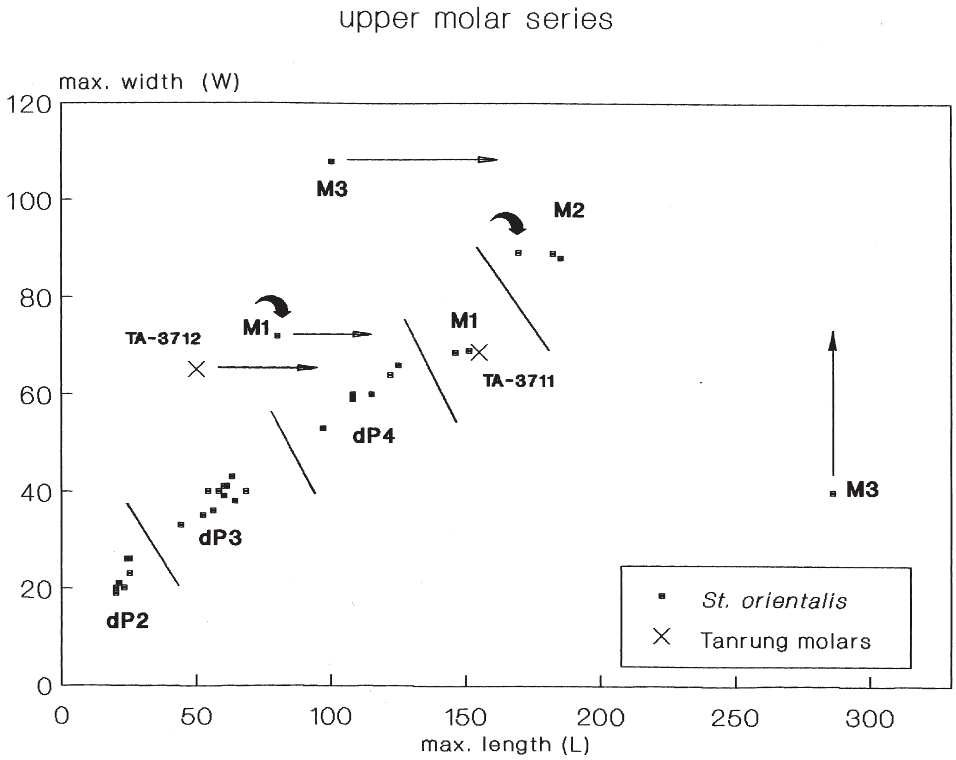


Fig. 56. Scatterdiagram of L versus W for the upper molars in the AMNH which have been attributed to *Stegodon orientalis* by Colbert & Hooijer (1953) and for various *S. orientalis* molars in the BMNH examined during this study. Like in Fig. 55, the successive molars fall into distinct clusters. Molars on which only one of the two parameters could be measured, are shown with straight arrows. Also added are the L-W plots of the successive molars TA-3711 and TA-3712 of a single individual here attributed to *Stegodon* sp. B and originating from the Tanrung Formation, South Sulawesi (see also Fig. 55). The size of TA-3711 matches perfectly with the only complete upper M^1 (BMNH-M10270) of *S. orientalis*. An other incomplete M^1 of *S. orientalis*, which occurs in a sinistral maxilla together with the M^2 (scatter points of the associated M^1 and M^2 are indicated with curved arrows) has a similar W as the complete isolated M^1. Note that the W of TA-3712 falls within the W range of the dP^4 of *S. orientalis*.

Most likely, the successive molars of the Tanrung individual represent dP^4s and M^1s of a *Stegodon* species with a more derived ridge formula and degree of hypsodonty than in *S. orientalis*. The fact that the W increase between the successive Tanrung molars is very limited, suggests that they represent a form with reduced jaw size compared to its direct ancestor. This would also be in accordance with the relatively high hypsodonty indices, which are usually only encountered in insular *Stegodon* species with reduced body-sizes. The possibility that the Tanrung dentition represent an M^1-M^2 succession cannot be excluded, however. In that case size reduction would presumably have been in a more advanced stage. However, this interpretation would imply that this species had very small tusks, which is unusual in the genus *Stegodon*.

The unworn posterior Tanrung molars have a comparable h/w index as in upper molars attributed to *S. florensis* in this thesis (h/w indices varying between 64 and 69 in the M^1 and between 60 and 81 in the M^3). Both also have a heavy cementum development in common. The ridge formula of the M^1 is x7x in *S. florensis*, that of the M^2 is not known. Their W corresponds well with the W of the only fragmentary M^2 known of *S. florensis* (see Table 37). No dP^4s of *S. florensis* are available for study yet, which hampers further comparison with this species. (Note that *S. florensis* is considered in this thesis as a distinct species, whereas Hooijer (1957a, 1972a) considered it as a subspecies, *S. trigonocephalus florensis*).

Mandible with M_3 fragment from the Tanrung Formation — The specimen under consideration (GRDC TA-3723) is a sinistral mandibular ramus fragment with the posterior fragment of an M_3 still in place. The mandibular fragment consists of the posterior portion of the horizontal ramus and the lower portion of the ascending ramus. The coronoid process is broken completely and the jaw has suffered much superficial damage. The posteriorly tapering molar is broken through the fourth ridge from behind. The ventral border of the ramus describes a wide rounded curvature as is characteristic for adult *Stegodon* mandibles. The molar fragment, which is subhypsodont and has roof-shaped ridges lacking median pillars, clearly indicates *Stegodon*. The M_3 has been fully erupted, but all posterior ridges were not yet touched by attrition. The transverse diameter at the level of the ascending ramus (measurement M18) is at least 115+ mm, but cannot be measured exactly because the lateral surface is much damaged. The only other measurement that could be taken on mandible TA-3723 is the vertical diameter of the lateral side of the ramus just in front of the (broken) ascending ramus (measurement M6), which amounts to 104e mm. The crownbase of the TA-3723 M_3 is concealed by the alveole so that the width of the successive ridges can only be estimated. These estimated values are given in Table 34. The original maximum width of this molar may be estimated as lying between 75e and 80e mm. Ridge III is 39.5 mm high, giving an height/width index of 54e. This rather low value may not be characteristic, because the height/width indices obtained at the posterior three ridges of *Stegodon* M_3s may deviate considerably from those of the more anterior ridges, and are not included in the various tables with summary measurements given in this thesis. The same applies for the rather large LF of 6.2, which was obtained from measurements taken on ridges II and III. The anterior portion of the molar probably had a lower LF value. The ET varies between 4 and 5 mm. Like in the upper dentition from the same stratigraphic layers (TA-3711/TA-3712), cementum is abundantly developed between the ridges and on the flanks of the ridges.

Comparison — The dental wear stage of specimen TA-3723 is similar to that of *Stegodon sompoensis* mandibular ramus CMTL/271285-1, both corresponding approximately with stage M3-C of Beden (1979). The maximum transverse diameter of the horizontal ramus (M18 = 115+ mm) is larger than in this *S. sompoensis* mandible (115 mm) and also larger than in the three other mandible fragments attributed to this species (Table 14, Fig. 74). Also the height of the ramus in front of the ascending ramus (measurement M6) is larger in the Tanrung mandible (104e mm versus 85 mm in CMTL/271285-1; Fig. 58). The size of the M_3 is considerably larger in the Tanrung specimen. The estimated maximum width (W) of between 75e and 80e mm is outside the range observed in the M^3 of *S. sompoensis* (W varying between 45 and 62 mm).

The estimated width of the M_3 in mandible TA-3723 falls within the range of the M_3 of *S. t. trigonocephalus* (though on the lower side of the variation) and also falls within the range of the M_3 of *S. florensis* (compare Tables 31 & 37). In the holotype mandible of *S. florensis*, which is in a comparable dental wear stage as the Tanrung mandible, measurements M6 and M18 amount 78 mm and 135 mm, respectively. Measurement M6 is considerably smaller in the Flores mandible, whereas M18 may be larger or of approximately equal size as compared to the Tanrung mandible. In *S. t. trigonocephalus* mandible CD-2896 from the locality Trinil on Java (2 ridges of the M_3 worn) these values are 99 mm and 134 mm respectively, the latter corresponding better in proportions with the Tanrung mandible (Figs. 58 & 74). The fragmentary nature of TA-3723 hampers its designation to any *Stegodon* species. However, like the upper dentition from the same lithostratigraphic unit (TA-3711/3712), the specimen belonged to an individual of clearly larger size than *S. sompoensis*. It is assumed that the present mandible belonged to the same large-sized *Stegodon* species, of which the upper dentition TA-3711/3712 was found in the same deposit and which was treated above.

Upper dentition from Sangihe — The dental material from Sangihe consists of three upper molar fragments and a distal portion of a dextral tusk (GRDC PS1/6), all of a single individual. Of the dextral side there are a completely worn molar remnant (GRDC PS1/1) and the anterior portion of a slightly worn molar broken behind ridge 6 (GRDC PS1/2). The slightly worn dextral molar forms a pair with an incomplete sinistral molar, broken behind ridge 5 (GRDC PS1/3). Specimens PS1/1 and PS1/2 have been figured by Aziz (1990: pl. VI, figs. 1 and 2, respectively).

Of specimen PS1/1 all preserved ridges (-$^{1}/_{2}$5x) are worn, including the posterior halfridge. The anterior -$^{1}/_{2}$1- ridges are worn down to the crownbase, their dentine being connected lingually. The length of the molar, as far as preserved, amounts to 119+ mm. The widths of the individual ridges are given in Table 34. The successive widths from posterior to anterior direction first increase to a maximum of 69.9 mm at ridge II and than decrease in the more anterior ridges, showing that the maximum width (W) corresponds with a value of 69.9 mm. The more anterior ridges are damaged buccally and lingually. The occlusal wear surface is convex antero-posteriorly. The enamel loops are fully developed apart from the posterior ridge and halfridge. The enamel loop of ridge II is characterized by 4 enamel constrictions, dividing the enamel wear pattern into five parts: one large axial one, two minor adaxial ones and two narrower lateral ones. In the more anterior ridges no constrictions are developed and the enamel loops are weakly expanded medially. The LF is 5.4. The enamel is heavily wrinkled with 4-5 folds per cm and an amplitude of between 0.5 and 1.5 mm. The ET varies between 2.8 and 3.2 mm. Cementum only remains between the ridges, but seems to have been worn away at the flanks of the ridges. As cementum has disappeared from the ridge flanks, it can be seen that the enamel of these flanks bears weakly developed vertical grooves, such as the ones which are usually developed in stegodont milkmolars and M1s, but which are rarely seen in M2s and M3s. A small contact facet is present posteriorly. The roots are broken largely, but what is left of them does not include the anterior hook and the antero-medial root, indicating that at least 1$^{1}/_{2}$ ridges are lacking in front.

Specimen PS1/2 has an anterior contact facet, which fits perfectly to the posterior contact facet of PS1/1. It is likewise of the right side and has the digitations of only the anterior ridge worn. The crownbase is convex in apical direction indicating that it is of the upper dentition. There can be no doubt that PS1/1 and PS1/2 were succeeding molars belonging to a single individual. PS1/2 has x6- ridges preserved, all intact. The length as far as preserved is 133+ mm. The anterior halfridge is only developed on the buccal half of the crown. Of ridge 1 the digitations, of which there are 7, are slightly abraded without exposing the dentine. Cementum leaves only the apices of the abraded ridges free, enough however, to distinguish the presence of a pronounced median cleft in the anterior ridge. The more posterior ridges are unworn. Ridge 2 has nine digitations, but the digitations of the more posterior ridges are partly covered with cementum. The w and h measurements of the successive ridges are given in Table 34. The maximum width (W) is 71.9 mm (at ridge 4). The h/w indices of individual ridges vary between 62 and 65. In transverse direction the apical profile of the ridges is weakly convex and the largest width occurs at the crownbase. The LF is 4.9. If two more ridges are lacking posteriorly, the total length of the molar would be c. 170e mm. The ET can not be measured at this specimen, but it varies between 3.1 and 3.6 mm in the sinistral counterpart (PS1/3), in which the first ridge is slightly more worn. The roots are best preserved in the sinistral molar. The antero-lateral root or hook is placed below the buccal side of the crown and supports x$1^1/_2$- ridges. The antero-medial root is smaller and situated below ridge 2. It projects slightly in medial direction.

The distal tusk fragment (PS 1/6), which was found associated with the molars, has a length of 55 cm from the preserved apex to its broken proximal end. The most proximally preserved diameter (nothing of the pulpa cavity is included) is 70 mm.

Comparison — The Sangihe molar sequence was interpreted by Aziz (1990) as an M^2-M^3 succession. This seems unlikely however, because at the same spot where the molars were found also a phalanx and astragalus were recovered, all belonging to the same individual. In these postcranial elements the epiphyses have not yet been fused. In an adult individual with the M^2s completely worn these epiphyses would have certainly been fused.

The worn anterior molar of the Sangihe upper dentition (PS1/1) corresponds very well in overall proportions (W, LF, ET; see Table 34) with the unworn posterior molar of the Tanrung dentition, which was assumed to represent an M^1 in the foregoing part. On the other hand, PS1/1 is 7% wider than the anterior worn molar of the Tanrung dentition, and more importantly, it has a lower LF (5.4 versus 6.2). The two succeeding molars from Sangihe have in common with the Tanrung dentition that there is only a very small increase in maximum width between the worn anterior and the largely unworn posterior molar. The width increase is even smaller than in the Tanrung upper dentition, amounting to only 2.9% in the Sangihe dentition (against 6.8% in the Tanrung dentition). As already mentioned before, such a low width increase is not encountered in dP^4-M^1 and M^1-M^2 successions of *S. t. trigonocephalus* nor of *S. orientalis*, but is usually only developed in diminutive forms. As argued above, the Tanrung upper dentition most probably represents a dP^4-M^1 succession. The Sangihe molar succession likely represents an M^1-M^2 succession on the contrary, as deduced from the slightly larger W and lower LF. Both dentitions are attributed to the same species here. In both dentitions the h/w indices of individual ridges are overlapping (60-68 in the Sangihe and 63e-71 in the Tanrung specimens), and the unworn molars (M^1 of the Tanrung and M^2 of the Sangihe dentition) are both characterized by the presence of a marked median cleft developed in the anterior ridge and a comparable degree of cementum development. Also other characters, such as the degree of enamel folding, the number of digitations and the transverse profile over the digitations is similar.

The distal tusk fragment associated with the Sangihe molars is larger in diameter (70 mm at the most proximally preserved end) than the proximal tusk fragments associated with the Tanrung molars (57 mm at the distal end of the pulpa cavity). This is in accordance with the determination of the associated Sangihe molar succession as M^1-M^2. With a more advanced dental wear stage the Sangihe individual should have possessed larger tusks than the Tanrung individual. Also a mandible fragment (GRDC PS-63) lacking dentition and found in association with the upper molars treated here, is of relatively large proportions (see below). This further corroborates the interpretation that the Sangihe molar succession is an M^1 and M^2.

In W and LF the posterior Sangihe molar (PS1/2) corresponds well with the M^2 of *S. florensis*. The h/w indices of the unworn Sangihe molars are lower than is usual for upper molars of the Flores stegodont, but fall within the range of variation of the latter (Tables 34 & 37). The W of the worn anterior molar of the Sangihe dentition (PS1/1 W = 69.9 mm) is slightly larger than in the 3 known M^1s of *S. florensis* (W ranging between 54 and 60c mm). The M^2s of *S. t. trigonocephalus* and *S. orientalis* on the other hand, are wider than the unworn posterior Sangihe molar (PS1/2) and have a lower LF, whereas the M^1s of these species are narrower and have a higher LF (Tables 31-32).

Based on the considerations given above, it is assumed that the succeeding Sangihe molars represent a worn M^1 and a largely unworn M^2. Apart from having slightly larger proportions, the Sangihe dentition agrees well with the Tanrung dentition in morphology. However, the latter presumably represents a dP^4-M^1 succession. It has further been demonstrated that both dentitions differ in size and/or morphology from those of other stegodonts known from the region.

Mandible fragments from Sangihe — The relatively older age of the Sangihe individual as compared to the one from Tanrung also follows from the relatively large dimensions of the mandible fragment (GRDC PS-63), which was found associated with the upper molars from Sangihe. The fragment, of the left side, lacks the dentition and is broken at the onset of the ascending ramus and along the medial side. In front the symphysis is broken, as well as a ventral portion of the horizontal ramus. The height of the horizontal ramus just in front of the ascending ramus (measurement M6) is c. 100e mm. The height in front of the alveole (measurement M5) is 100+ mm as far as preserved (excluding the missing ventral portion), but can be estimated to have been c. 130e mm judging from the lateral profile of the mandible.

An isolated mandibular symphysis (GRDC PS-66) of the same mandible but without fit, has a small pointed rostrum protruding forward and slightly downward. It measures 105 mm antero-posteriorly along the median axis and over the tip of this rostrum (measurement M21).

Comparison — The present mandible lacks the dentition, but from the wear stage of the associated upper dentition, we can roughly estimate its dental wear age class by using the system elaborated by Beden (1979: figs. 24-25) for *Loxodonta africana* upper and lower molars (see chapter 8 for an explanation of this dental wear age class division). According to this division, the dental wear stage of the mandible should correspond with dental wear stage M1/M2-B' or M1/M2-C, assuming that the associated upper molars are an M^1 and M^2. With this age class in mind we can compare the Sangihe mandible with other stegodont mandibles with a similar age class.

In two *S. t. trigonocephalus* mandibles from Kedung Brubus with the same dental wear stage measurement M5 (height in front of the anterior alveolar rim) was found larger than in the Sangihe individual. This is graphically shown in Fig. 57, in which measurement M5 taken on various mandibles in a whole range of dental wear age classes is plotted against the age class. A mandible from Trinil (NNM CD2893) with dental wear stage M1-B, and thus from a younger age class than the Sangihe mandible, has a value of 130 mm for measurement M5, which is the same value as in the ontogenetically more advanced Sangihe mandible. It follows from Fig. 57 that the Sangihe individual had a mandibular ramus which was lower anteriorly (measurement M5), or, with measurement M5 just within the lower part of the size range of *S. t. trigonocephalus* mandibles. Unfortunately, no M6 measurements could be taken on mandibles from Java in a comparable dental age class as the Sangihe mandible. Fig. 58, is a similar graph as Fig. 57, but now measurement M6 is plotted against dental wear age class. Some *S. t. trigonocephalus* mandibles from older age classes have a larger or equal vertical height in front of the ascending ramus as the Sangihe mandible, and it follows that measurement M6 of the Sangihe mandible falls amply within the range of variation of *S. t. trigonocephalus*.

A mandible attributable to *S. florensis* (GRDC DD4160) and with either dental wear stage M1/M2-B' or M1/M2-C, similar as PS-63, is clearly smaller with respect to both measurements M5 and M6 (Figs. 57 & 58). This is also the case for the holotype mandible of the Flores stegodont, which, though in a more advanced dental age class (stage M2/M3-C), clearly has a lower mandibular ramus than in PS-63 (both M5 and M6 are smaller). Also the already described *Stegodon* mandible from Tanrung (GRDC TA-3723), on which only measurement M6 could be taken and which supposedly belongs to the same species as the the Sangihe mandible, has a larger M6 value than the *S. florensis* type mandible, but this value falls within the lower range of variation observed in *S. t. trigonocephalus* (Fig. 58). Three *S. sompoensis* mandibles, though all with an more advanced dental wear age class than the Sangihe mandible, are all smaller in size with respect to measurements M5 and M6 (Figs. 57-58).

These comparisons suggest that the *Stegodon* individuals from Sangihe and Tanrung had a mandible of intermediate size between *S. t. trigonocephalus* (though with some overlap in measurement M6) on the one hand, and the smaller *S. florensis* and *S. sompoensis* on the other. The upper M^2s of the Sangihe individual are slightly narrower than the range of variation observed in the M^2 of *S. t. trigonocephalus*, but wider compared to the M^2 of *S. florensis*, which corroborates the size differences observed on the mandibles. However, the W of the dP^4 and M^1 from Tanrung and the M^1 from Sangihe are slightly beyond the upper size limits of the range of variation observed in *S. t. trigonocephalus*. The M^1s do correspond in size, plate formula and hypsodonty indices with the upper M^1 of *S. trigonocephalus ngandongensis*.

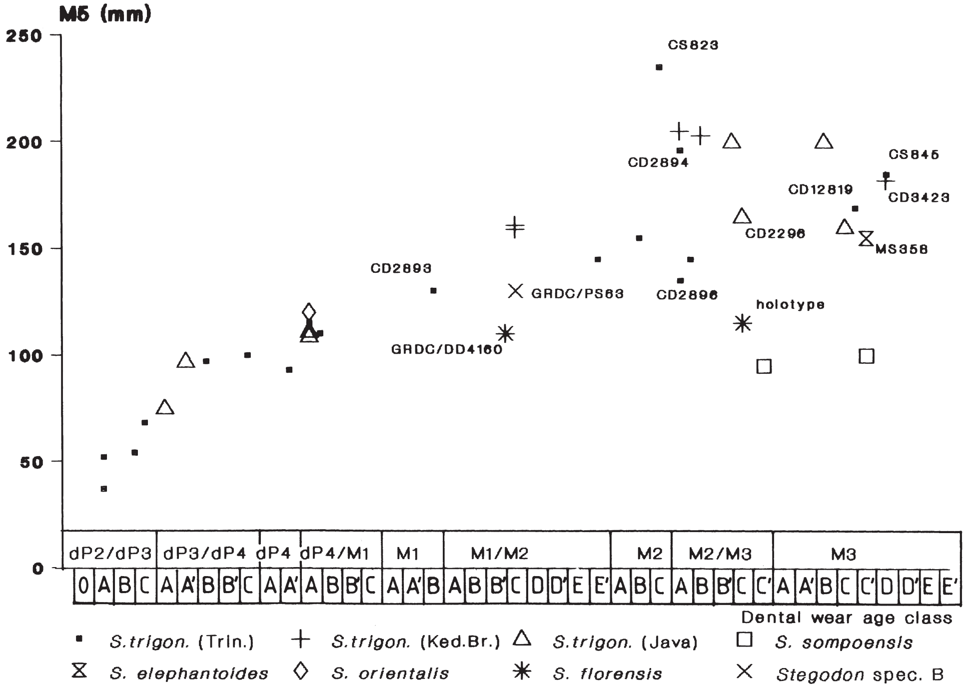


Fig. 57. Mandible size parameter M5 (height of the horizontal ramus measured at the level of the anterior margin of the dental alveoles) plotted against dental wear age class (DWAC), for various *Stegodon* mandibles in the NNM, GRDC and BMNH collections and from the Selenka expedition as given by Janensch (1911). The 43 successive DWACs, designated with lettercodes, are based on the dental wear stages as defined by Beden (1979, tables 7 & 8, fig. 24; see also Fig. 75 of this thesis) for *Loxodonta africana*. *S. t. trigonocephalus* mandibles from the localities Trinil and Kedung Brubus are shown with different symbols. The very large mandible from Trinil indicated with 'Selenka 823' does not originate from the 'Hauptknochenschicht', as do the remaining specimens from Trinil plotted in this scatterdiagram, but was excavated 5 m above the main fossiliferous layer in a younger layer according to the data given in Oppenoorth (1911). Datapoints representing adult individuals from Trinil (of which the dental wear stage is equal or more advanced than stage M1/M2-A = when the M_2 has been subject to initial wear anteriorly) appear to split into two groups: 5 smaller mandibles and 3 larger ones (including Selenka 823), supposedly representing females and males. The adult mandibles originating from Kedung Brubus are larger on average than the Trinil specimens. Furthermore are shown for comparison the datapoints of mandibles referred to *S. florensis*, *S. sompoensis*, *Stegodon* sp. B (note that the dental wear stage of this mandible fragment lacking dentition (GRDC PS-63) was estimated based on the associated upper dentition), and *S. orientalis*. Note that measurement M5 of the *Stegodon* sp. B mandible corresponds with the lower size range of that measurement in *S. t. trigonocephalus* mandibles of comparable dental wear age, but is larger than in mandibles of *S. florensis* and *S. sompoensis*.

Discussion

The upper dentition from the Tanrung Formation (TA-3711/TA-3712 and associated tusk fragments TA-3714 and TA-3715) can be distinguished from *S. t. trigonocephalus*. As has been shown above, the *Stegodon* upper dentition from Sangihe, which has been referred to earlier as *Stegodon* sp. B cf. *trigonocephalus* (Aziz, 1990), shows the same characteristics as the Tanrung individual, though it pertained to an older indi-

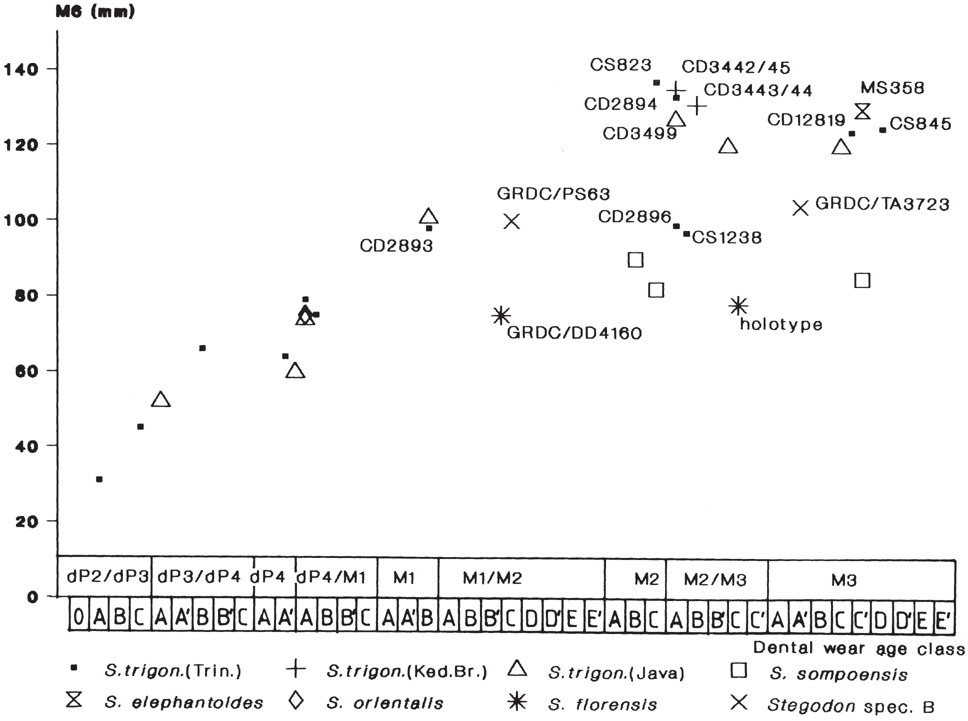


Fig. 58. Mandible size parameter M6 (heigth of the horizontal ramus measured at the level of the anterior onset of the ascending ramus) plotted against dental wear age class. For further explanation, see Fig. 57. Again, the datapoints of two mandibles here attributed to *Stegodon* sp. B correspond with the lower size range observed in mandibles of *S. t. trigonocephalus* with a comparable dental wear age, but show larger values than in mandibles of *S. florensis* and *S. sompoensis*.

vidual with a more advanced dental wear age stage and larger tusks. The fossil *Stegodon* remains from both Tanrung and Sangihe presumably represent the same species, and can be distinguished from *S. t. trigonocephalus* in having a slightly larger dP^4 and M^1 but a slightly narrower M^2, one ridge more in the M^1 and on average smaller mandible proportions in individuals with the same dental wear stage, though there is some overlap in size with the smallest *S. t. trigonocephalus* mandibles.

The Tanrung and Sangihe molars have also been shown to be distinct from homologue elements of *S. orientalis*, which has a similar M^1 size but a wider M^2 in combination with a lower ridge formula of the M^1, a lower hypsodonty index and weaker development of cementum.

Much smaller than the present species are the dwarfed *S. sompoensis* and *S. sondaari* sp. nov. These are both species from the SE Asian region, of which the intermediate molars are reasonably well known now, but which have different plate formulas than the Tanrung and Sangihe molars.

The molars from Sangihe and Tanrung differ from those of *S. florensis* in having slightly larger and broader molars and slightly larger mandible proportions. The M^1 of *S. florensis* has one ridge less than the M^1 of the present species. Comparison with

S. florensis is hampered by insufficient material for comparison. When more fossil material of *S. florensis* will be available, the Tanrung/Sangihe species may eventually turn out to be only distinguishable on the subspecies level from the Flores stegodont. The M^1 of the Tanrung/Sangihe species corresponds with the single complete true molar known of *S. trigonocephalus ngandongensis* in size, plate formula and hypsodonty indices. However, the M^3 of *S. t. ngandongensis* is very large (W is greater than 95+ mm), indicating that this subspecies was not size-reduced such as *S. florensis* and the present species.

In addition to the above-mentioned species, there are various *Stegodon* species known from the Siwaliks and northern China, of which the ridge formula of intermediate molars is insufficiently known or not at all, which hampers comparison. Saegusa (1996) gave the most recent review of the validity of the various species that have been described before. Material of some of these species has been examined in the course of this study. A cranium fragment attributed to *S. insignis* (BMNH-M3016, figured in Falconer & Cautley, 1846, pl. 24A, figs. 2a, 6) has the much worn M^1s and the slightly worn M^2s in place. The M^1s are only slightly wider (W = 73 mm) than the M^1s from the Tanrung formation (Table 34) and have a similar LF (= 5.7). However, the M^2s from the same cranium are clearly wider (W = 81 mm) than the homologue from Sangihe and more importantly, have a significantly lower range of h/w indices of unworn molar ridges (varying between 43 and 47). Besides, the M^2 of *S. insignis* has x7x ridges, while that of the M^1 of the present species possesses x8x ridges. The referred *S. ganesa* skull in the BMNH (M3008) has both M^3s in place, which have lower h/w indices (varying between 43 and 55) than encountered in the Tanrung and Sangihe upper molars (Table 34). Besides, this Siwalik species has a larger overall size than *S. t. trigonocephalus*, and is therefore no match for the stegodont from Sangihe and Tanrung, which appears to have been even smaller than the Javanese form.

The small increase in W between successive molars of the present species suggest that it represents a form with reduced body size, in which growth stopped at an earlier ontogenetic stage than its full-sized ancestor. Because there is the possibility that it is very closely related to *S. florensis* or *S. ngandongensis*, the Tanrung/Sangihe stegodont will be tentatively named *Stegodon* sp. B. Its characteristics are as follows: A *Stegodon* with relatively large dP^4 and M^1 but narrow M^2 and M_3 when compared with *S. t. trigonocephalus*. Molar ridges are sub-hypsodont, with h/w indices of individual unworn ridges varying between 60 and 71. Advanced plate formula, with 8 fully developed ridges in the upper M^1. A deep median cleft is well developed in the anterior ridges of the molars only. Cementum is strongly developed, covering the lateral flanks and digitations of unworn ridges. W increase of succeeding upper molars very small, with the W of the M^1 (68.5-69.9 mm) only slightly larger than that of dP^4 (65.0 mm), W of the M^2 (71.9 mm) only slightly larger than that of the M^1. Number of digitations of individual ridges varies between 7 and 9. The enamel is double layered with scalloped structure and stepwise wear surface. The transverse profile over unworn ridges is rounded.

Large-sized *Stegodon* sp.

Hooijer (1972b) mentioned two molar fragments from South Sulawesi (one from

Sompoh and one from Celeko), which he attributed to *Stegodon* cf. *trigonocephalus*. These fragments had been earlier referred to as *Stegodon* spec. (Hooijer, 1953b: pl. V, figs. 1-5) and subsequently to *Stegodon sompoensis* (Hooijer, 1964a: 43). Now that more material of *S. sompoensis* has become available it follows that these fragments fall within the ranges of variation of the M3 of *S. sompoensis* (see the description of that species elsewhere in this chapter). Three other *Stegodon* molar fragments collected during the 1970 expedition were also attributed to *Stegodon* cf. *trigonocephalus* (Hooijer, 1972b: pl. 3, figs. 4-5 (= the posterior portion of an upper molar comprising two ridges, originating from the excavation at Marale); pl.4, figs. 2-3 (= an isolated molar ridge fragment from the surroundings of Beru) and pl. 4, fig. 4 (= an isolated molar ridge fragment from the surroundings of Marale)). These fragments seem to belong to a large-sized *Stegodon*, despite of their fragmentary state. To these large-sized *Stegodon* molar remains can be added a molar fragment surface collected by us (GRDC L/III-3040) and a posterior portion of a large upper molar in the collection of the MPC (C-3/27/86), which has been figured by Bartstra et al. (1994: fig. 3) as *Stegodon* cf. *trigonocephalus*. According to Hooijer (1972b: 10) one rolled upper molar fragment was found in situ in 'the second excavation at Marale, 20/7/1970, at a depth of 125-150 cm', which corresponds with our FVL-18, according to the locality data given by Keates & Bartstra (1994: fig. 1). The other fragments attributable to a large-sized *Stegodon* species were all surface collected. Both the excavated fragment as well as the surface collected specimens have in common that they were found in the fault-bounded structural unit which has been designated in chapter 3 as the Lakibong Triangle, in an area where the uppermost layers of the Beru Member (Subunit B) crop out (van den Bergh et al., 1994; this thesis).

In addition to these molar fragments, four tusk fragments were collected during our field campaigns, which clearly belonged to a large-sized elephantoid. Three of them originate from the Tanrung Formation (FVL-29) and have a diameter larger than 85 mm, which is the diameter of the tusk alveole in the adult *S. sompoensis* skull BC-3050 and which has been taken as the upper size limit of the tusks of that dwarf species. These are specimens TA-3724, TA-3727 and a tusk fragment observed in a large block of conglomerate of the Tanrung Formation, which was left in the field. An other large-sized tusk fragment was found semi-in situ at FVL-12 in a conglomeratic layer pertaining to Subunit B of the Beru Member.

Description of the material

Molars — Specimen MPC C-3/27/86 is said to 'have been eroded from conglomeratic sandstone some two hundred meters east of Marale' (Bartstra et al., 1994: fig. 3). There is some well cemented pebbly sandstone matrix attached to the specimen. Marale is one of the locality names which has been used to indicate the 1970 archaeological excavation south of Beru (Keates & Bartstra, 1994: 20) and which is designated as FVL-18 in this thesis. This location does not correspond with the name Marale on the topographic maps, which is located c. 1.5 km SSE of FVL-18. Together with the curator of the MPC, Mr Anwar Akib, we visited the collecting locality of the specimen, which appeared to correspond with FVL-17 of this thesis. Well-cemented horizontal-layered conglomeratic sandstones crop out in small steeply sloping hills. These layers correspond with the uppermost exposed levels of Subunit B of the Beru Member.

FVL-17 is situated within a 500 m radius of the locality name Marale indicated on the topographic maps. The two sources concerning the origin of the specimen thus contradict each other. In any case, at both FVL-18 and FVL-17 the conglomeratic layers of Subunit B crop out.

Specimen MPC C-3/27/86 is a worn posterior fragment of a *Stegodon* upper molar, as follows from the convex wear surface and the well developed scalloped pattern of the worn enamel surface. It has been interpreted as an M^{3} (Bartstra et al., 1994: 13) based on the lack of a posterior contact facet and the suggestion of tapering in posterior direction. The specimen may represent an M^{3}, but the possibility of an M^{2} can not be excluded, as contact facets between succeeding molars are not always developed. The widths of the successive ridges are as follows according to our own measurements: posterior halfridge = 63 mm; I = 82 mm; II = 88 mm. The enamel loop of ridge III is only preserved on one side (buccal or lingual?) and no width can be given, while of ridge IV one quarter of the enamel loop remains. Judging from the preserved side of ridge III, this ridge may have been only a few mm wider than ridge II. In 9 *Stegodon trigonocephalus* M^{3}s the proportional width increase from ridge I to ridge II was found varying between 5% and 18%, with an average width increase of 13.4%. In 3 M^{2}s of the same species the width increase from ridge I to ridge II varied between 5% and 8% with an average increase of 5.9%. In specimen C-3/27/86 the width increase of the two equivalent posterior ridges is 7.3%, which comes closer to the average value for *S. trigonocephalus* M^{2}’s than for the M^{3}’s. The posterior tapering is thus not very marked, as can be also seen on fig. 3 of Bartstra et al. (1994). The molar fragment agrees better with a typical M^{2} than with an M^{3} in its degree of tapering. The LF, which is 3.6, falls within the range observed in the M^{3}’s of *S. t. trigonocephalus* but lies just below the range for the M^{2}’s of that same species (compare Table 31A-B). The ET, which varies between 4.3 and 4.5 mm, falls within the ranges observed in the M^{2} and M^{3} of *S. trigonocephalus*. Though clearly belonging to a large-sized *Stegodon*, the specimen is too fragmentary to allow determination to the species level. As we now know, a medium to large-sized *Stegodon* once lived on South Sulawesi, which has been shown to be clearly different from *S. trigonocephalus*: *Stegodon* sp. B. The present fragment is certainly too large for even an M^{3} of *S. sompoensis*. The maximum width (W) of the molar, which may have been c. 90e mm in case of an M^{2} and up to c. 110e mm in case of an M^{3}, is clearly too large to allow attribution to *S. sompoensis*, and also its LF is much lower (3.6 versus 6.6-7.7e in the M^{3} of *S. sompoensis*, Table 33). Also the ET falls outside the range observed in the M^{3}s of *S. sompoensis* (3.4-4.3 mm). It may be concluded that specimen C-3/27/86 certainly belonged to a large-sized *Stegodon* species.

Another molar fragment originating from the upper stratigraphic reaches exposed in the LT and clearly of large-sized proportions, is specimen GRDC L/III-3040 (Pl. 8, figs. 3-4). The fragment was surface collected in the surroundings of FVL-2, and has caliche crust attached to it. The fragment consists of $-^{1}/_{2}2^{1}/_{2}-$ ridges. The enamel of the posterior ridge is slightly abraded by wear, but the dentine is not yet exposed. The enamel of the ridge in front of it is broken largely at the occlusal surface except for a small lateral portion, which is worn down more than the in the ridge behind it. The enamel apices of the anterior and posterior preserved remnants of two more ridges are also broken, so that it could not be determined whether the wear surface was originally convex or concave in antero-posterior direction. The bases of the ridges are aligned in a horizontal plane. All ridges are damaged slightly on one side, but the opposite preserved border of the molar is strongly convex laterally, suggesting that the molar is a lower one. Having identified the fragment as a lower molar with its convex border placed lingually, it can be concluded that it is of the left side. The anterior ridge is only slightly damaged at the base on the buccal side. It is 77+ mm wide as far as preserved. The original width must have been near 80e mm. The same holds true for the succeeding ridge, which is 75+ mm wide as far as preserved with an estimated width of 2 or 3 mm more. This is outside the range of the M_3 of *S. sompoensis* (W varies between 45 and 62 mm), but within the W ranges of the M_2 and M_3 of *S. trigonocephalus* or *S. orientalis* (compare with Figs. 55-56). The unworn height of the posterior ridge is 58 mm, which gives an h/w index of 75e. This is rather high compared to the h/w ranges of lower molars of the last two mentioned mainland species, but could fit well with the relatively high-crowned Tanrung molars, which are here attributed to *Stegodon* sp. B. Further measurements that could be taken all point in the direction of a large-sized stegodont as well: The lamellar frequency amounts 4.6 buccally and 3.7 lingually (the relatively large difference expressing the strong lateral curvature of the molar), giving an average LF of 4.2. The scalloped, double layered enamel has an ET varying between 4.1 and 5.1 mm. The enamel is wrinkled with 1 to 3 folds per cm and an amplitude of 0.5-1.5 mm. Cement is prolific. The number of preserved digitations on the slightly abraded posterior ridge is 9. The apices are all of subequal size and neatly arranged in a straight row, separated by very weak and shallow grooves. The ridge forms an almost perfect wedge, which strongly reminds of the characteristic wedge shaped crests usually observable in *S. orientalis* molars, rather than of the usually more blunt ridges encountered in *S. trigonocephalus* and its closest relatives. A peculiarity of the present specimen is the presence of tiny intravalley conules on the damaged buccal side, which is an aberration sometimes encountered in *Stegodon* molars.

Tusks — Specimen GRDC TA-3727 is a proximal tusk fragment, which was found in the Tanrung River in a block of calcareous pebbly matrix clearly showing it to originate from the Tanrung Formation. The fragment is 29 cm long. Its maximum proximal diameter is 122 mm. The diameter perpendicular to the maximum proximal diameter is 119 mm. It is almost perfectly circular in cross section. At the same level the pulpa cavity has a diameter of 58 mm. At the distal broken surface the largest diameter is 118 mm and the smaller one 110 mm, while the pulpa cavity is 36 mm in diameter at this level.

Specimen GRDC TA-3724, likewise with matrix of the Tanrung Formation attached to it, is a shorter, 7.5 cm long proximal fragment. It is more weathered than the foregoing specimen. Its maximum proximal diameter is c. 105 mm and that of the pulpa cavity 42 mm at the same level.

The cross section of a tusk was found exposed on the surface of a large block of Tanrung Formation conglomerate. A diameter of 12.5 × 11 cm was measured in the field, with the pulpa cavity being 4 cm in diameter. A large but poorly preserved tusk fragment, with a diameter of c. 12 cm, was found on the surface at FVL-12, but was not brought to Bandung.

All the above mentioned tusk fragments are characterized by the 'guiloche' pattern and can be distinguished from the radiate cross-sectional pattern seen in *"Elephas" celebensis* tusks. They are considerably larger than *S. sompoensis* tusks. The tusks from the Tanrung Formation probably belonged to *Stegodon* sp. B, from the same deposit, but the possibility remains that they belonged to *Elephas* sp., which is also known from a single, surface collected molar fragment from the Tanrung River.

Stegodon sp.

There remain several *Stegodon* molar fragments, which can not be attributed with certainty to any of the *Stegodon* species treated above. These molar fragments have double layered, wrinkled enamel, showing the scalloped structure at the occlusal wear surface, which allows ascribing these fragments to *Stegodon*. The serial position could not be ascertained due to their fragmentary nature. Their W falls just beyond the observed upper size limit of the ranges of *S. sompoensis* M3s, and morphologically they appear slightly different from characteristic molars of the latter species. They have further in common that they all originated from the surroundings of locality Sare Batue (FVL-3, 4 and 4a).

Description of the material

Molars — Specimen SB-3760 was obtained from local villagers near Sare Batue. It represents a strongly laterally curved portion of a lower right molar consisting of -$^1/_2$3- ridges. The anterior ridges are worn slightly. Cementum fills the valleys but leaves the ridge flanks free. The maximum width of the second ridge from behind is 62.5e mm, against an estimated height of 41e mm of this slightly abraded ridge. These two measurements give a h/w index of 64e. In the last two ridges there are 6 digitations. The strong lateral curvature of the molar fragment suggests that it represents an M_3. However, the LF of 4.8 seems very low, even for an M3 of *S. sompoensis* and also the W is slightly above the maximum width range of the M_3 of this species (Table 33). The strong lateral curvature indicates that it doesn't represent a milkmolar of a large-sized *Stegodon* either. Its W would fall within the W range of the M_1 of *S. t. trigonocephalus* and slightly below the maximum width range of the M_1 of *S. orientalis*. Its LF is below the ranges of the M_1 of both these species, but it comes closer to that of the latter (compare with Tables 31-32).

Specimen LCL-221086-1 originates from locality 18 of Aziz (1990), which is located south of Sare Batue village in the surroundings of FVL-3 of this thesis. The occlusal wear surface of this fragment is convex, indicating that it is of an upper molar. The fragment consists of -$^1/_2$3- apically tapering stegodontine ridges, all worn and incomplete. The most posterior ridge is damaged on one side (buccal or lingual?). It is worn to such a degree that the dentine of most digitations (c. 9) is interconnected. Its worn height is 33+ mm, but the original height may have been 40 mm at most judging from the longitudinal profile of the ridge at the broken side. In the second ridge from behind wear has advanced slightly further. This ridge is damaged on both sides. However, it is preserved far enough to observe that its enamel loop shows three constrictions, the central one corresponding with a median cleft. The enamel is regularly wrinkled with c. 4 folds per cm with an amplitude of up to 1 mm. A clear scalloped enamel wear pattern is indicative for *Stegodon*. The width of this ridge as far as preserved is 63+ mm. The third ridge from behind, likewise damaged on both lateral sides, has a preserved width of 65+ mm as well. The original width can be estimated at 67e mm, judging from the outline of this ridge in occlusal view. In this ridge only one, median, constriction of the enamel loop marks the location of the median cleft. The enamel loop is weakly expanded on both sides of this median cleft, a feature often developed in worn ridges of *S. sompoensis* molars. The ET varies between 3.4 and 4.4 mm. The enamel shows 3-4 folds per cm with an amplitude of up to 1 mm. The LF is c. 4.5. Again, the width (between 65+ and 70e mm) of this specimen is slightly larger than the upper limit of the range of variation of the M^3s of *S. sompoensis* (Table 33). The width corresponds with an M^1 of *S. trigonocephalus* (Table 31), but the LF is again too low. The width and LF could correspond with an M^1 of *S. orientalis*. An other character corresponding with *S. orientalis* would be the very weak development of cementum, only present in the deepest parts of the intra-ridge valleys.

Specimens SB-2791 and SB-2792 constitute two portions of the same lower molar. The two portions cannot be fitted and one or more ridges may be missing in between them. Thus the ridge formula of this fragment can be given as $-^1/_2 2$-2-. All the wedge-shaped ridges are unworn. The ridges converge to the left (with the anterior side pointing away from us) and the lateral border of the tooth appears strongly curved laterally, which indicates that it represents a lower molar. This lateral curvature is expressed by the relatively large difference between the lamellar frequency on the left and right side, which is 5.6 and 4.0 respectively (giving a LF of 4.8). The convex molar border is to the right and is the lingual side and thus the molar is of the left side. The half preserved ridge in front has some of the median digitations preserved and has an unworn height of 35 mm. Its width cannot be taken. The ridge behind it is almost intact except for the broken basal part buccally. It is 65e mm wide and 38e mm high, which gives an h/w index of 59e. The next ridge behind it is too damaged on both lateral sides to give its width, but its height is 38 mm. The anterior ridge of the posterior fragment is 37 mm high but likewise damaged on both lateral sides. The most posteriorly preserved ridge is 66 mm wide and 43e mm high (h/w index 64e). Cement is deposited between the ridges but leaves the digitations and ridge flanks free. The ridges have 7 or 8 digitations of subequal size. The unworn ridges are, like in specimen L/III-3040, comparatively ‘sharp’ instead of blunt, resembling much the unworn ridges of characteristic *S. orientalis* molars. The ET, which could be measured on the broken surfaces, varies between 4.4 and 5.0 mm. Nothing of the roots is preserved. Like the foregoing specimens from Sare Batue, this fragment fits better with the dimensions of an M_1 of *S. orientalis* than that of *S. trigonocephalus*, but the fragment may also represent an M_2 or M_3 of a smaller species. It seems too big for an M_3 of *S. sompoensis* (compare with Table 33).

Elephas sp.

Description of the material

An advanced *Elephas* species from South Sulawesi (Bone District) is represented by a single molar fragment consisting of two posterior lamellae. The fossil (GRDC

TA-3920) was found in the Tanrung riverbed, and has been already briefly described and figured in another paper (van den Bergh et al., 1994). The specimen is rather abraded by transport, and the left side (seen from behind) is rather damaged. The S-shaped curvature of the lamellae in lateral view suggests that a lower molar is concerned here, but it is not possible to determine whether from the left or the right side. The height of the unworn posterior lamella measures 102+ mm as far as preserved, the penultimate lamella over 107+ mm (it is not possible to give exact measurements because the crownbase, and of the penultimate lamella also the apex, are damaged). The width can be given as 45e mm for the posterior and 53 mm for the penultimate lamella. The maximum height and width of the original molar were presumably larger because the maximum size does usually not occur in the ultimate or penultimate lamella. The ET amounts to 2 mm. The h/w index of the penultimate lamella is approximately 200 and it has an antero-posterior thickness of 15.3 mm near the crown-base, which gives a LF of 6.5. On the exposed anterior surface of the foremost lamellae it can be observed that the enamel is considerably wrinkled and that a median pillar or expansion is lacking completely.

Discussion

The width of lamella II of TA-3920 lies just within the range of variation of the W of the M^3 of *"E." celebensis* (45-56 mm), but its maximum width would have probably fallen beyond that range of variation. Besides, the lamella height of specimen TA-3920 is much too large to allow reference to *"E." celebensis*. In addition, the 2 mm thick enamel is too thin for an *"E." celebensis* molar (compare with Table 30). But more importantly, strongly developed median pillars, which are highly characteristic for *"E." celebensis* molars, are totally absent in the present molar fragment, as can be seen on the anterior surface of the foremost lamella. Thus, specimen TA-3920 can certainly not be referred to the Sulawesi dwarf elephant.

The h/w ratio of 200 is twice as high as in molars of *"E." celebensis* or *E. planifrons* (Maglio, 1973; van den Bergh et al., 1992). It is also slightly higher than the ratio in the Javanese species *E. hysudrindicus* Dubois as given by Maglio (1973: 49; hypsodonty index varies between 177.5 and 182.3 in the M_3). Of the South Asian elephants such an high h/w index is only reached by *E. namadicus* Falconer & Cautley (h/w varies between 145 and 302 in the lower M3; Maglio, 1973) and in *E. maximus* with h/w indices of individual lamellae between 200 and 300 (Hooijer, 1955b). *E. antiquus* from Europe has to be considered as a synonym of *E. namadicus*, and is at most subspecifically different (Maglio, 1973). From Indonesia only one molar, possibly from the surroundings of Samarinda, Kalimantan, has been referred to *Palaeoloxodon* cf. *namadicus* (Hooijer, 1952). From the island Luzon (Philippines) a poorly known dwarf elephant, *E. beyeri* von Koenigswald (1958) has been reported (see also chapter 7). Based on its large hypsodonty index (= 2.09) the latter was thought to be derived from *Elephas namadicus*.

If specimen TA-3920 is considered as belonging to a large-sized *Elephas* species (the finding of two large-sized cf. *Elephas* metacarpalia in the Tanrung River bedding also adds evidence to the occurrence of a large-sized *Elephas* in South Sulawesi, whereas no pygmy elephantoid remains have been found so far along this river), than it could represent either a M_1 or M_2 based on the width, height, LF and ET. All the size measurements of TA-3920 fall within the ranges of variation of either the M_1 or M_2 of *E. namadicus* as reported by Maglio (1973). If considered as *E. maximus*, the specimen would most likely correspond with a lower M1, using the size histograms given by Roth & Shosani (1988). Though the fragmentary nature of TA-3920 does not allow to determine it at the species level, it is clear that its advanced characteristics point to a Middle or Late Pleistocene, highly evolved elephant, likely *E. namadicus*. The supposedly Middle Pleistocene age of the fragment speaks against an attribution to *E. maximus*. The fragment is of great importance as it proves that at least a second migration of *Elephas* to South Sulawesi took place after the earlier immigration, which led to the evolution of the dwarfed *"E." celebensis*.

Elephantoidea, postcranial elements

C. 50 elephantoid postcranial elements have been collected in South Sulawesi during the 1989-1994 GRDC-NNM expeditions. All are currently stored in the collection of the GRDC in Bandung. There is also a small number of postcranial elements in the MPC and GRDC collections, which were recovered in earlier years. In addition, Hooijer (1949, 1955b) attributed various postcranial elephantoid elements in the van Heekeren Collection to *Archidiskodon celebensis*. This material is stored in the NNM.

Most of the recently collected postcranial fossils were recovered from the surface at various localities (Table_6). At excavation site FVL-24c near Lonrong 12 postcranial elements in total were recovered from the fossiliferous layer there. All the postcranial elephantoid elements which originated from the Beru Member of the Walanae Formation (both surface collected and in situ collected specimens) are without exception of small size and belong either to *Stegodon sompoensis* or *"Elephas" celebensis*. Postcranial elephantoid elements recovered along the Tanrung River on the other hand (FVL-29), were all attributable to large-sized elephantoids (Table 6). Six of these fossils were found in a small gully eroding the top layers of the Tanrung Formation, some with the characteristic conglomerate matrix of the Tanrung Formation still attached to them (indicated as semi in situ findings in Table 6). Two large-sized elephantoid metacarpalia with a distinct matrix and surface collected at this locality, may originate from younger alluvium covering the Tanrung Formation. The dwarf elephantoid material from the Beru Member will be dealt with in the next section of this chapter, followed by the large-sized postcranials.

Elephantoidea, dwarfed species

Those postcranials from Sulawesi which are here attributed to dwarf Elephantoidea, are all of inferior size compared to the smallest homologue elements from Java that have been attributed to *S. trigonocephalus* by Hooijer (1955b). The small-sized postcranials from the Beru Member of the Walanae Formation are generally between 50% and 70% smaller than the average size of homologue elements in the Javanese species. As no other small-sized taxa than *"E." celebensis* and *S. sompoensis* can be distinguished amongst the dental and cranial materials from the same stratigraphic interval, the small-sized postcranials should belong to either one of them. For most postcranial elements it has not been attempted to distinguish the postcranial elements of *"E." celebensis* from those of *S. sompoensis*. Pohlig (1911) and Hooijer (1955b) mentioned some diagnostic criteria of *Stegodon* postcranials, which enabled them to distinguish *Stegodon* bones from *Elephas*. For most postcranial bones these criteria involved length/width ratios. Because only very few postcranial longbones from the Beru Member are complete, these criteria were of limited use here. No associated skeletons together with diagnostic dentitions have been found either. Recently, Ariëns (1995) studied the morphological differences between postcranials of *S. trigonocephalus* and *M. primigenius*, and listed a number of diagnostic criteria between these two taxa. Based on these criteria it was possible to attribute some humerus fragments to either *"E." celebensis* or *S. sompoensis*. For other bones such a distinction may also be possible, but this would require a reexamination of the fossils in the GRDC and MPC collections.

Vertebrae — There are only 6 dwarf elephantoid vertebrae represented in the GRDC collection, none of which is complete (GRDC 1830, BC-3033, LR-2591, LR-2706, LR-3563-65, SB-3743). A corpus vertebrale originating from FVL-12 is in the collection of the MPC (no number). Measurements are given in Table 18.

The most complete specimen is LR-3563-65, a thoracic vertebrae with the corpus and a large portion of the arch and spinous process preserved. As the epiphyses of the corpus are lacking it belonged to an unfullgrown individual. Only the right transverse process is partly preserved. The spinous process is inclined backward with an angle of 50° relatively to the articulation plane of the corpus. On the right side anterior and posterior articulation facets for the costae are present below the transverse process.

Of two other vertebrae from the same locality (LR-2591 and LR-2706) only the corpus remains. They both belonged to adults with the epiphyses of the corpus fully fused. Of specimen LR-2706 the anterior margin of the right side is covered with a laterally protruding outgrowth, suggesting that it belonged to a very old individual.

Specimen 1830 is a corpus of a juvenile individual lacking the epiphyses.

Specimen BC-3033 consists of a dorsal spine, which is broken at the tip. Its height as far as preserved is 63 mm, the basal width is 57 mm.

Specimen SB-3743 is the only cervical vertebra in the collection. Only the corpus is preserved. The transverse processes are largely broken, but enough remains to observe that there were no lateral foramini, indicating that this specimen is the most posterior cervical vertebra.

The specimen without number finally, represents the corpus of a vertebra lumbare with the epiphyses fused.

All these vertebrae specimens, including the mature ones, are of inferior size compared to *S. trigonocephalus* and those originating from the Tanrung Formation (Table 18). The dimensions of the vertebrae from the Beru Member are on average larger than those of the dwarfed *Stegodon sondaari* from Flores (compare with Table 20).

Scapula — Measurements of the scapula fragments examined are listed in Table 21. There is one sinistral scapula fragment in the GRCD Collection (1351-52) consisting of the distal extremity broken just above the narrowest part of the collum scapulae. A small portion of the spine is included. The maximum antero-posterior diameter of the distal epiphysis is 125 mm, that of the glenoid articulation surface is 94 mm.

The maximum transverse diameter of the distal epiphysis is 68 mm. The antero-posterior diameter at the collum scapulae is 103 mm.

Another distal fragment of a sinistral scapula is in the MPC collection (C1-23/171086 from Marale, surroundings of FVL-15). It is poorly damaged and the only measurement that could be taken is the maximum distal antero-posterior diameter (measurement S2 = 119 mm).

A third distal scapula fragment in the NNM collection and originating from Tjeleko, was mentioned before by Hooijer (1955b: 90). It has a distal antero-posterior diameter (measurement S2) of 119e mm, similar as the Marale specimen. The antero-posterior diameter of the collum scapulae (measurement S4) is 117 mm.

In various fullgrown scapulas from Java, most of them from the locality Trinil and all attributed to *Stegodon trigonocephalus* (Hooijer, 1955b), the antero-posterior diameter of the collum scapulae varied between 150 and 200 mm, with an average of 170 mm (n = 13). This clearly indicates that the three specimens from the Beru Member belonged to elephantoids of small stature. They are also much smaller than two elephantoid scapula fragments originating from the Tanrung Formation (Table 21).

Humerus — The humerus is the best represented postcranial element in the various collections from South Sulawesi. Measurements are given in Table 22.

The most complete humerus recovered so far was excavated in situ at FVL-24c (GRDC LR-3707: Pl. 9, fig. 1). It is a dextral humerus, which is broken just above the epicondilar crest. A fragmentary portion of a distal epiphysis, which lacks the lateral condyle and epicondyle completely, belonged to the same humerus as followed from their close association in the excavation. The specimen belonged to a subadult individual, as the proximal epiphysis is not yet completely fused. Unfortunately there is no exact fit between the two portions but a reasonable estimate of the total length can be made. A few millimeters to at most two centimeters are missing between the two portions, and the total length between the caput and the medial condyle is estimated to lie between 44.5e cm and 46e cm. The anterior margin of the proximal epiphysis is superficially damaged. The deltoid crest of LR-3707 has a similar shape and prominence compared to that of *S. trigonocephalus* humeri. In both, the lateral margin of the deltoid crest has a curved, convex profile in posterior view, without any straight parts.

Hooijer (1955b: 71) noted that in *S. trigonocephalus* the proximal third of the humerus, including the deltoid crest, is heavier built than in the modern Asian elephant. Ariëns (1995) carried out a comparative study between the postcranial elements of *S. trigonocephalus* and *M. primigenius* in the NNM, and concluded that the humeri of both species can be distinguished by the shape of the deltoid crest. In *M. primigenius* the deltoid crest runs straight down and terminates distally in a marked nod before merging into the distal portion of the shaft, contrary to the convex margin without such a nod in *Stegodon*.

There is another proximal humerus from Sulawesi (PL-3736; Fig. 59), which corresponds in morphology with the deltoid crest as developed in *M. primigenius* humeri. The transverse diameter over the distal end of the deltoid crest (measurement H4) is relatively smaller in the latter mentioned specimen than in specimen LR-3736 (Table 22). The two Sulawesi specimens are further distinguished by the shape of the medial

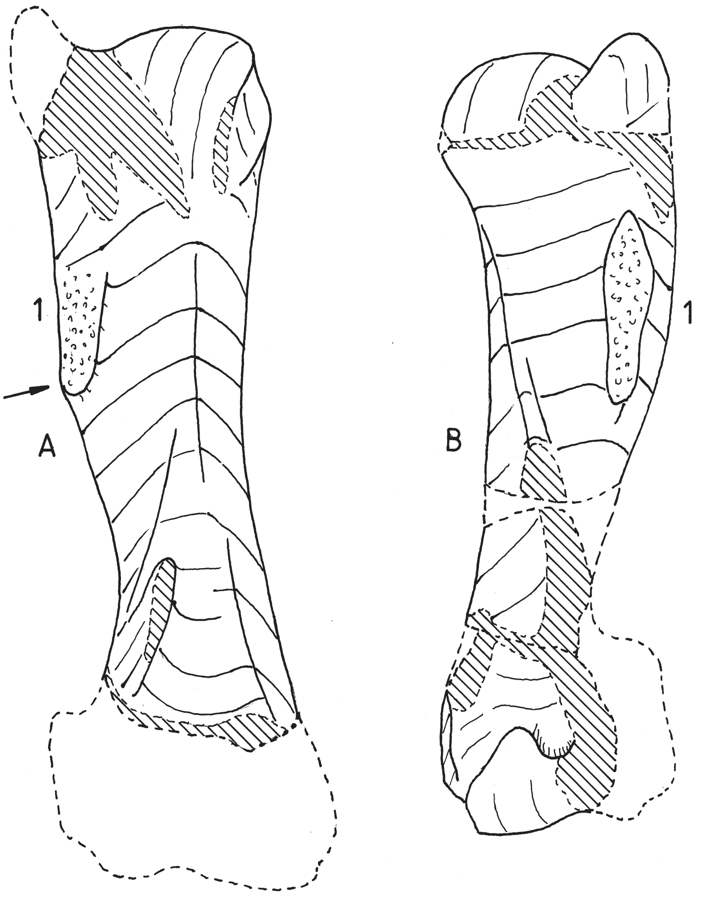


Fig. 59. A: proximal sinistral humerus fragment attributed to *"Elephas" celebensis* (GRDC PL-3736) and B: fragmentary dextral humerus attributed to *Stegodon sompoensis* (GRDC LR-3707). Both humeri are shown in caudal view, but are not drawn on the same scale. Note the more pronounced deltoid crest (1) with its convex lateral margin developed in *S. sompoensis*, whereas in *"E." celebensis* the lateral margin of the deltoid crest runs straight with a distinct nod (arrow) at the distal termination.

border of the proximal shaft. In LR-3736 this border is strongly curved concavely just below the caput. In PL-3736 this border is only very weakly concave. This difference was also noted between the humeri of *S. trigonocephalus* and *M. primigenius* respectively by Ariëns (1995). These observations suggest that specimen LR-3707 belonged to a *Stegodon* and specimen PL-3736 to a member of the Elephantidae. Specimen LR-3707 is here attributed to *S. sompoensis* and PL-3736 to *"E." celebensis*.

In the GRDC collection there are several additional proximal humerus fragments, which all lack the distinctive deltoid crest, but which clearly belonged to one of the two dwarf species from Sulawesi based on their small size. These are specimens SB-2842 (sinistral adult), SB-2850 (dextral adult), BC-3034 (sinistral adult), LR-2708 (dextral adult), LR-3706 (dextral adult) and ABTL/161186-1 (dextral juvenile). There is also a sinistral diaphysis fragment of a juvenile individual (2324-L1) and one distal dextral epiphysis fragment (LR-2709) (see Table 22). In this Table are also included the measurements of a dextral distal humerus fragment (C3/27-B) and two sinistral proximal humerus fragments (C1/23/171086 and C3/28-83) from the collection of the MPC. The proximal transverse diameter (measurement H2) varies between 118 mm in the juvenile specimen LR-3707 and 137 mm in the second largest adult specimen. In the largest specimen from Sulawesi, LR-3706, measurement H2 could not be taken, but the antero-posterior diameter of the caput (measurement H3) is c. 130e mm. In *S. trigonocephalus* humeri from Java, measurement H2 varies between 180 and 240 mm and measurement H3 between 155 mm and 200 mm (Hooijer, 1955b), which indicate a significantly larger size.

Radius — There is only one radius represented in the GRDC collection, which happens to be complete and of the right side (LR-3546, Pl. 9, figs. 2-3). It was excavated in situ at FVL-24c. The proximal epiphysis is fused with the diaphysis but the unfused distal epiphysis was found separately at close distance. This radius probably belongs to the same individual as humerus LR-3707, as both specimens were found within a radius of half a meter from each other in the same level, and also because the epiphysal fusion stage in both specimens indicates a similar age and is in agreement with fusion data on modern elephants (Roth, 1984; Haynes, 1991), according to which the elbow epiphyses fuse prior to the shoulder or wrist epiphyses. Because humerus LR-3546 can be attributed to *Stegodon sompoensis* on morphological grounds, the present radius of the same individual should be also attributed to *S. sompoensis*. The radius, with a total length (R1) of 365 mm and the proximal epiphysis fused, clearly belonged to a small-sized elephantoid. Other measurements are: greatest proximal transverse diameter (R2) = 62 mm; greatest proximal antero-posterior diameter (R3) = 33 mm; minimum transverse diameter of shaft (R4) = 23 mm; minimum antero-posterior diameter of shaft (R5) = 16 mm; greatest distal transverse diameter (R6) = 66 mm; greatest distal antero-posterior diameter (R7) = 82 mm; greatest transverse diameter of distal articulation surface with lunatum (R8) = 61 mm; greatest antero-posterior diameter of distal articulation surface with lunatum (R9) = 62 mm.

Are there any indications that point in the direction of *Stegodon*? Hooijer (1955b) distinguished the radius of *S. trigonocephalus* from that of fossil *Elephas* from Java based on size differences, and further noted that the shaft of the radius is slightly less curved in *Stegodon* as compared to modern *E. maximus*. Under the present circumstances, size differences are unsuitable for the distinction between *S. sompoensis* and *"E." celebensis*. Ariëns (1995) noted several morphological differences between the radius of *S. trigonocephalus* and *M. primigenius*. One is the shape of the elevated ridge running over the postero-lateral surface of the shaft. In *M. primigenius* this ridge bifurcates close to the distal end of the shaft while in *S. trigonocephalus* the bifurcation is situated halfway the shaft. The flattened surface between the two ridges on the distal shaft represents the contact facet with the antero-medial surface of the ulnar shaft. In LR-3546 there is no bifurcation at all, which could mean that the contact between the shafts of radius and ulna was very limited and the two bones were perhaps more movable with respect to each other. However, it is more likely that the crest is not yet well pronounced due to the immature ontogenetic stage. An other distinctive feature mentioned by Ariëns (1995) is the presence of a clear nod on the proximal half of the shaft visible in lateral view in *M. primigenius*, but not in *S. trigonocephalus*. In LR-3546 such a nod is not developed and the shaft is, like in *S. trigonocephalus*, straighter than in *M. primigenius* and extant *Elephas*. Other differences are the more strongly undulating and larger distal articulation surface, the relatively thicker shaft and the relatively large ulnar contact surface on the distal epiphysis in *S. trigonocephalus* than in *M. primigenius* (Ariëns, 1995). Because there is no dwarf elephantoid radius from Sulawesi with which to compare specimen LR-3546, these qualitative characters are difficult to judge. The only feature that seems to point towards *Stegodon* is the straight shaft of this radius.

Ulna — Two distal ulna fragments in the van Heekeren collection of the NNM were mentioned by Hooijer (1949: 215; 1955: 91). Both were attributed to *Archidiskodon celebensis*, because at that time Hooijer was not yet aware of the occurrence of a dwarf *Stegodon* in the same deposits. In the GRDC collection there are 8 ulnas represented, none of which is complete. Three proximal fragments originate from FVL-5. These are specimen 1306, a dextral ulna of a young individual in which the olecranon epiphysis was not yet fused, and specimens 1379 and 2028, a sinistral and dextral fragment consisting only of the processus anconeus and olecranon. Two diaphysis fragments, specimens 2002 (dextral) and 1387 (sinistral), are broken below (proximally) and above (distally) of the epiphysal fusion. Three distal portions, all broken above the fused epiphyses, are specimens 2006 (dextral), 2325-L1 (dextral) and LR-2620 (sinistral).

Pohlig (1911) mentioned that the olecranon of the *Stegodon* ulna is rather elongated and the processus anconeus more prominent than in *Elephas*. Hooijer (1955b) does not find these differences between the *S. trigonocephalus* ulnar material from the Dubois Collection and modern *Elephas* ulnas, but instead mentions that the surface for articulation with the humerus is wider relatively to the total length in *Stegodon* than in the modern species. Our material from Sulawesi is too fragmentary to evaluate these characters. The size measurements are given in Table 24, which show that all Sulawesi ulnas in the GRDC collection are of small size. The distal fragments are even smaller than the two specimens mentioned by Hooijer (1949, 1955b; measurements also included in Table 24), of which one belonged to a juvenile individual. The transverse diameter for the articulation facet with the triquetrum (measurement U7) varies between 47 and 73 mm in the five distal fragments from Sulawesi. In the distal ulnas of *S. trigonocephalus* measurement U7 varies between 75 and 95 mm (measurements of *S. trigonocephalus* given by Hooijer, 1955b, tables 31 and 33, n = 6; the triquetrum facet is called the cuneiform facet).

Pelvis — Only one fragment represents a dwarf elephantoid pelvis amongst the vertebrate fossils recently recovered from South Sulawesi. The fragment (Coll. GRDC L-3966/3969) consists of the anterior half of the acetabulum, the corpus ossis ilium and a portion of the dorsal margin of the ala ossis ilium of a dextral pelvis. The only measurements which could be taken are the dorso-ventral diameter of the articular surface of the acetabulum (P2 = 75 mm), the dorso-ventral diameter of the acetabulum between the outer margins (P3 = 96 mm) and the least width of the ilium just above the acetabulum (P4 = 108 mm). Hooijer (1955b: 91) gave some measurements of a similar fragment originating from Celeko, also consisting of the anterior half of the acetabulum and the corpus ossis ilium of a sinistral pelvis. Measurements P2 and P4 amount 85e mm and 100e mm respectively in this specimen.

These measurements indicate dwarfed elephantoids: in *S. trigonocephalus* from Java measurement P2 varies between 125 and 150 mm (average of 131 mm, n = 11) and measurement P4 varies between 120 and 190 mm (average of 154 mm, n = 15; measurements taken from Hooijer, 1955b). Hooijer (1955b) found the corpus ossis ilium to be relatively longer in *S. trigonocephalus* than in modern *E. maximus*, a difference which was also found by Ariëns (1995) when comparing *S. trigonocephalus* with *M. primigenius*. Considering the ilium from Celeko, Hooijer stated that 'as far as this specimen permits judgement, the expansion of the ilium is more rapid than that in *Stegodon*, and resembles that seen in *Elephas*.' Qualitative examination of specimen L-3966/3969 shows that the ilium is less rapidly expanding than the Celeko specimen. It is attributed here to *S. sompoensis*.

Femur — Hooijer (1955b: 91) mentioned a distal fragment of a dextral femur from Celeko. After removal of the matrix covering the shallow fossa intercondyloidea, it followed that both the lateral and medial condyles merge with the facies pattelaris without marked boundaries. Ariëns (1995) found this to be a distinctive character in which *M. primigenius* differs from *S. trigonocephalus*. In the latter the fossa intercondyloidea is wide and deep and the connection between the condyles and facies pattelaris is narrow and discontinuous. This suggests that the Celeko femur belonged to *"E." celebensis*.

Furthermore, there are two distal diaphysis fragments in the van Heekeren collection, which were left undescribed. Both are broken above the distal epiphysal fusion. One fragment is of the left side and bears the inscription "S.", which stands for the locality Sompoh. The other, of the right side originates from Beru (inscription "B."). The diaphysis from Sompoh is more compressed antero-posteriorly (compare measurements F4 and F5 in Table 25), but this may be due to post-depositional deformation, as this fragment is heavily fractured in longitudinal direction. Like in the dwarf *Stegodon* femur diaphysis from Flores, rough tuberosities for attachment of the biceps femoris are well developed on the disto-lateral edge of the Sompoh shaft, but are lacking on the Beru specimen. The latter probably belonged to an immature individual.

There are 6 more dwarf elephantoid femurs represented in the South Sulawesi vertebrate collections of the GRDC and MPC. Two are proximal fragments in which the caput was already fused with the shaft but in which the great trochanter is damaged (GRDC 2001 and 2323-L1). The only measurement which could be taken on these two fragments was the antero-posterior diameter of the caput (F8 is 78 mm and 91 mm, respectively). In adult *S. trigonocephalus* femurs from Java measurement F8 varies between 125 and 165 mm (average 137 mm, n = 11; measurements taken from Hooijer, 1955b). Distal fragments of either *S. sompoensis* or *"E." celebensis* are 4 in number (GRDC 2320 (sin.) and PL-3737 (dex.); MPC C1/23/171086 (sin.) and D2-35/86 (dex.)). They all have their distal epiphyses fused and their measurements are included in Table 25. The largest distal fragment, PL-3737, has a maximum distal transverse diameter (F9) of 153 mm, which is still 85% smaller than in the smallest adult *S. trigonocephalus* femur from Java (measurement F9 varying between 180 and 255 mm, average 207 mm, n = 13; measurements given by Hooijer, 1955b). The distinction between the femur of *Stegodon* and *Elephas* can be made based on the ratio of the transverse diameters relative to the total length, which is consistently larger in *Stegodon* (Hooijer, 1955b). In addition to the distinctive characters on the distal condyles and facies pattelaris already mentioned, Ariëns (1995) found that the *Stegodon* shaft is more curved as compared to *M. primigenius*. These diagnostic characters have not yet been studied in the Sulawesi femur material in the GRDC and MPC collections.

Tibia — In addition to the two tibia fragments described by Hooijer (1949: 216; 1955b: 92) there are four proximal tibia fragments of dwarf elephantoids in the GRDC and MPC collections from South Sulawesi (GRDC 1349 (sin.), 2005 (dex.), 1345 (sin., proximal portion of shaft lacking epiphysis) and MPC A1-2/85 (sin.)). Except for the proximal fragment mentioned by Hooijer (1949), they are all in a poor state of preservation. Their measurements are given in Table 27. Comparison with the data of Hooijer (1955b) learns that the largest Sulawesi specimen (A1-2/85) has a maximum proximal transverse diameter (T1) that is 89% smaller than in the smallest *S. trigonocephalus* tibia, and 65% smaller than the average T1 value of the Javanese species (T1 varying between 140 and 255 mm, average is 191 mm, n = 14). In a proximal tibia fragment from the Tanrung Formation measurement T1 was found at least 180+ mm wide.

Fibula — One dextral fibula of a juvenile dwarf elephantoid (GRDC LR-3500) was excavated near Lonrong at FVL-24c. The proximal epiphysis is lacking completely and the distal one is not yet fused. The total length excluding the proximal epiphysis is 330 mm. The minimum transverse diameter of the shaft (Fi1) is 21 mm, the minimum antero-posterior diameter (Fi2) measures 13.5 mm. The distal epiphysis measures 56 × 47 mm (Fi3 × Fi4). The inclined concave surface for articulation with the tibia measures 43 mm antero-posteriorly (Fi5). The diaphysis of an immature *S. trigonocephalus* fibula from Trinil, lacking both epiphyses, is 340+ mm long (Hooijer, 1955b).

Tarsus — There is only one dwarf elephantoid tarsal bone in the GRDC collection. It is a dextral cuneiforme secundum (LR-3555, excavated in situ at FVL-24c). The proximal facet for articulation with the astragalus has the shape of a right-angled triangle and is almost flat. Its maximum transverse diameter (anteriorly) is 23.3 mm. The posterior margin of the same facet is damaged slightly, but its antero-posterior diameter can be estimated at c. 25e mm. The maximum height measured anteriorly at the lateral side is 19.5 mm. The distal facet for articulation with the metatarsale II has an obtuse-angled triangular shape and a flat surface. Its antero-posterior diameter is 32 mm, its transverse diameter 30 mm. There is an elongated oval facet for articulation with the cuneiforme primum distally on the medial side. The maximum antero-posterior diameter measured along the medial surface is 39 mm. On the lateral side there are two oval facets, one distal and one proximal, for articulation with the cuneiforme tertium. The maximum antero-posterior diameter measured along the lateral surface is 43 mm. Toepfer (1957) gives measurements of the cuneiforme secundum belonging to the adult *Mammuthus* skeleton from Pfännerhall, Germany. This skeleton is 3 m high at the shoulders. The sinistral cuneiforme secundum belonging to this skeleton measures 66 mm along the medial surface and 89 mm along the lateral surface, and has a maximum height on the lateral side of the anterior surface of 37 mm. The cuneiforme from Lonrong is c. 50% smaller in linear dimensions.

Metatarsalia — Four metatarsalia of dwarf Elephantoidea are represented in the South Sulawesi collections. Their measurements are given in Table 28. Specimen LR-3552 (Pl. 10, figs. 1-2) is a dextral metatarsus III, excavated at FVL-24c. The distal epiphysis is completely fused anteriorly, but the suture is still well visible posteriorly. The flat proximal facet for articulation with the cuneiforme is slightly damaged anteriorly.

Specimen 1520 is a sinistral metatarsus IV excavated at FVL-5. The proximal facet for articulation with the cuboid is weakly concave. The distal epiphysis is fused. The anterior surface of the distal articulation is damaged slightly.

The remaining two metatarsalia are badly damaged. Specimen 1369 represents a dextral metatarsus IV of a juvenile individual, lacking the distal epiphysis. Specimen 1397 is an heavily weathered fragment of a sinistral metatarsus I.

Phalange — Only one third phalange (LR-3691) attributable to a dwarf elephantoid has been recovered from South Sulawesi to date. It has a single articulation facet, which is concave in antero-posterior direction. Distally it tapers. It could not be ascertained whether it belonged to the hand or foot. Its measurements are: transverse diameter = 37 mm, height at articulation facet = 16 mm, antero-posterior diameter = 21 mm.

Elephantoidea, large-sized species

All postcranial elements referable to large-sized Elephantoidea originate from either the Tanrung Formation or they were found along the Tanrung River. Three vertebrae, a distal scapula fragment, a proximal humerus fragment and a proximal tibia fragment were recovered 20 m east of the Tanrung River bank in a small gully eroding the weathered top layers of the Tanrung Formation (FVL-29, see also Fig. 37). A scapula originated from a well cemented eroded conglomerate block in the bedding of the Tanrung River. This conglomerate had the same characteristic composition as the conglomerates of the Tanrung Formation, which crops out along the river. Two large-sized elephantoid metacarpalia were found in the Tanrung River bedding downstream of all other findings and lying close together on the surface of a sandbank as if laid down by somebody. Their sandy matrix and brown fossilization color differs from those of the fossils originating from the Tanrung Formation conglomerates.

Based on morphological characters, the humerus and tibia fragments could be assigned to *Stegodon* and the two metacarpalia to *Elephas*.

Vertebrae — Three elephantoid thoracic vertebrae of large proportions all lack the arch and transverse processes. The corpii of all three specimens (GRDC TA-3064, TA-3065 and TA-3066) are much damaged and cracked and partly covered with caliche matrix. From the size measurements (Table 18) it follows that the three corpii from FVL-29 have a transverse diameter between 32% and 91% larger than the dwarf elephantoid thoracic vertebrae originating from the Beru Member of the Walanae Formation.

Scapula — Two elephantoid scapulas of large proportions were found along the Tanrung River. One of these (GRDC TA-3068) originates from the same site where the three vertebrae were recovered. The other one (TA-3725) was found in the Tanrung River bedding with a lump of cemented conglomerate of the Tanrung Formation still attached to it. Both are distal fragments that are heavily damaged superficially due to erosion, rounding and partial dissolution. The measurements that could be taken are given in Table 21, showing them to be much larger than the scapula fragments from the Beru Member. The minimum antero-posterior diameter of collum scapulae (measurement S4) of the two specimens (180e mm and 166e mm respectively) falls within the range of variation of scapulae attributed to *Stegodon trigonocephalus* by Hooijer (1955b: table 26; S4 ranges between 140 mm and 200 mm; mean = 166 mm, n =15).

Humerus — The only elephantoid humerus from the Tanrung Formation is represented by a sinistral proximal fragment of very large size (GRDC TA-3063). The fragment includes a large portion of the shaft with the deltoid tuberosity. The superficial substantia compacta is largely eroded exposing the spongiosa over large surfaces. Approximate measurements that could be taken on this specimen are given in Table 22. The transverse diameter over the superficially damaged caput and lateral tuberosity (measurement H2) is 222+ mm. The original width may be estimated to have amounted between 230e and 240e mm. This size corresponds with the largest proximal humerus from Java (CD-4260) which has been attributed to *S. trigonocephalus* by Hooijer (1955b: tables 27-28). The deltoid tuberosity is very prominent and projects, when seen in posterior view, beyond the lateral margin of the lateral tuberosity. The deltoid tuberosity has a rounded margin, which, together with the prominence of it, suggest that TA-3063 belonged to *Stegodon* and not to *Elephas*.

Metacarpalia — GRDC TA-3061 (Pl. 10, figs. 3-4) and TA-3062 (Pl. 10, figs. 5-6) are two well preserved dextral metacarpalia, probably of the same individual (Mc. III and Mc. V, respectively). In both specimens the epiphyses are fully fused. The maximum length (measurement Me1) of TA-3061 is 196 mm, which is 12 mm shorter than the Mc. III of the *Mammuthus* skeleton from Pfännerhall, Germany (Toepfer, 1957), which was already mentioned before. This shows that the specimens clearly belonged to a large-sized individual. Additional measurements of TA-3061 and TA-3062 are given in Table 29A-B, together with the measurements of homologue elements attributable to other elephantoid taxa for comparison.

Pohlig (1911) had the disposal of only a single *Stegodon* metacarpus from Trinil in the Selenka collection, a Mc. III, which however, lacked the distal epiphysis. He mentioned that, compared with *Elephas*, the proximal articulation surfaces of the Mc. III in *Stegodon* are inclined more steeply upwards and backwards, a character also expressed in the metacarpals of *Mastodon*. This character could not be examined in any of the metacarpalia present in the Dubois Collection, nor is there any metacarpus preserved amongst the dwarf elephantoid material from Sulawesi or the *Stegodon* material from Flores. However, there are some data on other elephantoids metacarpalia for comparison. Mol et al. (1999) state that steep proximal articulation surfaces were also developed in the Mc. III of *Anancus arvernensis*, when compared to that of *Mammuthus meridionalis* and *M. primigenius*. They also found that the Mc. III and Mc. V of *A. arvernensis* had wider epiphyses (both in transverse and antero-posterior direction) relatively to their length when compared with *Mammuthus*. This is expressed by the smaller length/width and length/depth ratios in *Anancus* as compared to *Mammuthus* and is graphically shown in Fig. 60A-B. These figures present the ratios between measurements taken on various elephantoid metacarpalia (based on the measurements presented in Table 29). Data of metacarpal material of the following taxa are included in the present comparison: *M. meridionalis* and *M. primigenius* (specimens dredged from the Eastern Scheldt Estuary, The Netherlands), *A. arvernensis* (dredged from the Eastern Scheldt Estuary), *E. maximus* (from a female skeleton of c. 40 years old, housed in the VFUU collection) and both Tanrung specimens, TA-3061 and TA-3062. Some measurements of a Mc. III and V from the complete skeleton of *Stegodon huanghoensis* from China (= synonym with *S. zdanskyi* according to Saegusa, 1996) were taken from Zheng et al. (1975), and have been used for comparison as well.

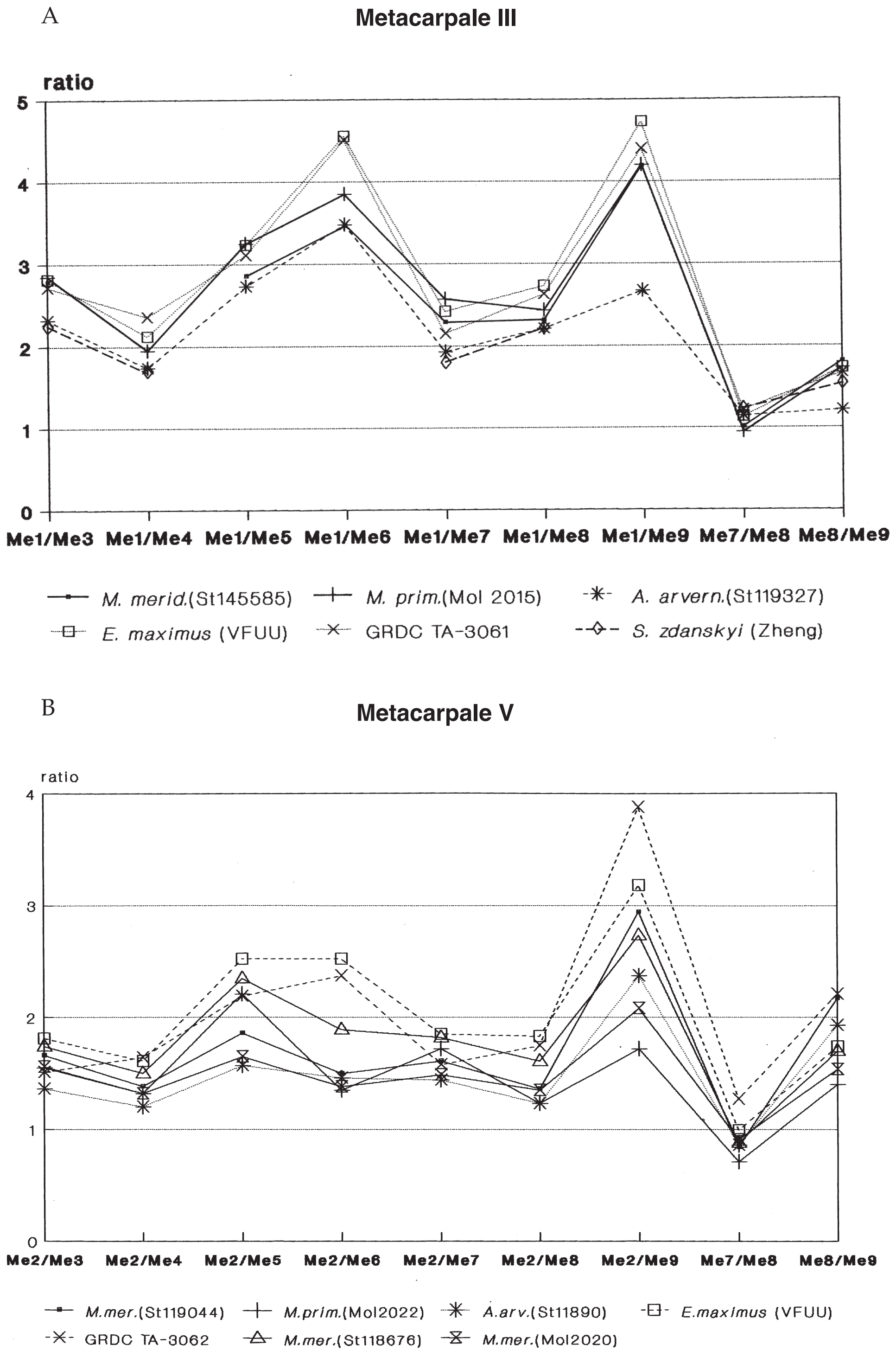
The Mc. III of *S. zdanskyi* and *A. arvernensis* do not differ much in their relative proportions, despite the fact that the latter mentioned species has a Mc. III which is c. 40% smaller than the Chinese species. Metacarpalia III of these two species posses the smallest length/width and length/depth ratios when compared with the other taxa. This trend is also present in the Mc. V, though less marked.

Specimen TA-3061 agrees closely in absolute size with the Mc. III of *E. maximus* (Table 29), and also its size ratios fit best with those obtained in the Mc. III of the Indian elephant, as shown in Fig. 60A. TA-3061 agrees with the Elephantidae morphology in the more horizontally oriented proximal articulation surfaces, and contrasts with the more inclined articulation surfaces in *Anancus* and *Stegodon*. The top angle of the proximal crest dividing the surfaces for articulation with the magnum and uncinatum can be taken as a measure for the degree of inclination of the proximal articulation surfaces of the metacarpus III. The smaller this angle, the steeper the articulation surfaces. In TA-3061 this top angle is even blunter (115°) than in the *Elephas maximus* Mc. III (100°). These observations strongly suggest that specimen TA-3061 did not belong to a stegodont, but instead to a member of the Elephantidae, most likely an *Elephas*. Its large dimensions further indicate that this elephant was not dwarfed.

Fig. 60. Ratio diagrams of measurements from an elephantoid metacarpale III (TA-3061) and metacarpale V (TA-3062) from South Sulawesi and from homologue elements of various other elephantoid taxa for comparison.

A: metacarpalia III. Specimens NNM-St145585 (*Mammuthus meridionalis*) and NNM-St-119327 (*Anancus arvernensis*) were dredged from the Eastern Scheldt Estuary, The Netherlands. Specimen Mol-2015 (*M. primigenius*) originates from the West Brown Bank, North Sea. The metacarpale III of the Recent *Elephas maximus* belonged to a female individual, older than 40 years with the M3s in function (Coll. VFUU). Ratios of *Stegodon zdanskyi* are based on measurements published by Zheng et al. (1975). Note the close similarity in proportions between specimen TA-3061 and the metacarpale III of *E. maximus*.

B: metacarpalia V. Specimens NNM-St119044, NNM-St118676 (*M. meridionalis*) and NNM-St118902 (*A. arvernensis*) were dredged from the Eastern Scheldt Estuary, The Netherlands. Specimens Mol-2020 (*M. meridionalis*) and Mol-2022 (*M. primigenius*) were dredged from the North Sea. The metacarpale V of *E. maximus* belongs to the same individual as the metacarpale III of that species included in Fig. 60A. Again, the specimen from South Sulawesi (TA-3062) shows the closest similarity with *E. maximus*. Note that the *A. arvernensis* and various *Mammuthus* specimens have comparatively thick shafts as expressed by lower Me2/Me6 ratios.


A
Metacarpale III
ratio
0
1
2
3
4
5
Me1/Me3
Me1/Me4
Me1/Me5
Me1/Me6
Me1/Me7
Me1/Me8
Me1/Me9
Me7/Me8
Me8/Me9
M. merid.(St145585)
M. prim.(Mol 2015)
A. arvern.(St119327)
E. maximus (VFUU)
GRDC TA-3061
S. zdanskyi (Zheng)
B
Metacarpale V
ratio
0
1
2
3
4
Me2/Me3
Me2/Me4
Me2/Me5
Me2/Me6
Me2/Me7
Me2/Me8
Me2/Me9
Me7/Me8
Me8/Me9
M.mer.(St119044)
M.prim.(Mol2022)
A.arv.(St11890)
E.maximus (VFUU)
GRDC TA-3062
M.mer.(St118676)
M.mer.(Mol2020)

Now let us consider the Mc. V (TA-3062). The length/width ratios of Fig. 60B are calculated using the length between the medial border of the proximal articulation surface and the distal joint (measurement Me2), instead of using the maximum length (Me1), as was done in the Mc. III. This has been done to avoid the inclusion of the highly variable lateral tuberosity of the Mc. V in the total length measurements. Unfortunately, Zheng et al. (1975) did not give measurement Me2 for the *S. zdanskyi* Mc. V. Theoretically it is expected that the proportions of the Mc. V are subject to more variability on the genus and even species level, because the degree of reduction of the lateral finger is in different stages amongst the various taxa. For example, the Mc. V of *A. arvernensis* is even larger in most size measurements than in *E. maximus*, though the Mc. III of *Anancus* is much smaller than in *E. maximus* (Table 29). Because of the small sample size caution has to be taken with these observations, but it is considered possible that the Mc. V is more reduced in *E. maximus* than in the more primitive *Anancus*, instead of being the result of body size differences. The Mc. V from Sulawesi, TA-3062, has again the closest resemblance in both size and proportions with that of *E. maximus* (Table 29 and Fig. 60B), and shows the largest differences in size with the Mc. V of *M. meridionalis* and *M. primigenius* and in proportions with the Mc. V of *A. arvernensis*. Based on the closest resemblance between both Tanrung metacarpalia and their homologues in *Elephas maximus*, TA-3061 and TA-3062 are here attributed to *Elephas* sp. The occurrence of an high-crowned, large-sized *Elephas* sp. in the deposits cropping out along the Tanrung River is also proven by the molar fragment described earlier (van den Bergh et al., 1994).

Tibia — A proximal fragment of a dextral elephantoid tibia (GRDC TA-3067) is much eroded and little detail can be distinguished. The transverse diameter of the epiphysis (measurement T1) as far as preserved is 180+ mm (a rough estimation of the original width is 200e mm), the antero-posterior diameter of the epiphysis (T2) is approximately 155e mm. In the largest adult dwarf elephantoid tibia from the Beru Member measurements T1 and T2 amount to 125e mm and 100 mm, respectively (Table 27), whereas these measurements vary between 140 and 255 mm and between 120 and 165 mm, respectively, in tibias attributed to *S. trigonocephalus* by Hooijer (1955b). This clearly shows that TA-3067 belonged to a large-sized elephantoid. The eminentia intercondyloidus lateralis and its anterior protrusion are very prominently developed in this tibia fragment. Ariëns (1995) found this to be a distinctive character which enabled to separate *S. trigonocephalus* tibias from those of *M. primigenius*. In the latter mentioned species both articulation fovea for the condyles of the femur border each other without a well developed eminentia intercondyloidus in between. This suggests that TA-3067, where such a eminentia intercondyloidus is prominently present, belonged to *Stegodon*.

5. Flores: stratigraphy and faunal evolution of terrestrial vertebrates during the Pleistocene

Introduction

The study is primarily concerned with an investigation of the fossil fauna successions on various islands in Indonesia, including Flores. First, an historical account on the study of fossil vertebrates and Palaeolithic stone artefacts from Flores will be given. To get a better understanding of the palaeogeography and the local stratigraphy of the island, the geodynamic setting and geological history are briefly reviewed. After that an analysis of the stratigraphy and sedimentology of the fossil-bearing strata of the Soa Basin in west Central Flores will be presented, followed by new data concerning the age assessments of the various lithological units. Based on the sedimentological and stratigraphical data the palaeo-environmental evolution in the Soa Basin area is reconstructed. The fossil assemblages recovered from the various stratigraphic levels will be discussed. On the basis of sedimentological and taphonomical aspects, an attempt is made to explain the fossil accumulations of the two most important sites, Tangi Talo and Mata Menge. All data are integrated to arrive at a Quaternary terrestrial fauna succession for the island of Flores.

In chapter 6 the fossil *Stegodon* material from Flores will be described and discussed. Comparison of the dwarf *Stegodon* material from Tangi Talo with other stegodont species justifies the erection of a new species: *S. sondaari* sp. nov. Additional material of the large-sized *Stegodon* from Flores will also be described and the existing material evaluated. It is concluded that molars of this species are sufficiently distinct from *S. trigonocephalus*, to justify their designation to a different species, *S. florensis*. A description of the excavated artefacts from the locality Mata Menge is given elsewhere (Morwood et al., 1997).

History

On Flores fossil stegodont remains were first discovered by the raja of Nage Keo at Ola Bula in 1956. The finds were reported to the Dutch priest Theodor Verhoeven, who immediately visited the site, which is located in the Ngada District, west Central Flores (Fig. 3). He collected additional material, together with collaborators of the Museum Zoologicum Bogoriense. From Bogor the fossil material was sent to Leiden, where it was examined by Hooijer. Hooijer (1957a) attributed all the material to *Stegodon trigonocephalus* Martin, but considered it to be different from the Java stegodont at the subspecies level, and named the Flores subspecies *Stegodon trigonocephalus florensis*. This subspecies was considered to be only slightly smaller in size than *Stegodon trigonocephalus trigonocephalus* from Java, and characterized by a higher degree of hypsodonty.

In 1960 the Geological Survey of Indonesia carried out fieldwork in the surroundings of Ola Bula in order to clarify the stratigraphic sequence of the fossil vertebrate-bearing beds (Hartono, 1961). Hartono collected additional vertebrate material and found out that the stegodont-bearing beds had a much wider extension. Amongst the fossils he recovered were two *Stegodon* milkmolars of very small size, found on the surface in the surroundings of Ola Bula. Hooijer (1964c) examined these milkmolars and concluded that they represented a pair of lower dP_3s of a real pygmy stegodont, approximately half the size of *S. trigonocephalus*. Earlier, Hooijer (1949) had described a pygmy elephant from Sulawesi, named *Archidiskodon celebensis* Hooijer, and subsequently (Hooijer, 1954d) a pygmy stegodont from Java, *Stegodon hypsilophus* Hooijer. In the same year when the occurrence of a pygmy stegodont on Flores was presented, he also announced the existence of another pygmy stegodont from Sulawesi (Hooijer, 1964a), which he named *Stegodon sompoensis* Hooijer. It became clear that, like the Mediterranean islands, various islands from the Indonesian Archipelago had once been inhabited by dwarfed elephantoids.

In the meantime two more fossil vertebrate localities were discovered on Flores through the surveys of Verhoeven, both only yielding remains of *S. trigonocephalus florensis* (Mata Menge, Boa Leza; Fig. 3) but not of the small pygmy stegodont. These localities appeared to be very interesting because stone tools were said to occur in association with the stegodont remains (Maringer & Verhoeven, 1970). However, the claim that humans were once living together with stegodonts on Flores was not taken very serious in the following years.

In 1964 Verhoeven also found pygmy stegodont material on the island of Timor near Atambua. Sartono (1969) gave a new name to this pygmy stegodont, *Stegodon timorensis* Sartono, based on an incomplete molar. Additional pygmy stegodont material from Timor was entrusted by Verhoeven to Hooijer, who described two ten-ridged M^3s (Hooijer, 1969a). In the same paper it was concluded that the two pygmy *Stegodon* milkmolars from Flores which he described earlier (Hooijer, 1964c) were conspecific with *S. timorensis*, a pygmy stegodont which was found heaving more hypsodont molar ridges than *S. trigonocephalus trigonocephalus* from Java. In the Verhoeven collection from Timor also material of a large-sized stegodont appeared present, which was attributed by Hooijer (1972a) to the subspecies already known from Flores at that time, *S. trigonocephalus florensis*.

In 1970 Hooijer visited Timor, Flores and Sulawesi himself and collected more elephantoid fossils from these islands. However, the two dP_3s (Hooijer, 1964c) remained the only pygmy stegodont specimens known from Flores (Hooijer, 1972a). Hooijer presumed that *S. timorensis* had been derived from *S. trigonocephalus trigonocephalus* from Java with as intermediate stage *S. trigonocephalus florensis*. The fossil-bearing deposits on both Flores and Timor were considered as Middle to Upper Pleistocene, noting that *S. t. florensis* and *S. timorensis* might not have been strictly contemporaneous. He assumed that important tectonic changes had occurred causing the formation of a sea-barrier between Flores and Timor during the later part of the Pleistocene.

In 1980 a reconnaissance survey was held by collaborators of the Geological Department of the I.T.B. at Bandung, the Geological Institute of Utrecht University (now IESU), and the Museum of Natural History at Basel. The layer bearing the Flores pygmy *Stegodon* was discovered near a place called Bhisu Sau. During more recent studies it appeared that the name Tangi Talo should be used for the dwarf stegodont locality instead of Bhisu Sau (Sondaar et al., 1994). Therefore, this locality will be further referred to as Tangi Talo in this thesis. Tangi Talo (Fig. 3) is located only 250 m southeast of Verhoeven's excavation at Ola Bula. Stratigraphically, the Tangi Talo fossil-bearing layer is 31 m lower in the stratigraphy than the fossiliferous layer at Ola Bula. Surprisingly, the pygmy *Stegodon* thus appeared to be older than the *S. t. florensis* remains from Ola Bula (Sondaar, 1987) and, consequently, it could not have been derived from that species. At least two *Stegodon* immigrations to Flores were presumed to have occurred (Sondaar, 1987). Besides pygmy stegodont remains, consisting of molar fragments, an atlas and several vertebrae fragments, also carapace and plastron fragments of a giant tortoise were recovered from the same level at Tangi Talo (Sondaar, 1987; Turkawski, 1988).

In November 1991 and 1992 and in April 1994 Indonesian-Dutch joint expeditions were organized to the Ola Bula area in order to 1) clarify the stratigraphic relationships between the various sites, 2) check the claims of Verhoeven concerning the in situ association of stone tools and *Stegodon* fossils at Mata Menge and Boa Leza, 3) collect more fossil material, particularly of the dwarf stegodont, and 4) sample the various sections for absolute dating methods.

All previous sites were rediscovered and two sections were measured and sampled for palaeomagnetic dating, one near Mata Menge and the other at Tangi Talo/Ola Bula. Fossils were collected at Tangi Talo and Mata Menge by means of excavations. At Mata Menge artefacts appeared to be associated with large-sized *Stegodon* remains indeed. Based on the palaeomagnetic results it was concluded that the layer which had yielded pygmy *Stegodon* and tortoise remains at Tangi Talo should be older than the Brunhes-Matuyama boundary while the layer at Mata Menge, which had yielded artefacts and large-sized *Stegodon* remains should be considered somewhat younger than this transition (Sondaar et al., 1994; van den Bergh et al., 1996). No large-sized elephantoid remains were recovered from the Tangi Talo horizon. Instead, numerous remains of a large tortoise, some teeth and vertebrae of *Varanus komodoensis*, and one tooth of a small crocodile were found in association with pygmy *Stegodon* remains. Amongst the fossils of the latter there is now sufficiently complete material available for comparison with pygmy stegodonts from the other islands.

The study area and its regional setting

Location of the study area

The study area lies at the middle reaches of the drainage basin of the Ai Sissa River in west Central Flores. Administratively, this area belongs to the Ngada District, with the capital Bajawa. The area lies between 8°40′ and 8°45′S and between 121°0′ and 121°15′E. The study area corresponds with a relatively flat depression in between various active and inactive volcanoes, the Soa Basin (Fig. 3). Only a preliminary geological map covering the study area, published by the GRDC in 1981 (Ruteng Quadrangle, scale 1:250 000), could be used. A detailed topographic map of the study area on a scale of 1:25 000, prepared by Hartono (1961), was of great help. Black and white aireal photographs consulted at the GRDC only covered the southern margin of the study area.

Physiography

The length of the island is 350 km from west to east, while the width from north to south varies between 12 km and 70 km. Due to its active volcanism, the island of Flores has a very rugged topography and an irregular coastline. The highest volcanic peaks extend to heights of over 2000 m. Plain areas are of limited extent and are mainly situated along the major rivers and in some intramontane basins. Small coastal plains occur at a few places along the northern coast where major rivers, like the Ai Sissa, debouch into the Flores Sea. Most of the north coast is fringed by coral reefs, which are virtually absent along the south coast, where the sea bottom slopes rapidly to great depths in excess of 1000 m. Active volcanoes are mainly located along the southern part of the island, where their steep southern slopes enter directly into the Savu Sea. The western end of Flores is flanked by an archipelago of small islands, of which Komodo and Rinca are the largest. During Quaternary episodes of low sea level these islands must have been united with Flores. Further west, between Komodo and Sumbawa, and between Bali and Lombok, the straits have depths in excess of 200 m (Mammerix et al., 1976; Aziz, 1990). Towards the North, Flores is separated from Selayar and from some smaller islands halfway Sulawesi by an over 4000 m deep basin. With the present day bathymetry, connection of Flores with Sulawesi would require a lowering of the sea level in excess of 1000 m, and such a connection would take place only indirectly via the Java Sea area and Sundaland.

Flores forms part of the driest region of Indonesia. The island lies on the southern rim of the area where the northwest monsoon asserts its influence from December until March. During the southeast monsoon only some moist air reaches the south coast of the island. For two-third of the year, from April until October, virtually no rain falls except on the higher mountains. Along the north coasts and in the sheltered areas of the interior, the average annual rainfall is less than 1500 mm, on the driest places maximally 500-750 mm.

Due to the dry climate, the vegetation is open, with bushes and grasses prevailing in large areas of the northern part of the island and with some forest along the rivers. The vegetation in the lower areas is strongly influenced by local inhabitants, who frequently burn vegetation at the end of the dry season during hunting. Part of the land on the lower mountain slopes and plains is used for seasonal crop raising. The steeper mountain slopes are largely covered by semi-deciduous forests.

Geodynamic setting

The geodynamic setting presented below and schematically shown in Fig. 61, is based on the work of various authors (Audley-Charles, 1975; Hamilton, 1979; Charlton et al., 1991; McCaffrey, 1996; Hall, 1996; Simandjuntak & Barber, 1996). The island of Flores forms part of the Inner Banda Arc (Figs. 27, 61). The non-volcanic Outer Banda Arc is formed by the islands Sumba, Sawu, Roti and Timor in the proximity of Flores. According to most plate-tectonic reconstructions for the Paleogene, the subduction zone running south of Sumatra and Java, bended northwards east of Java, either by means of a transform fault (Daly et al., 1987) or as a more gradual bending but continuous subduction zone with an important strike-slip component (Hall, 1996). In this palaeo-Sunda Arc oceanic crust of the Indian Plate was subducted below the Sunda shelf, but more to the east oceanic crust with various microcontinental blocks was moving northwards. The Banda Arc, the eastern extension of the Sunda Arc, did not exist yet at that time. During Early to Middle Miocene times the subduction zone east of West Sulawesi shifted eastwards and southwards and an east-west trending subduction zone came into existence as an eastward prolongation of the Java trench. In the literature it is agreed that the Sunda Arc gradually got its present shape in the course of the Neogene, although details of the process are reconstructed differently by the various authors. Still a matter of debate is the presumed origin and formation of Sumba: Eurasian or Australian, while most workers agree nowadays that Timor has an Australian origin (Hamilton, 1979; Otofuji et al., 1981; Nishimura et al., 1981; von der Borch et al., 1983; Audley-Charles, 1985; Rangin et al.,

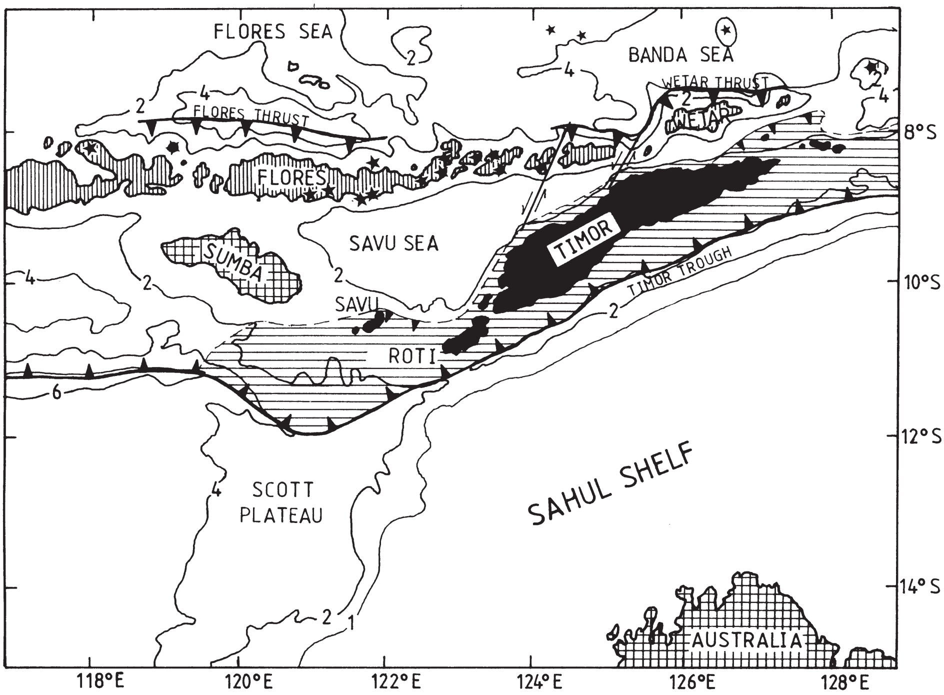


Fig. 61. Tectonic setting of Flores, showing the collision zone between the southern Banda Arc and the Australian Continent near Timor (after Hamilton, 1979, and Simandjuntak & Barber, 1996). Bathymetric contours in kilometres. Horizontal hatching: Outer Banda Arc collision zone with islands in black. Vertical hatching: Inner Banda Arc, consisting of Neogene and Quaternary volcanics. Active volcanoes are indicated by stars. The segment north of Timor is inactive nowadays. Crossed lines pattern: emerged continental crust.

1990; Wensink, 1994; Vroon et al., 1996; McCaffrey, 1996; Simandjuntak & Barber, 1996). Volcanism has come to an end in the segment of the Banda Arc north of Timor. Due to the collision of the Australian Continental Shelf with the Banda Arc, thought to have started at c. 2.4 Ma, subduction ceased in this segment, and at present Timor is being ‘bulldozed’ northwards by the advancing Australian plate. In response to the continuing north-south compression a new deformation zone has been generated directly north of the inner Banda arc in the form of the south dipping Wetar and Flores Thrusts (Fig. 61). At the present stage most of the convergent movement between Australia and the Banda Arc is being accommodated along these back-arc thrusts (Simandjuntak, 1996; Richardson & Blundell, 1996; McCaffrey, 1996). These southward dipping thrusts, on which the Inner Banda Arc overrides the oceanic crust of the Flores Sea, originated by the end of the Pliocene. The compression has resulted in strong uplift of Timor, some 700 m during the last 200 ka (Fortuin & de Smet, 1991). Also on Flores, where fewer geological data are available, uplift appears to have been strong, as evidenced by highly elevated Quaternary reefs and coastal terraces (Ehrat, 1925).

Geology

Relatively little is known of the geology of Flores. The first extensive geological expeditions to the interior of the island took place at the beginning of this century in order to investigate the rumours that there would exist large tin ore occurrences. These rumours, however, could not be substantiated (Pannekoek van Rheden, 1911; Ehrat, 1925; Kemmerling, 1929; Brouwers, 1940). The island appeared to be of interest for volcanologists, but received little further attention, due to a lack of economically interesting resources and the young age of its relatively undisturbed rocks. More detailed geological maps on a scale of 1:250 000, published by the GRDC, were not published until 1978 (Komodo Quadrangle, covering the westernmost tip of Flores) and 1990 (Lomblen and Ende Quadrangles, covering the eastern half of Flores). Most of the original data of Ehrat (1925) have been incorporated in these maps, a compilation of which is shown in Fig. 62.

As stated, the island of Flores was formed quite recently. The oldest sedimentary and volcanic rocks are of Miocene age (Ehrat, 1925). The oldest volcanic rocks of andesitic composition are locally interbedded with sandy tuffs, tuffaceous sandstones, limestones and *Globigerina* marls. Fission-track datings on these rocks yielded ages of 15-21 Ma (Nishimura et al., 1981). They mark the onset of island-arc volcanism in Flores. Intriguing, however, are two very old potassium-argon dates, suggesting that the history of Komodo and West Flores extend back well into the Mesozoic (Auffenberg, 1980). One sample obtained from a basaltic laccolith dome at Insilung Mountain, located south of Labuanbajo, Mangerrai District, West Flores, gave a date of 130 ± 10 Ma, whereas another sample obtained from basaltic rock of Banu Mate, Komodo, gave a date of 134 ± 19 Ma. A basalt from Ntodo Klea on east Komodo gave a date of 49.0 ± 4.3 Ma, while raised coral limestones on the flanks of this mountain contained Early to Middle Tertiary invertebrate fossils (Auffenberg, 1980). These older rocks on Komodo and westernmost Flores may represent the margin of the SE Asian plate during the Late Mesozoic and Paleogene.

Massive Miocene limestones containing lepidocyclinids are developed along the north coast of Flores, particularly on the western part of the island. Deformation of these oldest rocks has been moderate and the strata generally dip less than 50° towards the south with dominantly E-W trending fold axes. Faults generally have a NW-SE or NE-SW trend. The older volcanic and sedimentary rocks are intruded by granitic, granodioritic and quartz dioritic rocks of post-Middle Miocene age. Locally the magmatism has transformed the sedimentary rocks by contact metamorphosis.

Upper Miocene to Lower Pliocene tuffs and tuffaceous sandstones with some intercalations of sandy limestones, are unconformably overlying the older formations. Locally, these clastics intercalate with tuffaceous limestones and algal-coralline limestones. East of Maumere, these coralline limestones now reach an elevation of 300 m. Van Heekeren (1957) mentions coral reefs along the north coast, presumably of Neogene age, which are elevated to altitudes of 500-600 m. The Upper Miocene to Lower Pliocene strata have been folded gently with dips generally less than 20°.

The older volcanic rocks crop out mostly in the northern part of the island, whereas Late Pliocene and Quaternary volcanic centers and their products are located predominantly on the southern half of the island, where they cover the older strata. The recently and subrecently active volcanic centers are predominantly producing rocks

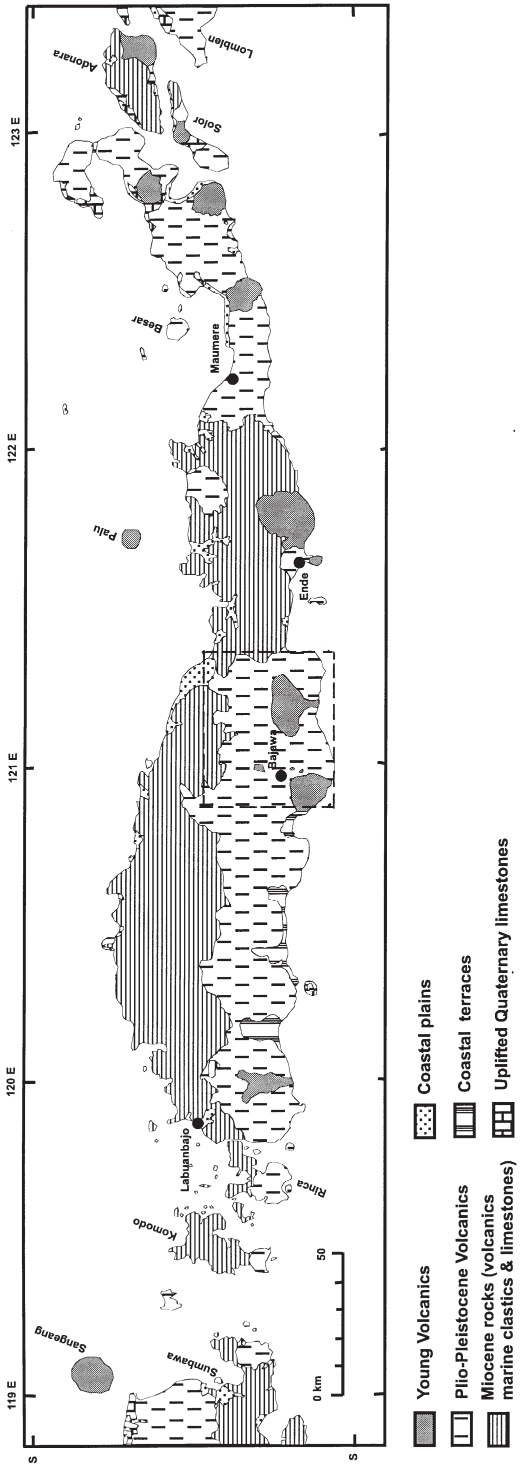


Fig. 62. Geological map of Flores. The outlined area comprises the Soa Basin and surroundings; its topography is shown in Fig. 3.

of andesitic composition. Quaternary coastal terraces can be locally found along the south coast if they are not obliterated by the volcanic activity. They attain elevations of up to 30 m above present-day sea level (PDS) (Koesoemadinata et al., 1981), but Ehrat (1925) also mentions subrecent beachgravel terraces intercalated with limestone layers at elevations of up to 150 m above PDS near Aimere on the south coast of West Ngada. Quaternary coral limestones are locally present along the north coast and may attain elevations of c. 200 m above PDS.

The Soa Basin, where the present study has been carried out, is a depression bordered in the south by Quaternary volcano complexes of high elevations and in the north by the folded Miocene and Pliocene marine and volcanic rock sequence. The horizontally layered sediments deposited in the Quaternary Soa Basin unconformably overly slightly southward tilted older Pliocene volcanics. Possibly, the Soa Basin was formed in response to subsidence generated by isostatic adjustments caused by the volcanic loads deposited to the south. Deposition in the Soa basin may have been triggered by blocking of the Ae Sissa River outlet with volcanic products from the now inactive Kelilambo Volcano.

Stratigraphy of the Soa Basin

Introduction

The study area (Fig. 3) corresponds with the central part of the Soa Basin. The basin is surrounded to the west, south and east by active and inactive volcanoes. The basin constitutes a depression extending over some 30 km in east-west direction and 15 km from north to south. Towards the north the basin is bounded by a topographic high with elevations of c. 500 to 1000 m. Miocene and Pliocene rocks crop out in this area. The highest hills in the central part of the Soa Basin attain elevations of c. 200-250 m above present-day sea-level (PDS) (according to the topographic map of the U.S. Army Map Service, Serie T 503, sheet SC 51-1, scale 1:250 000; Maringer and Verhoeven (1971) erroneously state that the Soa Plateau is elevated some 500 m above PDS). The basin is drained by the Ae Sissa River, with a single outlet located in the northeast of the basin. The area has been called Soa Plain (Ehrat, 1925) or Soa Plateau (Maringer & Verhoeven, 1971), named after the small town of Soa on the western margin of the basin. The original top surface has been incised to a depth of 200 m in the central river valley of the Ae Sissa, and has been dissected considerably in the southeast. Because the term ‘plateau’ suggests an inverted topography, while the area actually forms a depression, it is preferred here to speak of the Soa Basin. Deposition is nowadays limited to floodplains adjacent to the major streams in the wider valleys.

Pannekoek van Rheden (1911) and Ehrat (1925) both visited the Soa Basin during prospections for valuable minerals. The former author found fossil fishes, plant leaves and insects in the Soa layers, while Ehrat reported on the occurrence of undeterminable gastropods and pelecypods. Neither of them reported the occurrence of mammalian fossils, however. Ehrat (1925) mentioned that the Soa deposits constituted a sequence of volcanic products (ashes, tuffs and breccias), which cover a basement of andesitic rocks and andesitic breccias and which locally filled in depressions in these basement rocks. He also observed intercalations of thin-bedded limestones in the younger volcanoclastics. He assumed a Neogene age for the formation of the depression but supposed a Quaternary age for the upper part of the basin sequence.

The massive andesitic breccias forming the basement of the Soa Basin have been named Ola Kile Formation by Hartono (1961). These breccias have been slightly tilted (5° towards the south) and crop out at the bottom of the deepest valleys. No fossils have been found in the Ola Kile Formation.

The basin fill covering the Ola Kile Formation consists of a sequence of horizontally layered volcanoclastic products, named Ola Bula Formation by Hartono (1961). The Ola Bula Formation rests unconformably on the massive breccias of the Ola Kile Formation. The Ola Bula Formation, which wedges out towards the basin margins, is locally capped by a thin (up to 10 m) sequence of lacustrine limestones. Vertebrate fossils can be found in the Ola Bula Formation at places where the Ae Sissa River and its tributaries cut into these horizontal basin deposits. The deeper parts of the valleys, which cut through the resistant Ola Kile breccias, are usually steep-walled and V-shaped. Erosional terraces are often developed halfway the valleys on top of the resistant Ola Kile Formation. Locally, remnants of alluvium consisting of coarse and poorly consolidated gravels are developed along the valley margins. In the south erosion by north-south flowing tributaries of the Ai Sissa have shaped the topography into elongated ridges, which merge into the footslope of the active Abulobo volcano further southward (also called Ambulombo or Amboeromboe volcano). This volcano erupted for the last time in 1924 (van Bemmelen, 1949). Unconsolidated volcanic products from this volcano cover the Ola Bula Formation along the southern margin of the basin.

Description of the Ola Bula Formation

The outlines of the stratigraphy of the Ola Bula Formation have been given previously by Hartono (1961), Maringer & Verhoeven (1970), Sondaar et al. (1994) and van den Bergh et al. (1996). The stratigraphy is summarized below and schematically represented in Fig. 63, showing the subdivisions used here. Fig. 64 portrays an east-west profile through the Soa basin.

The Ola Bula Formation unconformably overlies the massive volcanic breccias (lahar deposits) of the Ola Kile Formation (Figs. 63-64). The Ola Bula Formation is up to 80 m thick in the south-eastern part of the basin, but thins out along the western basin margin. The formation can be subdivided into three members, which are designated here as Members A, B and C (Fig. 63). The lower part of the Ola Bula Formation is dominated by white, pumice containing tuffaceous sediments (Member A). This member is conformably overlain by fluvial sandstones and claystones (Member B). Locally thin-bedded lacustrine limestones form the top part of the sequence (Member C). These limestones tend to form small conical hills in areas where dissection by rivers has been limited.

Member A — Member A has a thickness of 30 m near Tangi Talo, but wedges out towards the west. Near Mata Menge the thickness of this member is only 10 m, and still further to the west it wedges out completely (Fig. 64). In the westernmost part of the basin the Ola Kile Formation is directly overlain by Member B of the Ola Bula Formation.

Member A is dominated by extensive, 25 cm to 1.5 m thick, loosely consolidated,

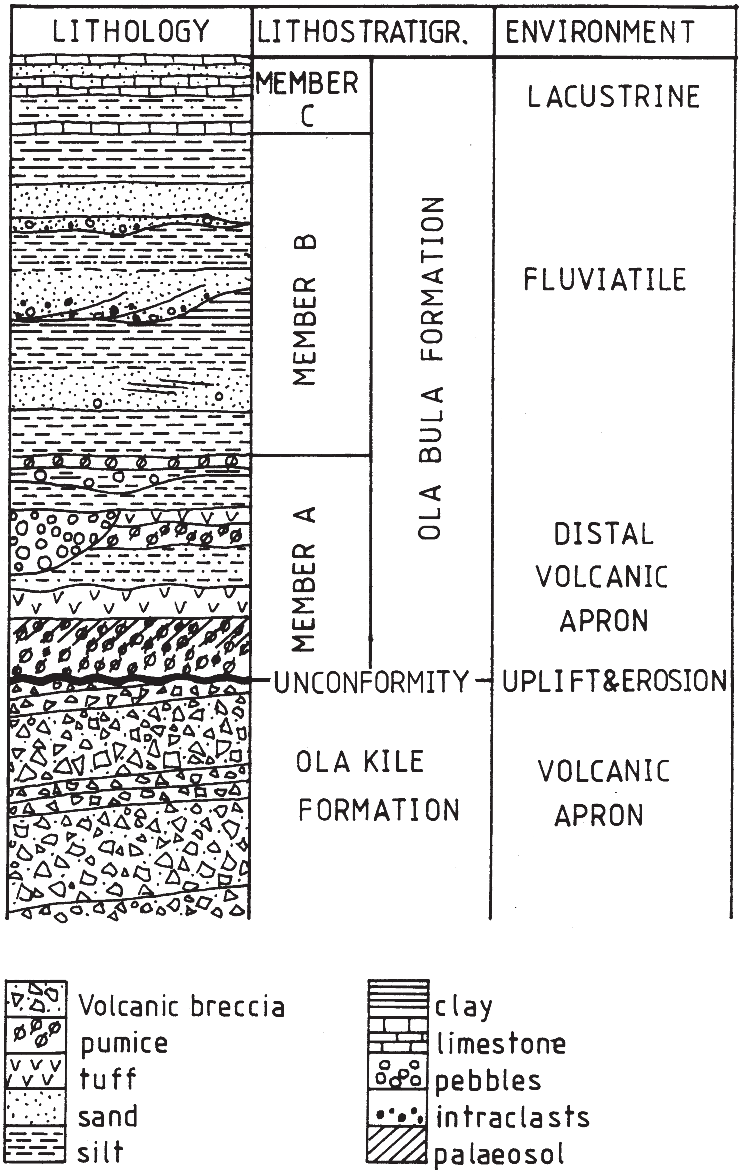


Fig. 63. Schematic lithostratigraphic scheme of the Soa Basin, Flores.

tabular sheets of, pumice-rich, volcanoclastic sandstones and siltstones, with intercalations of fine-grained tuffs, poorly sorted debris-flow deposits, and 30 cm to 3.5 m thick massive pumice beds (pyroclastic flow deposits). Rarely, deeply scouring, channelized bodies of pebbly sandstones or polymict conglomerates were observed in the field. In the section near Dozo Dhalu, the lithology of Member A is dominated by pumiceous sandstones showing low-angle and parallel laminations, while massive pumice beds are absent.

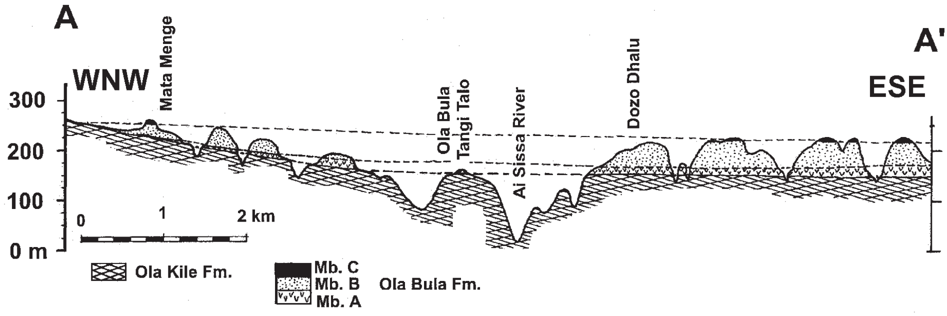


Fig. 64. WNW-ESE profile trough the central part of the Soa basin. The positions of the various FVL are projected on the profile. The profile line (A-A′) is drawn in Fig. 3. Vertical exaggeration 3 ×.

The coarser-grained layers of Member A are poorly sorted and usually lack internal structures. Some layers have a muddy matrix and may contain angular pebbles of volcanic products (debris-flow deposits). The sediments are dominated by vitric pyroclastic components, volcanic rock fragments and plagioclase. Quartz and hornblende may be encountered locally. Pumice generally contains no macroscopically visible crystals, but if present hornblende and biotite can be distinguished. Debris-flow deposits and conglomerates contain subangular to rounded clasts, consisting of andesite, basalt, silicified volcanic rocks and weathered volcanic rocks. The source volcano produced mainly volcanic products of a dacitic composition.

The fine-grained tuffaceous layers, which alternate with the coarser clastics, are silty or clayey and well sorted, but they may contain pumice fragments as well. In many of the fine-grained siltstones and claystones fossil plant-roots can be recognized.

In the western area of the Soa Basin the deposition of the sediments of Member A has time and again been interrupted by the development of various pinkish to reddish coloured palaeosols. Such oxidation colours, associated with ancient groundwater table horizons, were used by Smith (1987) to locate poorly developed, 1.5-20 cm thin palaeosols in well-drained sandy volcanoclastic sequences. Where Member A is not developed (west of Menge Ruda, Figs. 3, 64) the upper part of the Ola Kile breccias is capped by dark-red mottled palaeosols of various meters thick.

Member A can easily be recognized from large distances in the field by its bright white colour.

Member B — Member B is characterized by an alternation of fluvial sandstone layers and brown to buff coloured silty clays. Hartono (1961) subdivided the sandstone member into three biostratigraphic units: a mollusc zone, a fossil leaf zone and a *Stegodon* zone. As was already noted by Maringer & Verhoeven (1970) this subdivision appears to have no real significance, as fossil plant and mollusc remains occur in the same layers that yielded *Stegodon* remains. Member B reaches a total thickness of 60 m in the central part of the Soa Basin and, like Member A, wedges out towards the west. Near Mata Menge Member B has a thickness of 18 m. The transition between Members A and B is sharp at this site, but near the depocenter of the Soa Basin the transition between the two members is more gradual with intercalations of fluvial and tuffaceous layers. The fluvial sandstone beds of Member B are typically between 1 and 2 m thick with scouring bases and showing fining upward grain-sizes. They can be traced laterally over several hundreds of meters. Internal sedimentary structures are often obliterated by bioturbation, but occasionally parallel laminations and cross-bedding can be distinguished. Inclined accretionary surfaces, caused by the lateral shifting of channels, have also been observed. Two or more sandstone intervals may have amalgamated into multi-story layers. The sandstones are well sorted except near their erosive bases, where small amounts of rounded andesitic and basaltic pebbles are usually incorporated in the sandstones. Also eroded intraclasts (clayballs) are frequently present near the erosive bases of the sandstone layers. The clastics of Member B appear to have had a different source than those of Member A. The fluvial sandstones consist predominantly of plagioclase and volcanic rockfragments, with admixtures of orthoclase, augite and hornblende. Isolated pumice fragments present in Member B may have been eroded from the underlying Member A, but massive pumice layers characteristic for Member A, were not found in Member B.

The sandstones and siltstones of Member B frequently contain casts of fresh-water molluscs (*Melanoides*) and of fossil plant remains (mostly grasses, but also poorly preserved wood fragments, of which often only cylindrical molds remain).

Member C. — Member C is at most 40 m thick in the eastern part of the Soa Basin near the village of Gero (Hartono, 1961), but towards the west it thins to maximally 10 m. It conformably overlies Member B and the transition is rather gradual. Member C consists of thinbedded micritic limestones alternating with thinbedded sandstone, claystone and tuffaceous limestone layers. Some of the limestones are finely laminated. The top surfaces of the limestone layers frequently exhibit polygonal shrinkage cracks, which are filled in with sparitic calcite. Oogonia of Characea, ostracods and freshwater molluscs occur in the limestones. Member C of the Ola Bula Formation was designated as a separate formation, the Gero Formation, by Hartono (1961). Its limited thickness and gradual transition does not warrant the erection of a separate formation, and here it is included in the Ola Bula Formation. Hartono (1961) identified various non-vertebrate fossils from the Ola Bula Formation, which are indicative of marine conditions. These are ostracods of the genera *Bairdia* and *Cytherella* and foraminifera of the genera *Cymbaloporella* and *Amphistegina*, suggesting that the seashore was not far away.

Age control

Biostratigraphy

The Ola Kile Formation was assumed to be of Pliocene age by Hartono (1961), but since the formation has not yielded any fossils, it may therefore be older. Based on the occurrence of a highly evolved *Stegodon* in the fluvial layers of Member B of the Ola Bula Formation, a Middle or Late Pleistocene age has been assumed by Hooijer (1957a) and Maringer & Verhoeven (1970). The presence of tektites in the area has also been used as an argument for a late Middle Pleistocene age (von Koenigswald, 1958b). The tektites, however, were obtained from the local villagers and have not been found in situ. Hooijer (1957a, 1972a) considered the larger Flores *Stegodon* (not the rare dwarf form) as a slightly smaller and in dental morphology more advanced subspecies of the Javanese *S. trigonocephalus*, and named it *S. t. florensis*. On Java *S. trigonocephalus* ranges from Lower to Middle Pleistocene (Leinders et al., 1982) and has its youngest occurrence in the Ngandong Fauna. The age of the latter fauna is estimated at early Late Pleistocene or late Middle Pleistocene (van den Bergh et al., 1996; this thesis).

However, the close relationship between the Flores stegodont and the Javanese *S. trigonocephalus* as suggested by Hooijer (1957a, 1972a) is far from certain. Molars of the Javanese and Flores stegodonts can be easily distinguished. On the other hand, no skull material of the Flores *Stegodon* has been described to date, so that skull comparisons between the two stegodonts will have to await future findings. *Stegodon* species with highly distinctive skull architecture, such as *S. insignis* and *S. ganesa*, both from the Upper Siwaliks, have molars that are deceivingly similar. Taking these considerations into account, it may be well possible that the Flores stegodont did not descend directly from the Javanese *S. trigonocephalus*, but instead may have been derived from invaders from the north (Sulawesi).

The advanced stage of molar evolution observable in the Flores *Stegodon*, which has been used to estimate the age of the artefacts from the same layer, is not a good time indicator either. In Japan, for instance, *Stegodon aurorae* independently developed relatively high-crowned molars, an increasing number of molar ridges and reduced body size as compared to its direct ancestor, *S. shinshuensis* (Taruno, 1991; Saegusa, 1987, 1995). The appearance of the subhypsodont *S. aurorae* in Japan took place relatively early (at c. 2.5 Ma: Kamya, 1995) at a time when *S. trigonocephalus* was not yet present on Java. It is here believed that the development of high-crowned molars in *Stegodon* has taken place with an accelerated evolutionary rate on several islands as an adaptation to the island environment, whereas stegodonts present in mainland faunas were more conservative and changed very slowly in molar morphology. Therefore, the relatively high hypsodonty of the Flores stegodont does not necessarily imply a relatively young age.

On the other hand, the endemic *Stegodon* may have become extinct on Flores later than on Java, which makes its use for dating purposes unreliable (Bellwood, 1985; Allen, 1991).

Other faunal remains recovered from Member B are small crocodile teeth and bones and teeth of an endemic giant rat, *Hooijeromys nusatenggara*. A single tooth of the extant *Varanus komodoensis* was recovered at the site Dhozo Dhalu. These endemic faunal elements are not suitable for biostratigraphic purposes either.

Lithostratigraphic correlations indicate that the fossil-bearing horizon at Tangi Talo, pertaining to Member A of the Ola Bula Formation, is the oldest known vertebrate occurrence from the Soa Basin to date. The older age is expressed both by the superposition of Member B on top of Member A and the different faunal contents of the Tangi Talo locality relative to all other fossil localities in Member B. Tangi Talo yielded an insular fauna with the dwarf *Stegodon sondaari* sp. nov., a giant tortoise, a single tooth of a small crocodile and remains of the still extant *Varanus komodoensis.* Only the crocodile and *V. komodoensis* are also found in younger layers pertaining to Member B. The occurrence of the large-sized *Stegodon* at the localities Ola Bula, Boa Leza and Mata Menge, led Sondaar (1987) to conclude that these localities are all younger than the one near

Tangi Talo (called Bhisu Sau by Sondaar, 1987). Absolute dating techniques are required, however, to date the Ola Bula Formation more accurately.

Palaeomagnetic dating

In order to obtain absolute ages for the Flores sequence, two sections were sampled for palaeomagnetic dating, one near Mata Menge and one near Tangi Talo/Ola Bula (Fig. 65). The results have been published earlier (Sondaar et al., 1994), but a more detailed description of the palaeomagnetic data will be given below, with permission of B. Mubroto, who carried out the palaeomagnetic sampling and analysis. Samples from 19 levels in both sections were taken in order to determine the remanent magnetization. From each layer 5 to 6 oriented core samples were drilled, or an oriented block sample was cut using non-magnetic tools. The block-samples were further prepared in the laboratory. The Natural Remanent Magnetization was determined using a Schönsted DSM-2 spinner magnetometer. A stepwise alternating field demagnetization method was applied in steps of 5-20 mT up to a maximum peak field of 100 mT in order to examine the stability of magnetization. Three of the sampled horizons did not yield reliable demagnetization results; from each of the other layers 4 to 6 samples gave satisfactory demagnetization curves and the average declination and inclination was calculated from these measurements. The results are presented in Fig. 65 and Table 49.

Results — The lower part of the section at Tangi Talo, including the fossil-bearing level at Tangi Talo, is dominated by reversed magnetic polarities. It is concluded that this part of the section must be older than the Brunhes-Matuyama boundary at 0.78 Ma, according to the palaeomagnetic scheme of Berggren et al. (1995). An Early Pleistocene age is most likely. Two of the six levels in the lower part, however, have normal polarities (Fig. 65, Table 49). At present it is not clear whether these two normal polarities represent a short normal event, perhaps the Jaramillo Event at 1.0 Ma (according to the palaeomagnetic scheme of Berggren et al., 1995), or that a secondary normal magnetic overprint has not been successfully removed in these samples. In any case, the reverse polarities in the same interval indicate that this part of the sequence is at least older than the Matuyama-Brunhes boundary.

The fossil bearing layer at Tangi Talo is stratigraphically 31 m below the *Stegodon florensis* bearing layer of Ola Bula in which Verhoeven carried out his excavations (C in Fig. 65). There is an 18 m thick non-exposed and poorly consolidated interval in between, in which no samples could be taken. Above this non-exposed interval three sampled levels with normal polarities occur, situated 5-10 m below the excavation level of Verhoeven at Ola Bula. It follows that at least a transition from reverse to normal polarity should occur in the non-exposed interval. This transition most likely represents the Matuyama-Brunhes boundary as will be argued below.

At Mata Menge the Ola Bula Formation is thinner than near the type section at Ola Bula. At Mata Menge the lower part of the Ola Bula formation is 23 m thick from its base to the base of Member C (the equivalent lithostratigraphic interval is at least 36 m thick in the Tangi Talo/Ola Bula section 2 km more to the east, see Figs. 64, 65). Near Mata Menge a transition from reverse to normal polarity must have occurred between deposition of a 3 m thick oxidized palaeosol overprinted on a massive pumice layer (M in Fig. 65) and the accumulation of the top part of the brown clay-

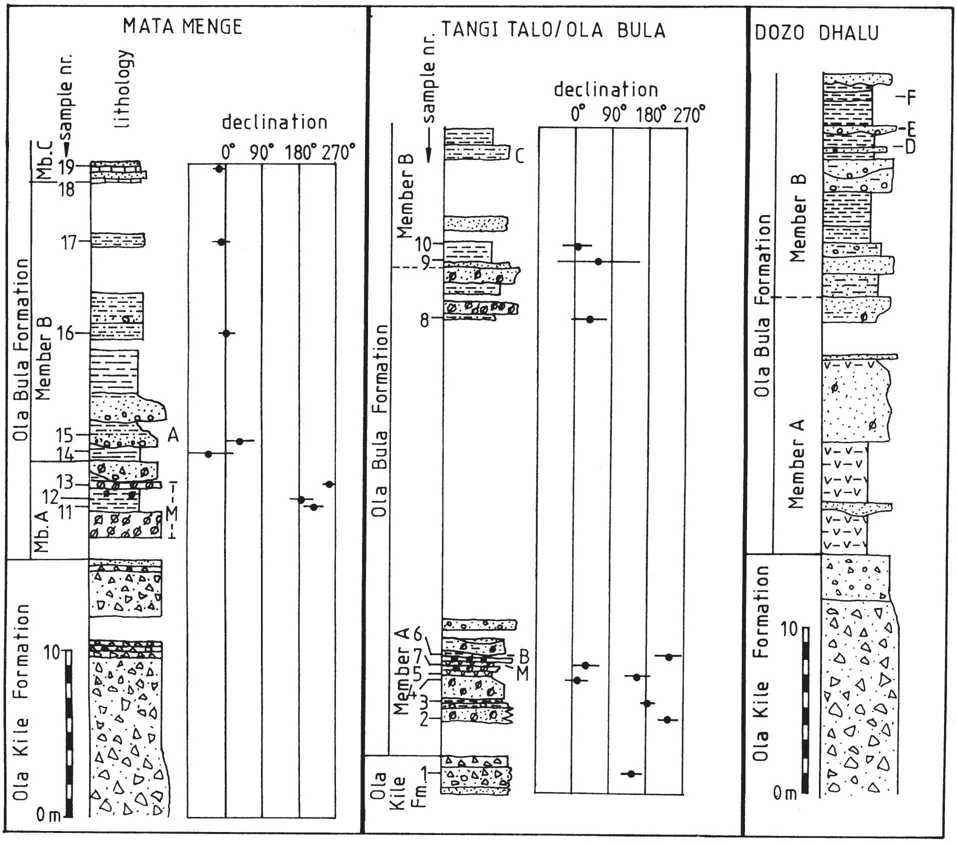


Fig. 65. Three columnar sections from the Soa Basin, Flores. For location of the sections see Fig. 3. For legend of the lithology see Fig. 63. Palaeomagnetic rocksamples (sample numbers to the left of sections) have been collected at the sections Mata Menge and Ola Bula/Tangi Talo. The declinations are shown to the right of the sections (see also Table 39). Declinations are averages of higher-coercivity remanences of various samples from single beds. Error bars represent limits of the 95% confidence cones.

Lettercodes to the right of the sections indicate: A = layer with *Stegodon florensis*, *Hooijeromys nusatenggara* and stone artefacts at Mata Menge; B = layer with *Stegodon sondaari*, *Varanus komodoensis* and *Geochelone* sp. at Tangi Talo; C = layer with *S. florensis* and *H. nusatenggara* at Ola Bula; D = layer with *S. florensis* and *V. komodoensis* at Dozo Dhalu; E = layer which yielded 2 flakes; F = layer with *H. nusatenggara*. M = pink/white mottled intervals.

stone underlying the artefact bearing fluvial sandstone layer. Samples from the middle of the palaeosol provided a reversed polarity (Fig. 65; Table 49). The magnetic transition above this palaeosol most likely represents the Matuyama-Brunhes boundary at 0.78 Ma. The in situ occurrence of artefacts just above this transition proves that Flores was inhabited by technologically skilled humans during deposition of this layer, and an age older than 1 Ma would be very unlikely. The palaeosol corresponds with a period of reduced volcanic activity, which followed a period of rapid syneruption deposition along the western margin of the basin.

Because of the depositional hiatus indicated by the palaeosol, the artefact bearing layer should be considered slightly younger than 0.78 Ma, though there are no indications (such as a major erosional contact) that the hiatus would be larger than a few hundred thousands of years.

ESR dating

Two samples of *Stegodon* molar enamel from Flores were sent to Japan for ESR analysis by Dr Motoji Ikeya of the Science Faculty of Osaka University. The samples were ESR dated together with the samples from Sulawesi already discussed before, and with a number of mammalian tooth enamel samples from Crete and other Mediterranean islands. The results on the samples from Crete, numbered 7, have been recently published (Reese et al., 1996). As already mentioned, no radiation assessment of the fossil sites was carried out and therefore the ESR ages are only suggestive for the order of magnitude.

As discussed in the section on the chronostratigraphy of Sulawesi, the relatively young ages of less than 0.85 Ma obtained on seven samples from Crete were in good agreement with the inferred faunal succession and with the ages obtained by AAR dating. Also the ages obtained on the three samples from Sulawesi were in agreement with palaeomagnetic and biostratigraphic data. Two samples from Sulawesi gave ESR ages of 2.1 ± 20% Ma, the oldest ages amongst the entire sample series. These ages were obtained from an *"Elephas" celebensis* and *Celebochoerus* molar enamel sample, yielding ED of 4323 Gy and 4255 Gy respectively.

The two Flores samples consist of a molar fragment of *S. florensis* from the locality Ola Bula and a molar fragment of *S. sondaari* sp. nov. from the locality Tangi Talo. The two Flores samples gave ED of 3096 Gy and 3204 Gy (roughly corresponding to ages of 1.5 Ma ± 20% and 1.6 Ma ± 20%, which is intermediate between the oldest Sulawesi samples and most Mediterranean samples. Probably, the background radiation at the Flores sites was higher than at the fossil sites on Crete, where the fossils originated mostly from non volcanic cave deposits. The fossil bearing deposits in Flores are of volcanic origin and presumably received higher doses of background radiation. This may explain the rather old ESR ages for Flores when compared to the Crete ESR ages. It is safest to discard the old ESR ages obtained on the Flores samples, especially because the Ola Bula Formation has yielded man-made stone artefacts. The late Middle Pleistocene age obtained by the palaeomagnetic results is considered here as more reliable.

Palaeoenvironmental reconstruction

Member A is characterized by a homogeneous volcanoclastic composition of most of its deposits. The larger components of many layers consist exclusively of pumice fragments. This is one of the criteria used to distinguish sediments that are produced geologically instantaneously, following the release of large amounts of pyroclastic fragments during volcanic eruptions. Such rapidly accumulated sediments are called syneruption deposits (Smith, 1991). Another aspect of syneruption pyroclastic deposits mentioned by Smith (1991) is the dominance of coarse-silt to fine-gravel particle size. This criterion also applies to Member A of the Ola Bula Formation. During inter-eruption periods, which usually extend over much longer time-periods than the syneruption phase, preeruption conditions are restored, aggradation ceases and stream beds are incised to form narrower, typically more sinuous, gravel-bedload channels.

Smith (1991) distinguishes various facies types for deposits that accumulated on volcanic aprons. The facies geometry of Member A corresponds with his facies type 1, which is characterized by extensive syneruption sheets of ash-rich, sandy flood and debris-flow facies and hardly any inter-eruption gravel-bedload facies preserved. This facies type 1 is produced by rapid syneruption aggradation of wide and shallow, flashy discharge streams in tectonically stable sites or slowly subsiding basins, in which the long-term subsidence rate is lower than the volcanic sediment production. In such a setting there is little or no record of the intereruption periods preserved. During deposition of Member A of the Ola Bula Formation rapid aggradation in supposedly shallow, braided streams and by debris-flows occurred during syneruption phases. The massive pumice beds may represent pyroclastic flows (ignimbrites), though no traces of welding were found.

During the inter-eruption phases only limited incision and deposition in deeper bedload channels is recorded in Member A, but depositional hiatuses are clearly marked by the well developed palaeosols and bioturbated horizons, particularly in the western part of the Soa Basin.

After deposition of Member A volcanic activity probably ceased and/or shifted to another, more distant area. Deposition of Member B was dominated by normal fluvial processes, though the source material was partly volcanoclastic. However, the clastic sediments of Member B document a wider range of erosion products, like weathered volcanics, chert and silicified volcanic rocks. The clastics were deposited in small sinuous rivers with laterally shifting channels, which indicates that sediment input was not excessive. Deposition of muds took place laterally of the fluvial channels on the floodplains or in lakes. Finally, perhaps due to a decrease in sediment input, lacustrine limestones were formed (Member C). Limited influxes of clastic material are recorded by the admixture of tuffaceous sand in some of the micritic limestones. The lakes must have been shallow as follows from the lack of limestone layers thicker than 10 cm, and may even have dried up occasionally (mudcracks), suggesting relatively dry climatic conditions.

The shift from almost exclusively syneruption facies of Member A to a normal fluvial facies of Member B may have been triggered by the closure of the basin outlet in the northeast, where the present Ai Sissa river cuts trough volcanic products of the now extinct Kelilambo volcano (Koesoemadinata et al., 1981). However, increased subsidence rates, decreased volcanism or tectonic uplift of the northern hills could all have played a role in this transition and to resolve this question requires more detailed, basinwide sedimentological studies.

The present study concentrated mainly on the western part of the Soa Basin. During deposition of Member A, the volcanic source feeding the apron probably was located in the west, which would explain the higher elevation of the units A, B and C in the west (Fig. 64) and the more frequent occurrence of palaeosols west of the present Ae Sissa River. However, a basinwide facies analysis should reveal if perhaps more than one source provided sediment simultaneously.

Quaternary faunal succession of Flores

Fossil vertebrate localities of the Ola Bula Formation

Vertebrate remains can be found at several places throughout the Soa Basin, like the sites Mata Menge, Ola Bula, Boa Leza, all discovered by Verhoeven, and the locality Dozo Dhalu (Fig. 3). The fossils at these localities all originate from fluvial sandstone and siltstone layers pertaining to Member B of the Ola Bula Formation (Figs. 63, 65). The Member B localities have all in common that remains of *Stegodon florensis* are present, while remains of the pygmy *S. sondaari* sp. nov. and of giant tortoises are lacking. In the only known FVL pertaining to the tuffaceous Member A, Tangi Talo (Figs. 63, 65) fossil vertebrate remains occur in a tuffaceous layer and include a giant tortoise, a dwarfed stegodont, named here *S. sondaari* sp. nov., and *Varanus komodoensis*. Fossils attributable to *S. florensis* are absent from the fossiliferous layer at Tangi Talo. Based on superposition, this allows to conclude that an older fauna with giant tortoises and *S. sondaari*, is succeeded by a younger fauna characterized by *S. florensis*. A more detailed correlation of the FVL occurring in Member B would require more intensive study of the basinwide stratigraphy. The following sections of this chapter will concentrate on the sedimentology and taphonomy of the two most important FVL where we have carried out our excavations, Tangi Talo and Mata Menge. Both localities have yielded important new fossil material. The newly recovered *Stegodon* material is described in chapter 6.

FVL Tangi Talo — At Tangi Talo the vertebrate fossils were concentrated at one horizon pertaining to Member A of the Ola Bula Formation. The fossiliferous horizon coincides with the transition between a clast supported pumice layer and a tuffaceous silty clay layer containing some pumice fragments (at the transition between layers 1 and 2 in Fig. 66).

The pumice layer (1 in Fig. 66) underneath the fossiliferous horizon crops out on a steep hillslope and can be traced over a lateral distance of c. 50 m, until it is covered by dense vegetation. The pumice layer is homogeneous and does not show internal sedimentary structures. It has a weakly scouring base and an undulous upper boundary. The only clasts with a diameter larger than coarse sandsize are subrounded to rounded pumice fragments with a maximum diameter of up to 5 cm, but with an average diameter of 5 mm. The pumice fragments are relatively well sorted. The matrix between the pumice fragments consists of light gray tuffaceous mud, but in patches both pumice and matrix are mottled with pink colours, suggesting some degree of soil formation. The uniform composition of the pumice layer indicates that deposition of the layer must have been related to a single volcanic event. Perhaps, the layer represents a (reworked) air-fall tephra deposit, though clast-size gradations are hardly recognizable. More likely, the layer may represent a distal pyroclastic flow deposit. Distal, because no signs of welding could be observed and because the poorly sorted texture of the layer suggests viscous flow prior to deposition.

The boundary with the overlying tuffaceous mud layer is sharp but undulous. This tuffaceous mud layer (2 in Fig. 66) has a thickness varying between 10 and 30 cm, and has a buff colour when wetted but white when dry. Some pumice fragments are dispersed throughout the silty clay layer, which is otherwise well sorted. This

Fig. 66. Fossil-bearing horizon at Tangi Talo. Fossils are concentrated on top of a clast-supported pumice layer (1) and covered by a silty clay layer with scattered pumice fragments (2). The long bone to the right of the center is a *Stegodon sondaari* femur diaphysis (TT-4083). Layer 2 is overlain by poorly sorted debris flow (3).

tuffaceous mud covers the fossils completely.

The tuffaceous mud layer is in turn overlain by a brown-coloured, poorly sorted sandy mudstone layer with pumice clasts and angular volcanic granules (3 in Fig. 66). The base of layer 3 is strongly erosive, locally cutting down 25 cm into the underlying tuffaceous mud. The layer is up to 1 m thick. It has no internal structures, except for some up to 15 cm high channel-fill crossbedding structures at the top. The entire layer, including the channel-fill structures, is capped by a 2-15 cm thick palaeosol, indicating a longer depositional hiatus. A few small tortoise carapace fragments were found in layer 3. Possibly, these fossils were eroded from the underlying fossiliferous horizon prior to deposition of layer 3. The upper part of layer 2 was partly eroded, presumably prior to deposition of layer 3, which has a massive, poorly sorted appearance characteristic for a debris-flow deposit. The composition of this debris-flow is more heterogeneous than layer 1, and may not be directly related to a volcanic event. Small gullies were active for some time after deposition of layer 3.

Apart from the few fossils recovered from layer 3, the bulk of the fossils was found at the undulous transition between pumice layer 1 and tuffaceous mud layer 2. Some larger fossils are partly embedded in the pumice layer with their base and covered by the tuffaceous clay. Fossil remains must have accumulated after deposition of pumice layer 1. Subsequently, fine-grained sediments of layer 2 covered the fossils. The question is whether the deposition of the tuffaceous clay followed relatively shortly after deposition of layer 1 or not. The observation that the pumice layer 1 is locally mottled with pink colours suggests a longer period of soil formation after deposition of the pumice layer, but the reddening may have also been formed after deposition of layer 2 at the groundwater level. This pink mottling is not developed in the overlying silty clay layer, though at other places in the basin similar clayey deposits may show pink mottled levels. Thus, the available evidence suggests that locally at Tangi Talo there was a sedimentation hiatus of some extent between the deposition of pumice layer 1 and tuffaceous clay layer 2. The good sorting of the latter (excluding the isolated pumice fragments, which can float temporarily until becoming water saturated, as followed from a small experiment in the field) suggests that after this depositional hiatus, a pool or lake of standing water developed, from which sedimentation out of suspension could take place. Pumice fragments entering this pool may have floated temporarily on the water table before settling down and becoming incorporated in the clayey deposit. The vertebrate fossils may have either accumulated prior to the formation of this pool of standing water, or more likely, the presence of the waterpool itself may have attracted the animals.

Higher up the slope above the fossil level with *Stegodon sondaari* sp. nov., the layers become more sandy and grade into the well sorted fluvial sandstones of Member B. These sandstones contain fossil remains of the large-sized *Stegodon florensis*. Therefore, surface findings at Tangi Talo must be handled with care, and were only considered as originating from the main fossiliferous level if their fossilization and adhering matrix indicated so.

Taphonomy at FVL Tangi Talo — Due to time constraints, the position and orientation of the fossils were not recorded at Tangi Talo. However, some remarks can be made concerning the taphonomy of the fossiliferous layer, based on sedimentological aspects and preservation and composition of the fossil assemblage.

The fossils are dispersed over an undulating surface, which follows the boundary between pumice layer 1 and tuffaceous clay layer 2. Of the pygmy *Stegodon sondaari* sp. nov., dental elements are over-represented relative to postcranial elements (Table 7). The minimum number of individuals present (MNI) as based on the dental remains is 12. However, there are only 3 mandible fragments, 2 small skull fragments, 12 vertebra fragments, 6 proximal costa fragments besides a dozen costa fragments without articulation facets, 1 femur diaphysis and 1 phalanx. None of the mentioned non-dental elements are complete. A few vertebrae seem to have been intact prior to deposition, but were poorly fossilized, especially the materia spongiosa of the transverse processes. Many very small fragments of the pneumatic skull bones were found isolated. These, and many other small indeterminable bone fragments are not included in Table 7. Broken fragments could generally not be fitted either to other fragments from the direct surroundings or to more distant fragments. It is concluded that much of the bone fragmentation must have taken place prior to sediment coverage.

In contrast to the low numbers of postcranial elements of the dwarf *Stegodon*, intact postcranial elements of the giant tortoise are more frequent in the same layer. Besides a large tortoise plastron-carapace fragment with associated pelvic girdle and right hind leg, more than 10 large fragments of femurs, humeri and scapulae of other tortoise individuals could be excavated. Of *Varanus komodoensis* 6 vertebrae, 6 isolated teeth, 1 femur diaphysis and several other smaller bone fragments were recovered. Four teeth of this carnivorous reptile were found inside the tortoise shell mentioned above. The better preservation of the tortoise material as compared to the stegodont material might indicate that the tortoises died at a later stage prior to sediment coverage than the pygmy stegodonts. It is also possible that tortoises died in larger quantities at the same site.

It seems that much of the *Stegodon sondaari* sp. nov. bone fragmentation and removal of postcranial elements occurred prior to sediment burial, though not all. The scarcity of postcranial material is thought to be primarily due to two factors: 1) deterioration of bone due to physical conditions and trampling prior to burial and 2) scavenging activity of *Varanus komodoensis*, of which teeth and vertebrae were found in the same layer. In addition, further fragmentation of especially spongeous bone seems to have occurred after sediment burial due to compaction and poor fossilization.

In any case, final coverage of the fossils must have been relatively rapid. This follows from the largely intact tortoise shell (plastron and carapace) in the tuffaceous sediments of layer 2. As already mentioned, a large portion of the pelvic girdle and the sinistral femur and tibia were found inside the shell, though not in articulating position (unfortunately, this carapace was already largely destroyed by erosion). Though many fragmentary carapace fragments have been found in the same layer, the intact plastron-carapace must certainly have been buried within a period of several years.

A scenario for the formation of the Tangi Talo fossil site, based on the above mentioned observations, might be as follows: A volcanic eruption caused the rapid formation of the pumice layer, presumably as a mass-flow. Subsequently, deposition was halted for a considerable time, during which soil formation processes caused the reddening of the pumice layer. Due to unknown reasons (damming of river outlets by volcanic eruptions?), a pond or shallow lake could develop at Tangi Talo. Fine-grained products washed into the pond and settled out of suspension. At this stage bones of local faunal elements accumulated on the surface, either in the pond or on the soil surface prior to pond formation. Prior to total sediment coverage of the bones, which must have taken place in a few years at most, the bones had been disarticulated and fragmented to a large extent, either due to trampling, removal by scavengers or physical weathering, or a combination of these factors. The cause of death of the pygmy stegodonts will be discussed further on in the section on the age mortality profiles.

FVL Mata Menge — Like at Boa Leza and Ola Bula, the fossil-bearing stratum at Mata Menge represents a fluvial layer pertaining to Member B of the Ola Bula Formation. The layer crops out halfway the slope of a small valley and can be laterally traced over several tens of meters in both directions along the slope. In association with *Stegodon florensis* and giant rat fossils several in situ artefacts were obtained from this layer. The artefacts have been analyzed by Mike Morwood and are described elsewhere (Morwood et al., 1997). A description of the newly recovered *Stegodon florensis* remains from Mata Menge is given in this thesis.

The excavation at Mata Menge was conducted in the same layer and at the same spot where Verhoeven had made his excavations (Maringer & Verhoeven, 1970). Ini-

Fig. 67. Excavation at Mata Menge, west Central Flores.

tially, in 1992, a test excavation was made during two successive days, by excavating a pit of 1 by 1 m adjacent to the wall of Verhoeven's excavation. A *Stegodon* tusk and three vertebrae were excavated together with four basalt pieces showing fresh brakes. One of the pieces possessed a very clear percussion bulb (Sondaar et al., 1994). This suggested that the original claim of Maringer & Verhoeven (1970), of in situ association of artefacts and *Stegodon* remains, was correct. As these results looked very promising, a larger excavation was carried out at the same spot during the next field campaign in 1994. Sediments were removed to a maximum depth of 2 m over an eastward sloping area of 13.5 m^2. Removal of the sediments took place in 10 cm spits, using a grid of 1 by 1 m (Figs. 67-68). Coordinates of fossils and stone pieces, as well as data concerning the matrix in which they were found, were recorded during the excavation. During the excavations we were assisted by 7 local laborers. A total volume of c. 19.5 m^3 was removed during the 1994 excavation.

Besides stone artefacts and stones lacking artefactual characteristics, 33 fossils, all attributable to *Stegodon florensis*, were excavated. All the fossil material and most of the artefacts originate from a well consolidated fluvial layer of 1.5 m thick (Unit 1, Fig. 69). The layer has an erosional base (lower arrow in Fig. 69) and is fining upwards. The lower part of Unit 1 contains intraclasts of the underlying silty clay. The grain-size is coarse to medium grained with a few rounded pebbles. Upwards the sandstone grades into siltstone. The siltstone interval of Unit 1 is overlain by a younger fluvial unit, consisting of an alternation of sands and silts and lenses of gravel (Unit 2). The two units are bounded by an erosional surface (upper arrow in Fig. 69). Cylindrical potholes were eroded into the siltstone of Unit 1, with rounded peb-

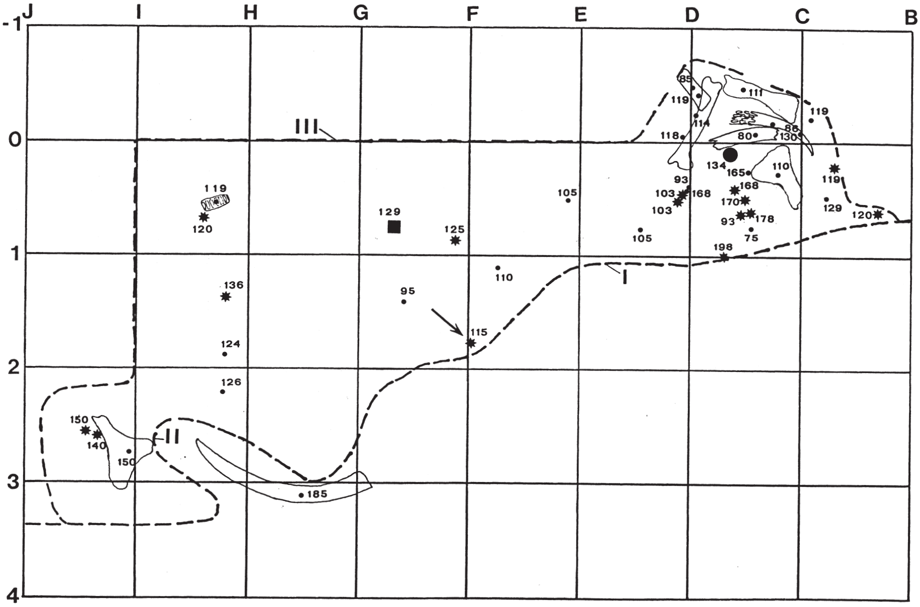


Fig. 68. Horizontal plan of the Mata Menge excavation, showing the location of the various artefacts and fossils. The highest point of each object as it was found in situ is indicated in cm below the zero reference line indicated in Fig. 69. Small dots = fossil (larger fragments are drawn); stars = flakes; large dots = pebble tool; square = multiplatform core. I: Wall of the original Verhoeven excavation. II: Wall of the 1992 test excavation. III: Wall of the 1994 excavation. The North is to the right.

bles at their bottom. This indicates that the siltstone was well consolidated when it was eroded, and therefore the overlying Unit 2 may be considerably younger than Unit 1. This is also suggested by the fact that the coarse clastics of Unit 2 are hardly consolidated, in contrast to those of Unit 1.

The internal layering of Unit 1 dips 7-15° in eastern direction (towards the spectator in Fig. 69). The silty interval at the top thickens in the same direction and must have been deposited under calm conditions, perhaps in a shallow pool or (partly) abandoned fluvial channel.

Stegodon florensis fossils occur throughout Unit 1, but were not found in Unit 2. A tusk, which occurred in the upper part of the siltstone interval of Unit 1, was found broken and heavily fragmented at the point where it reached the erosional contact with Unit 2. Freshwater gastropods (*Melanoides*) and plant remains (grasses and wood fragments) were found only in Unit 1, especially in the silty interval. In addition some small bones and teeth of the giant rat *Hooijeromys nusatenggara* were unearthed from Unit 1, as well as a few teeth of a small crocodile.

During the 1994 excavation 39 stone pieces were found in situ, several of which showed unambiguously artefactual characteristics. From the in total 39 stone pieces recovered in situ from the excavation at Mata Menge (from both Units 1 and 2), 11 have characteristics which suggest that they are artefacts, and some of them are difficult to explain otherwise (Morwood, 1995; Morwood et al., 1997).

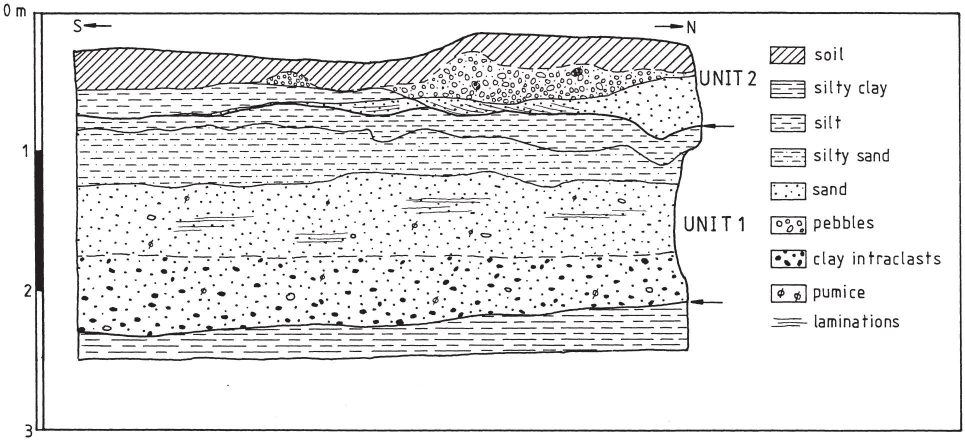


Fig. 69. N-S profile (visible in the wall of the 1994 excavation, III in Fig. 68) of the Mata Menge site. Vertebrate fossils and artefacts were found present throughout the entire fluvial layer between the two arrows (Unit 1). They are most densely concentrated in the upper siltstone interval of Unit 1. A second fluvial unit (Unit 2) overlies Unit 1 with an erosional contact. Unit 2 is poorly consolidated, contrary to Unit 1. Two chert flakes were recovered from the sandy gravel lense of Unit 2, but no fossils have been recovered from this unit so far. Depths of objects indicated in Fig. 68 correspond with the scale bar to the left. The base of the siltstone layer of Unit 1 is inclined in western direction (downwards towards the spectator). 3 m west of the profile this boundary occurs at a depth of ca. 1.45 m below the zero reference level.

Taphonomy of FVL Mata Menge — The *Stegodon florensis* fossils excavated from Unit 1 at Mata Menge tend to be rather poorly fossilized. For example, the materia spongiosa of the epiphyses of a femur and humerus from the silty upper interval of Unit 1 has not been preserved, and the superficial materia compacta of the epiphyses is poorly fossilized. A dark halo in the sediment marks the original surface boundary of the bone, indicating that the bones were complete prior to burial. Two tusk fragments, which had been exposed partly prior to deposition of Unit 2, were found heavily fragmented in the sediment. These observations suggest that bones with a low density and/or juvenile bones may have disappeared from the site after burial.

In Table 8 the *Stegodon florensis* fossils from the localities Ola Bula, Boa Leza, Menge Ruda, Dozo Dhalu, and Mata Menge are listed. The material includes fossils collected by Verhoeven between 1956 and 1968 (and described by Hooijer, 1957b, 1967, 1972a) and material collected by Hooijer in 1970, by Sondaar in 1980 and by our own team between 1991-1994. As there was not sufficient time for preparation of all the fossil material from Mata Menge after the last fieldwork period, some elements that are listed in Table 8 have to remain without further description in chapter 6. Likewise, most of the fossil material excavated at Dozo Dhalu in 1994 awaits examination as well. It can not be excluded that the list of *S. florensis* fossils from the Verhoeven collection, which are also included in Table 8, is incomplete. Some of the material collected by Verhoeven may not have reached Hooijer for study. Some of the *Stegodon* fossils had ended up in the Museum Blikon Blewut, pertaining to the Roman Catholic Theological College at Ledalero near Maomere. This museum was largely destroyed during the 1992 earthquake in East Flores. Furthermore, it followed that Hooijer selectively treated the more or less complete material in the Verhoeven collection, and that small bone fragments, like for example costa fragments, have been omitted. Part of the Flores collection has been sent back to Indonesia, but the present depository is not known.

For Mata Menge all the *S. florensis* bones excavated in 1992 and 1994 are grouped per sublayer of Unit 1 (Table 8/C3-C4). The coordinates of these bones, 37 in total, were recorded in most cases. The coordinates of the highest point of the bone as it laid in the sediment are included in this list. In addition, there are 10 fossil specimens from Mata Menge from the Verhoeven collection (Table 8/C5), which were described by Hooijer (1972a).

Most excavated bones originate from the transition between the lower sandstone interval and the upper siltstone interval (larger bones were found with their base in fine sandstone and their top in sandy siltstone), or from the upper siltstone interval (14 and 13 out of 37, respectively). The lower sandstone interval yielded only 6 stegodont fossils, while of the 5 remaining specimens the level was not recorded. Larger amounts of bones were recovered from the siltstone interval despite the fact that the total volume of siltstone removed was lower than the volume of sandstone removed during the excavation (c. 7.3 m^3 of siltstone versus c. 10.5 m^3 of sandstone). Using these values, the bone densities can be estimated at 3-5 bones/m^3 for the siltstone interval and less than 1 bone/m^3 for the sandstone interval.

A similar distribution was found for the positively identified artefacts, which appeared to be concentrated at the transition between the lower sandstone interval and the upper silty interval of Unit 1. Most stone fragments positively identifiable as artefacts originated from Unit 1 (9 in total, in addition to 5 possible artefacts). Of these 9 artefacts, 2 were derived from the lower sandstone interval of Unit 1 and 6 from the upper siltstone interval of Unit 1 or from the transition between sand and siltstone. Of 1 artefact the coordinates were not recorded, but it certainly originated from Unit 1 as was indicated on the sample bag. Only 2 positively identified artefacts and 1 indeterminate artefact came from Unit 2. However, it must be noted that the total volume of sediment removed from Unit 2 has been much less (c. 1.6 m^3) than from Unit 1 (17.8 m^3). The artefact densities can be given as follows: sandstone interval of Unit 1: 0.3 artefacts/m^3; siltstone interval of Unit 1: 0.8-0.9 artefacts/m^3; Unit 2: 1.2 artefacts/m^3.

Stone fragments that could not be positively identified as artefacts, amongst them pebbles and angular stone fragments, were occurring more frequently in the sandstone interval, though they were also recovered from the siltstone of Unit 1.

Apart from the vertical differentiation of bone and stone concentrations, there is also a horizontal differentiation. The relatively dense concentration of bones and artefacts, vertically occurring in the siltstone interval and at the transition between the sandstone and siltstone intervals of Unit 1, was found in the most northern quadrants (Fig. 68).

Comparison of the Mata Menge *S. florensis* fossil assemblage with the *S. sondaari* fossil assemblage from Tangi Talo shows that the percentage of dental material versus postcranial elements is relatively low at Mata Menge, while at Tangi Talo dental elements are over-represented. In Mata Menge 7 (18%) out of the in total 38 *Stegodon* fossils represent molar or tusk remains. Of the in total 73 dwarf *Stegodon* fossils excavated at Tangi Talo, 48 (66%) represent dental elements. The MNI at Tangi Talo is 12, while at Mata Menge the MNI is 2 or 3.

The collected data are still limited, and more extended excavations are required to get a better picture of the bone accumulating circumstances at Mata Menge. A few remarks may be made, however. It seems that bone removal prior to burial has been limited at Mata Menge compared to the *Stegodon* bones at Tangi Talo. Some damage to the bones may have been caused by trampling, but contrary to Tangi Talo, damage to the bones at Mata Menge seems to have taken place mainly after sediment coverage, due to poor fossilization circumstances, at least in the silty upper interval of Unit 1. The smaller bone fragments from the lower sandstone interval of Unit 1 may have been transported over considerable distances by water currents, but water transport in the upper siltstone interval was probably limited as indicated by the fine-grained sediments.

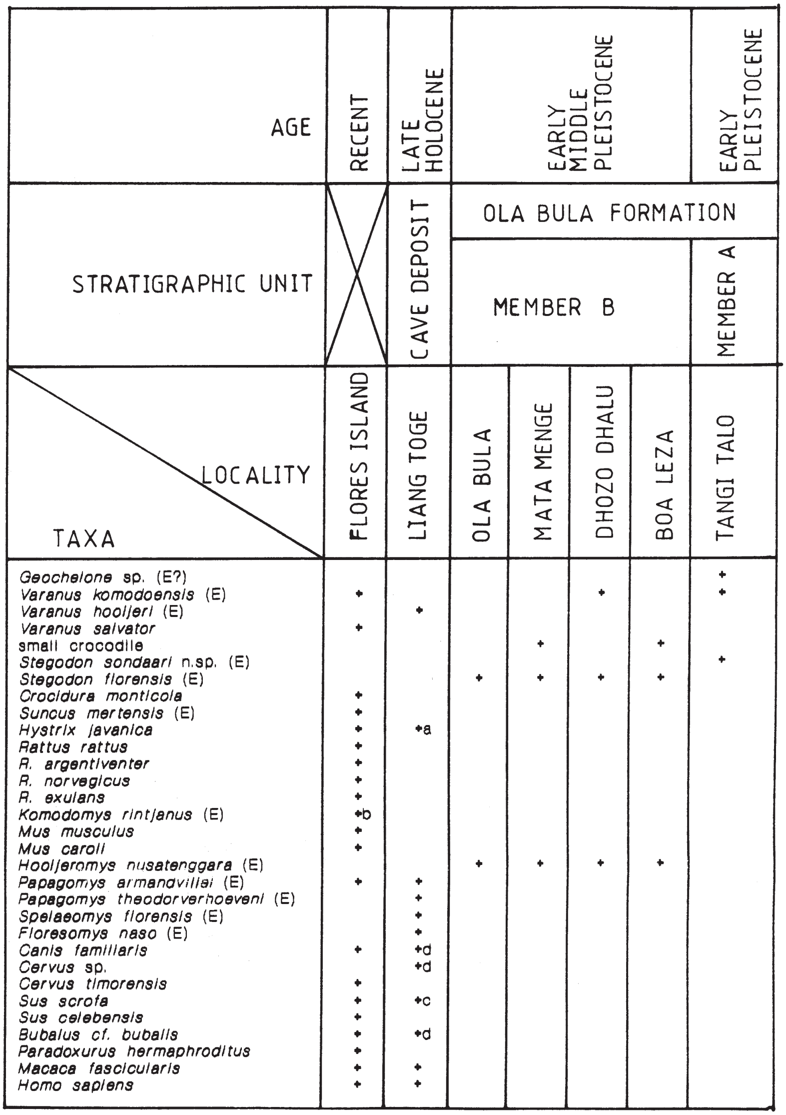
Perhaps the most important conclusion is that artefacts and *Stegodon* fossils do occur associated in the same layer. It is certainly too premature to assume any direct relation between the bone accumulation and the stone artefacts. For example Haynes (1991: 141) found stone tools associated with massive bone accumulations around various water seeps in the Kalahari. However, the bone accumulations could be shown to have originated non-culturally during a period of severe drought.

Faunal succession of Flores

The fossil faunal assemblages from the various localities are represented in Fig. 70. The FVL at Tangi Talo is the only one that yielded the *Geochelone-Stegodon sondaari* sp. nov. association. Besides these two species, also remains of *Varanus komodoensis* and a small crocodile were recovered from the same layer. No artefacts have been found in the fossiliferous layer at Tangi Talo or in the surrounding sediments of Member A in which this layer occurs. The fauna from Tangi Talo is tentatively called Fauna A.

The fossiliferous layers at the localities Ola Bula, Boa Leza, Mata Menge and the recently discovered Dhozo Dhalu on the other hand are all fluvial sandstone and siltstone layers pertaining to Member B. Neither *S. sondaari* nor *Geochelone* fossils have been found in Member B so far. Instead, all larger fossil fragments can be attributed to *Stegodon florensis*. In addition, fossil remains of the giant rat *Hooijeromys nusatenggara* have been found at Mata Menge, Ola Bula (Musser, 1981) and Dhozo Dhalu, in sediments pertaining to Member B. At Mata Menge also a few teeth of a small crocodile were recovered, while at Dhozo Dhalu a single tooth of *Varanus komodoensis* has been found in association with the younger fauna and artefacts. This still extant species seems to have been the only element from the older vertebrate fauna that continued into the younger fossil fauna and even in the extant fauna of Flores (Auffenberg, 1981). The fossil fauna from Member B of the Ola Bula Formation is tentatively called Fauna B.

The colonization of the island by humans, as evidenced by the stone artefacts, coincides with a faunal turnover on the island. An endemic insular fauna with a giant tortoise and a pygmy *Stegodon* was replaced by an endemic insular fauna with a large to medium-sized *S. florensis* and a giant murid. This younger fauna is associated with



AGE	RECENT	LATE HOLOCENE	EARLY MIDDLE PLEISTOCENE				EARLY PLEISTOCENE
STRATIGRAPHIC UNIT		CAVE DEPOSIT	OLA BULA FORMATION				
			MEMBER B				MEMBER A
LOCALITY / TAXA	FLORES ISLAND	LIANG TOGE	OLA BULA	MATA MENGE	DHOZO DHALU	BOA LEZA	TANGI TALO
Geochelone sp. (E?)							+
Varanus komodoensis (E)	+				+		+
Varanus hooijeri (E)		+					
Varanus salvator	+						
small crocodile				+		+	
Stegodon sondaari n.sp. (E)							+
Stegodon florensis (E)			+	+	+	+	
Crocidura monticola	+						
Suncus mertensis (E)	+						
Hystrix javanica	+	+a					
Rattus rattus	+						
R. argentiventer	+						
R. norvegicus	+						
R. exulans	+						
Komodomys rintjanus (E)	+b						
Mus musculus	+						
Mus caroli	+						
Hooijeromys nusatenggara (E)			+	+	+	+	
Papagomys armandvillei (E)	+	+					
Papagomys theodorverhoeveni (E)		+					
Spelaeomys florensis (E)		+					
Floresomys naso (E)		+					
Canis familiaris	+	+d					
Cervus sp.		+d					
Cervus timorensis	+						
Sus scrofa	+	+c					
Sus celebensis	+						
Bubalus cf. *bubalis*	+	+d					
Paradoxurus hermaphroditus	+						
Macaca fascicularis	+	+					
Homo sapiens	+	+					

Fig. 70. Stratigraphic occurrences of fossil and (sub)Recent terrestrial vertebrate taxa from Flores. Information concerning the Recent mammals of Flores is from Musser (1981). Information concerning the subfossil mammals from Liang Toge and other caves is taken from Hooijer (1967) and Musser (1981). Radiocarbon dating of Liang Toge deposits gave an age of 3550 ± 525 years as reported by Jacob (1967). Domestic animals recently occurring on Flores but not known from subrecent cave deposits, such as goats and cats, have been omitted. Bats have also been omitted from the scheme. E = endemic species. a: Subfossil remains were originally determined by Hooijer (1967) as *Acanthion brachyurus*. b: present occurrence of *Komodomys rintjanus* on Flores is not reported but this endemic species is still extant on the islands Komodo and Rinca. c: The suid fossils from Liang Toge and other caves on Flores were originally determined as *Sus scrofa* Hooijer (1967), but may belong to feral or domestic *Sus celebensis* (Grooves, 1981). d: species not recorded from Liang Toge, but its presence has been reported by Hooijer (1967) in other sub-Recent cave deposits from Flores .

artefacts at the localities Mata Menge and Boa Leza, indicating the co-occurrence with humans. This fauna in turn, was replaced by a Subrecent to Recent Fauna, which was presumably partly introduced by humans. The Late Holocene species list in Fig. 70 is based on material excavated by Verhoeven from the abri site Liang Toge (West Flores, near Warukia). He also excavated various other cave and abri sites, including Liang Michael, Liang Melima, Liang Momer, Liang Nintal, Liang Panas, Liang Rundung, Liang Toge, Liang Wakar, Liang X and Nderuk. The material from these sites was determined by Hooijer (in: Verhoeven, unpublished report, 1950; Hooijer, 1957b, 1967), Brongersma (1958: varanids), and Musser (1981: murids). Apart from the genus *Rattus* all murids appeared to represent endemic species of Flores. Jacob (1967) gives a date of 3550 ± 525 BP for Liang Toge. The material from different caves might vary considerably in age, though it is expected that most if not all material is of Late Pleistocene or Holocene age. The Recent mammalian fauna in Fig. 70 is based on Musser (1981). Chiroptera have been omitted from both the Recent and Subrecent faunal lists, while various *Varanus* species presently occurring on Flores have been included, based on the herpetofauna list provided by Auffenberg (1981). Most if not all large mammals in the Subrecent and Recent Fauna lists were probably introduced by humans, like pigs, deer and *Macaca*. The same holds true for the various *Rattus* species. The endemic murids must have evolved locally. Stegodonts, tortoises and *Hooijeromys nusatenggara* are entirely absent from the Subrecent cave deposits.

6. Description of the *Stegodon* remains from Flores

Introduction

To date, two *Stegodon* species can be distinguished on Flores. Remains of a dwarf *Stegodon* were collected by a team consisting of collaborators by the Institute of Technology at Bandung, The Institute of Earth Sciences at Utrecht, and the Museum of Natural History at Basel, in 1980. The fossils were found at the locality Tangi Talo. The fossil material of this pygmy *Stegodon* collected subsequently by our own team justifies the erection of a new species, *S. sondaari* sp. nov. Prior to 1980 this dwarf *Stegodon* from Flores was only known from a pair of isolated milkmolars from unknown stratigraphic position.

The remains of a larger *Stegodon* from the Soa Basin had been known since 1956 through the discoveries of Theodor Verhoeven. During our study it became evident that all his localities and some newly discovered ones yielding this larger *Stegodon* pertained to the fluviatile Member B of the Ola Bula Formation. The material was originally attributed to *S. trigonocephalus florensis* by Hooijer (1957a, 1967a, 1972a). The Flores subspecies he considered as a slightly more advanced variety of the Javanese *S. t. trigonocephalus*. Below the Flores stegodont will be given the status of a distinct endemic species, *S. florensis*.

Stegodon sondaari sp. nov.

Pl. 11, figs. 1-6; Pl. 12, figs. 1-5; Pl. 13, figs. 1-3; Pl. 14, figs. 1-6; Pl. 15, figs. 1-4; Pl. 16, figs. 1-5; Pl. 17, figs. 1-6.

pygmy *Stegodon*; Hooijer, 1964c: 49, fig. 1.
Stegodon cf. *timorensis* Sartono; Hooijer, 1972a: 13.
Stegodon sompoensis Hooijer; Hooijer, 1975: 53.
dwarf *Stegodon*; Sondaar, 1987: 162.
Stegodon species C; van den Bergh et al., 1992: 38.
pygmy *Stegodon*; Sondaar et al., 1994: 1258-9.

Holotype — The partial mandible with both M_1s, M_2s and the uncompleted sinistral M_3 (GRDC TT-3837; Pl. 13, figs. 1-3), excavated in 1992 by Reinier van Zelst at Tangi Talo, are designated here as the holotypes of *Stegodon sondaari* sp. nov.

Hypodigm — Amongst the material collected in 1992 and 1994 there is also the upper dentition of the same individual as the holotype mandible. This upper dentition, found as isolated teeth, consists of a dextral (TT-4035) and sinistral (TT-4037) M^1 and a dextral (TT-4031) and sinistral (TT-4030) M^2. These, and all other dental, cranial and skeletal elements housed in the collection of the GRDC, with collection numbers starting with TT are paratypes. Paratypes are listed with their collection numbers in Table 7. Further there are two lower dP_3s of one individual figured and described by Hooijer (1964c), but their present depository is unknown. In addition there is an M^2, 1 atlas, 2 vertebrae thoracales, 4 processus spinosus, and several isolated molar ridges, collected in 1980 at Tangi Talo by Sondaar. These are presently stored in the collection of the NNM.

Type locality — All material collected in 1980, 1992 and 1994 originates from the boundary between a pumice layer and a silty clay layer (Fig. 66). This level pertains to Member A of the Ola Bula Formation and is situated 6 m above the unconformable contact with the Ola Kile Formation (Fig. 65) at Tangi Talo, Ngada District, Flores, East Nusatenggara Province, Indonesia. Co-ordinates are 8°41'S and 121°7'E. *S. sondaari* sp. nov. has not been recovered from other, known localities so far.

Age — Based on palaeomagnetic dating techniques the fossiliferous horizon at Tangi Talo has been shown to possess a reversed polarity and can be placed below the Matuyama-Brunhes boundary (Sondaar et al., 1994). A late Early Pleistocene age is inferred.

Derivatio nominis — The species is named in honour of Dr Paul Y. Sondaar, who dedicated much of his scientific research to the study of fossil island faunas.

Diagnosis — A dwarf *Stegodon* with linear dimensions half the size of *S. t. trigonocephalus* from Java. The ridge-crest formula is as follows:

$$\text{dP2: }\frac{\text{—}}{\text{—}}\quad \text{dP3: }\frac{\text{—}}{6}\quad \text{dP4: }\frac{x6x/x7/7x}{-5x}\quad \text{M1: }\frac{x6x}{-5}\quad \text{M2: }\frac{x6x/x7/x7x}{x8/x8x}\quad \text{M3: }\frac{-{}^{1}/_{2}5x}{x8}$$

Cheek-teeth rather hypsodont for a *Stegodon* (hypsodonty indices for upper molar ridges varying between 59 and 90, lower teeth ridges between 70 and 92). Width and height of the last three molars within the same range, but upper molars slightly wider than lower ones. Largest width of the ridges occurs at the base, lateral and medial borders only weakly tapering in apical direction. Amount of tubercles per ridge variable between 5 and 10, the adaxial ones being slightly taller than the abaxial ones, giving a convex apical border in unworn ridges. Median cleft usually only developed anteriorly, and more frequent in lower than in upper molars. Wear pattern initially without median expansions. Upon further wear, the anterior and posterior enamel borders usually show 2 expansions, corresponding with the two central conules. In a more advanced stage of wear, these two expansions usually amalgamate to 1 weakly developed median expansion on the anterior and posterior enamel border of the enamel loop. ET of the last three molars is within the same range and relatively thick (ET = 2.8-4.3 mm). Scalloped enamel folding, enamel folding usually moderate, with a low amplitude (less than one-third of the ET). Enamel folding frequency tends to increase near the crown base. Enamel is double-layered, showing stepwise wear pattern. The outer enamel layer comprises c. 50% of the total ET. 3D enamel of the inner enamel layer is relatively weakly developed, comprising 0 to 20% of the total ET. Cement moderate, usually leaving the tubercles and ridge flanks free. Molars relatively large in proportion to the jaws. Anterior region of the horizontal ramii enlarged and thickened, providing space for an anteriorly expanded molar rootmass. Very short symphysis lacking a protruding rostrum. The atlas is dorso-ventrally compressed.

Differential diagnosis — S. sondaari differs from *S. timorensis* Sartono, 1969 in having on average slightly smaller mandible and molar dimensions (though overlap in molar W exists between the two species), less ridges on the M2 and M3 and relatively thicker, less folded enamel. The mandible of *S. timorensis* has a protruding symphysis, and does not have a thickened and enlarged horizontal ramus in front. It possesses smaller teeth relatively to the overall mandibular dimensions. The atlas of *S. timorensis* is less dorso-ventrally compressed as in *S. sondaari*, and resembles more the atlas of *S. trigonocephalus* Martin, 1887 in this aspect.

A dwarf *Stegodon* mandible fragment from Sambungmacan (Central Java), recently described by Aziz & van den Bergh (1995), has similar dimensions as the holotype mandible of *S. sondaari* sp. nov., but it can not be determined with certainty whether the molar present in this mandible represents an M_1 or M_2. Except for the slightly lower hypsodonty and smaller enamel thickness in the molar of the Sambungmacan mandible, which has not yet been designated a species name, there are no other morphometric differences with the M_2 of *S. sondaari*.

S. hypsilophus Hooijer, 1954, also known from Java, has a larger size and relatively thicker enamel than *S. sondaari*, but is similar in hypsodonty. *S. trigonocephalus* Martin 1887, *S. aurorae* Matsumoto, 1918, *S. florensis* Hooijer, 1957, and *S. sompoensis* Hooijer, 1964 are larger than *S. sondaari*, and all possess more ridges in homologue molars. Except for *S. florensis* and *S. aurorae*, their molar ridges are generally less hypsodont than in *S. sondaari*, though some overlap exists. All other mainland *Stegodon* species not mentioned here are of superior size and have different plate formulas compared to *S. sondaari* (Table 38).

Description and comparison of the material

Unfortunately no significant skull material of *Stegodon sondaari* sp. nov. has been found so far, but reasonable numbers of complete molars from the locality Tangi Talo on Flores are available now. The best material consists of a mandible, of which the sinistral ramus is almost complete including the condyle. The upper dentition of the same individual is also preserved as isolated molars. The dental material will be described first, followed by the mandibles and postcranial remains of the dwarf *Stegodon* from Flores. All identifiable material is listed in Table 7. All specimens with collection numbers starting with the lettercode TT are presently housed in the GRDC Collection. Additional material collected by Sondaar is housed in the NNM collection.

Dental elements — The 1992-1994 collection contains 37 molars and molar fragments. Of 24 specimens the rank of the molar can be positively identified. In addition, there is one M^2 in the Sondaar collection. Amongst the 25 identifiable molars 10 constitute pairs of opposite homologue molars or milkmolars. On 12 specimens length measurements could be taken. Except for the dP^2, dP_2, and dP^3, all molar elements are represented in the collection. Summary biometrics of the molar material is given in Table 35.

dP_3: n = 3 (GRDC: TT-4044. Hooijer, 1964c: fig. 1 (1 pair)) The specimens figured by Hooijer (1964c), pertaining to one individual, are reported to bear 6 ridges. However, it is not clear from the photographs if incompletely developed half-ridges are present or not. Our own specimen, of the left side, is incomplete in front (Pl. 11, figs. 1-2). Preserved are $-^1/_2 4x$ ridges, all very worn. The posterior root is largely preserved over a length of 19 mm and the milkmolar is broken just in front of it. In the specimens described by Hooijer the anterior two ridges are placed above the smaller anterior root, which suggests that in our broken specimen originally also 6x ridges were developed. The length and maximum width in both complete specimens measured 28 mm and 18 mm respectively, while the narrower frontal portion measured 14 mm transversely (Hooijer, 1964c). The maximum width in our specimen is 15.7 mm, occurring at the penultimate ridge. The crown is strongly curved, leading to a LF of 16.6 lingually and 19.1 buccally. The ridges are worn down to such a degree that the dentine inside the enamel loops coalesces along the medial axis of the crown. What is left of the enamel is hardly wrinkled and varies in thickness between 0.8 and 1 mm. On the buccal and labial sides of the crown the enamel shows clear vertical grooves, which is characteristic for milkmolars.

dP_4: n = 1 (GRDC: TT-3835) This is a sinistral, incomplete specimen that is broken in front, leaving -5x ridges preserved (Pl. 11, figs. 3-4). What is left of the molar measures 44 mm in longitudinal direction. The maximum width occurs at the penultimate ridge and amounts to 25.7 mm. All preserved ridges are worn. The dentine inside the enamel loops is constricted by the enamel along the median axis of the crown, which is reminiscent of an originally well developed median cleft. In each ridge the two adaxial conules on both sides of this median cleft are markedly stronger developed than the labial and buccal conules, resulting in weak double sinuses on the anterior and posterior margin of the enamel wear patterns. This pattern is also frequently developed in other stegodont molars. The lingual side of the crown is convex, giving a lamellar frequency of 12.2, while the concave buccal side has a lamellar frequency of 15.5. Like in the dP_3 the enamel on the buccal and lingual sides is grooved. The enamel is double layered and shows a step-wise wear on the occlusal surface. It is 1.6-1.7 mm thick and finely wrinkled with a frequency of c. 3 folds along a transverse distance of 10 mm. The amplitude of the folds is always less than 0.5 mm. Part of the posterior root is preserved and also the posterior portion of the curved anterior root. Because the anterior root in stegodonts is never capped by more than x2 ridges, we can deduce that only one ridge is missing in the front, giving a plate formula of 6x or x6x for the dP_4, similar as in the dP_3. The dP_4 can be distinguished from the dP_3 by its markedly larger size (Fig. 71) and the thicker enamel.

M_1: n = 3 (2 paired specimens are in the holotype mandible (TT-3837A+B; Pl. 13, figs. 1-3), both very worn and broken anteriorly; another unworn isolated specimen is lacking the posterior part (TT-3815)). Of both M_1 from the type mandible the sinistral one is the most complete. There can be no doubt concerning the rank of this molar as its size is considerably larger than the dP_4, and two molars are in place behind it, leaving only the possibility of an M_1. The anterior portion was shed during life and the molar as far as preserved is located in front of the mandible constituting the largest portion of the occlusal wearsurface. In total -5x worn ridges are left with a tiny posterior remnant left of the ridge VI. Ridge V is worn down to the root, while ridge I is very worn. The greatest width (W) occurs at ridges IV and V, measuring 39.9 mm. The width decreases slightly backward to 36.2 mm on the last ridge (including cement), thereby differing from the dP_4, which is broadest posteriorly. Cement is abundant on the lingual and buccal sides. The preserved length measures 68 mm. The lamellar frequency is 8.5 on the lingual and 9.0 on the buccal side, giving a LF value of 8.8. The worn enamel shows stepwise wear and ranges in thickness between 3.4 and 3.7 mm. The scalloped enamel contains 4 to 6 folds per cm with an amplitude less then one-third of the enamel thickness. With wear the two adaxial conules of the least worn ridges appear slightly wider in antero-posterior direction as compared with the abaxial conules, similar as in the dP_4. The occlusal surface is slightly concave.

There is another lower molar fragment in the collection, of which the posterior part is missing. All 5 preserved ridges are unworn. Based on its relative small width (38.9 mm in ridge 5) this fragment is thought to represent an M_1 (Fig. 71), but there remains a small possibility that it represents a small M_2. Its lamellar frequency is 8.3 on the lingual and 10.0 on the buccal side, giving a LF of 9.2. The h/w index varies between 85 and 92 in the ridges 2 to 5. The unworn ridges possess 4 main conules and 3 smaller accessory conules. The broken anterior root supports $x1^1/_2$ ridges.

M_2: n = 5 (a pair of complete and slightly worn M_2 belong to the holotype mandible TT-3837 (Pl. 13, figs.1-3)). Further there are three isolated specimens, one of which is complete and slightly worn (TT-3816; Pl. 14, figs. 3-4). The remaining two are worn and lacking a small anterior part (TT-4028 and TT-4029, the latter is figured in Pl. 14, figs. 5-6)) The two paired M_2 from the mandible differ slightly in morphology. The sinistral one has x8 ridges, while the dextral one possesses an extra posterior conule, giving a plate formula of x8x. In addition, the sinistral specimen has the buccal side of the valley between ridges 6 and 7 closed by an accessory conule of 14 mm high, an aberration reminding of the more frequent occurrence of such conules in *Stegolophodon* (e.g. the holotype M_3 of *Sl. lydekkeri* from Borneo (Medway, 1973: pl. XXVI) or the holotype M_3 of *Sl. nasaiensis* from Thailand (Tassy et al., 1992: pl. 1, fig. D)).

The number of ridges in specimen TT-3816 is also x8x. Specimen TT-4029 is half-worn and has $-^1/_27$ ridges preserved. As the anterior root is preserved completely it can be concluded that at most $x^1/_2$- ridges are missing, which would result in a plate formula of x8. The remaining specimen has $-^1/_26$x ridges preserved. Length of the

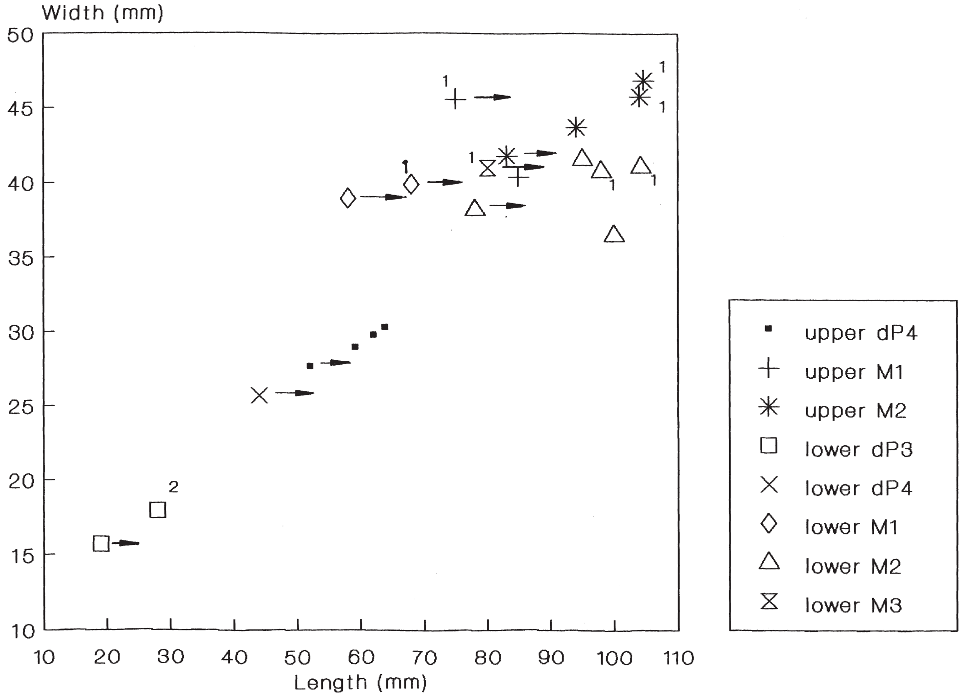


Fig. 71. Scatterdiagram of the Length and Width measurements of the various *Stegodon sondaari* molars from Tangi Talo. Data points with arrows indicate the length of incomplete specimens as far as preserved; the maximum Width could be measured in these specimens. Datapoints marked by '1' represent molars from one individual (molars of the holotype mandible plus associated upper dentition). Data point marked by '2' represents the sinistral and dextral lower dP_3 described by Hooijer (1964c).

complete specimens varies between 98 and 104 mm. The maximum width ranges between 36.5 and 41.6 mm, which matches the width range for the M_1 (Fig. 71).

The sinistral ramus of the mandible is preserved along the buccal side and it can be seen that of the M_2 six ridges had originally emerged from the alveole, 3 of which are lightly worn. The M_2 emerges from the alveole in a lingually inclined fashion, resulting in a wear-surface that is more advanced buccally than lingually. This is also the case in the dextral M_2 of the same mandible, and both teeth are strongly curved with the convex side lingually. The anterior ridge of both M_2s is divided by a median cleft, which is not present in the less worn 2nd and 3rd ridges. The anterior half-ridge is asymmetrically placed at the buccal side of both teeth. The lamellar frequency of both M_2s is 7.8 (sin.) and 8.0 (dex.) on the lingual side and 10.1 and 10.5 respectively on the buccal side. The remaining M_2 specimens show similar strong curvature in transverse direction, except the most incomplete specimen, which has a lamellar frequency of 9.1 lingually and 9.3 buccally. The LF values of the 5 specimens range between 8.6 and 9.4, similar as the LF range in the M_1. The h/w index of individual ridges varies between 73 and 89 (excluding the first and last fully developed ridges), overlapping the h/w indices of the M_1. The ET is similar as in the M_1, ranging between 2.9 and 3.7 mm. Enamel is clearly double-layered, scalloped, and exhibits a stepwise wear pattern. Enamel folding comprises 2-5 folds per 10 mm with an amplitude of less than 0.5 mm. Valleys are filled with cement and in the mandible specimens the internal and external surfaces are covered with cement as well. In all specimens where this is visible, the valley bottoms as seen in internal or external view are quite open and in some cases even U-shaped rather than V-shaped. The V-shaped valley morphology is generally considered as being characteristic for stegodont molars (Osborn, 1943; Maglio, 1973), but this character seems to loose its value in the relatively high-crowned pygmy stegodont molars, as was noted by Sondaar (1984). In the island dwarf stegodonts the molar ridges have lost their typical 'roof'-shape for which the genus received its name in the first place, and instead the ridges resemble more the laminae of elephantid molars. While mainland stegodontidae are quite conservative in their brachiodonty, the island dwarfs show a parallel evolutionary trend with the elephantidae in becoming high-crowned, and also the valleys in between ridges become U-shaped.

Roots are well preserved only in the most worn isolated specimen (Pl. 14, figs. 5-6). The external portion of the anterior root is curved and slightly pointing transversely, while all other roots are fused into a single backwards pointing root-mass. The more fragmented roots of the type specimens have a similar morphology. Here the anterior root carries x$1^1/_2$ ridges, while in an other specimen with only the anterior root partly preserved, x2 ridges are placed on the anterior root.

The crown-base lies more or less in a single plane in the M_2s from the mandible, but is clearly concave towards the crown in the remaining M_2 specimens. In all worn specimens the occlusal surface is concave as is normal in lower molars.

M_3: n = 2 (One sinistral incompletely formed M_3 occurs in the holotype mandible (TT-3837A; Pl. 13, fig. 3). The other specimen consists of a completely worn out fragment, of which nothing of the enamel is left (TT-4041)). The M_3 from the mandible has not yet erupted from the alveole and only the anterior x5 ridges are fused, while 3 isolated and incompletely mineralized ridges were found still present in the alveole. The smallest posterior one, in which a thin layer of enamel has already been formed, has a transverse width of only 25 mm, while the largest width of 41 mm occurs at ridge 3. This small ridge therefore must represent the last one, and the plate formula would be x8, a similar number as in the M_2. This is remarkable as in other stegodonts the M3 has a higher number of ridges than the M2. As the M_3 from the mandible is not yet fully fused, no length measurements can be given. The left mandibular ramus is broken away along the internal surface and only the buccal side of the molar is exposed. The lamellar frequency along the buccal side is 9.8, which should be larger than the average LF value of the tooth due to the transverse curvature. The width measurements can only be estimated. The maximum width occurs at ridge 3 and is approximately 41e mm, similar as the M_2 in front of it. The anterior ridge and the anterior half-ridge are curved backwards. The ridges possess 7 conules, 4 of which are larger than the remaining conules. Roots are not yet developed.

The second M_3 fragment is completely worn down. The wear surface is concave but smooth and nothing of the enamel crown is left. In fact only the posterior root-mass is preserved. It most likely represents a last molar as this is the only one that wears down to such a degree as in this specimen, without being shed.

dP^4: n = 4. (all complete specimens; 2 specimens (TT-4033 and TT-4034) form a pair in a beginning stage of wear (Pl. 11, figs. 5-6); both remaining specimens are half worn, one of which is isolated (TT-4032; Pl. 12, fig. 3) and one is situated in a maxillary fragment (TT-3836; Pl. 12, figs. 1-2)).

All specimens possess x6x ridges, though the posterior halfridge in the two paired specimens is quite strongly developed and could be classified as a completely developed ridge, which would give a plate formula of x7 (Pl. 11, figs. 5-6). In the other two specimens the posterior halfridge is rather small (Pl. 12, figs. 1-2). The length ranges between 52 and 62 mm, the width between 27.7 and 30.3 mm, the maximum width occurring at the penultimate ridges. Size variation is considerable, the length of the smallest specimen being only 84% of the largest one. The variability in h/w indices is very large. The h/w index of individual ridges ranges between 64 and 69 in the paired specimens and amounts to 90 in the penultimate ridge of the maxilla specimen and 59 in the same ridge of the remaining dP^4. In the latter specimen the slightly abraded third ridge from behind has a minimum h/w index of 66, which falls within the range of the paired specimens.

The dP^4 are not so markedly curved as the lower milkmolars, and consequently the difference between buccal and lingual lamellar frequencies within a single dP^4 is not so large as compared with lower milkmolars. Due to the relatively large size-range amongst the 3 individuals represented, the LF values of individual molars vary considerably between 12.6 and 13.5. Unworn ridges are largely covered with cement but the tips of the conelets are usually visible. Of the two paired specimens the anterior ridge is just abraded. A median cleft is not visible in these specimens, but in specimen TT-4032 (Pl. 12, fig. 3) ridge 3, which is slightly worn, shows a median cleft. In the same specimen a median cleft is not visible anymore in the more worn anterior ridges, indicating that it was not very deep. In the remaining specimen (Pl. 12, fig. 1), which is in the same stage of wear, only the first ridge bears posteriorly a weak indication for the development of a median cleft.

The enamel is somewhat thicker developed as compared to the dP_4, varying between 1.8 and 2.5 mm. Enamel frequency values are between 4 and 5 folds per cm in the two worn specimens, while the enamel amplitude is lower than two-third of the ET in one specimen and lower than one-third of the ET in the other worn specimen figured in Pl. 12, figs. 1-2. Variation in the number of conelets in the unworn ridges is considerable between the various specimens, and ranges between 6 and 10 conelets for the widest posterior ridges. Large parts of the roots are preserved in all specimens. The anterior root can be divided into a cylindrical internal portion, which is directed strongly transversely, and a more platelike external portion, which is inclined straight backwards (Pl. 12, fig. 3). The posterior roots are all fused below the crown into a single large posterior root.

M^1: n = 3 (One is an isolated slightly worn sinistral specimen (TT-4036), the other 2 constitute a worn and anteriorly incomplete pair (TT-4035 and TT-4037; Pl. 14, figs. 1-2); this pair fits to two complete M^2, and together all these elements were found within 1 m from the holotype mandible TT-3837. It is in the same stage of wear and the occlusal surface fits well to that of the mandible dentition. They must have belonged to the same individual).

The length of the isolated specimen, of the sinistral side, is 85 mm. The maximum width of 40.4 mm occurs at ridge 2. In both paired specimens it amounts 45.6 mm at ridge IV (Fig. 71). The h/w indices are less as compared to the M_1, as is usual in elephantoid dentitions, ranging between 61 and 71 for individual ridges.

The first ridge behind the anterior halfridge of the complete specimen is distinct from the normal stegodont morphology in consisting of a buccal and a lingual portion both twisted in clockwise direction (in occlusal view). Details are not visible due to the presence of abundant cement only leaving the slightly abraded tips of the conules free. The more posterior ridges show a regular stegodontine configuration with 6 to 8 conules aligned in a row. The LF ranges between 7.8 and 8.3, which is below the LF range of the M_1. The enamel morphology can only be studied in the worn pair of M^1 (Pl. 14, fig. 1). The ET is 3.0-3.3 mm. The enamel is delicately wrinkled (5-6 folds per 10 mm) with an amplitude of less than 0.5 mm, far less than one-third of the ET. In the enamel loop of the posterior ridge of the dextral specimen there is an irregularity consisting of a single median sinus, which is strongly developed on the anterior side of that ridge only. In the anterior border of the enamel loop of the same ridge of the sinistral specimen, as well as in the other enamel loops of both molars, there are only weak expansions visible along the median axis of the crown.

The unworn specimen has a large part of the roots preserved. The anterior root has its strongest development on the buccal side, pointing straight backward. The smaller and cylindrical antero-internal root points in medial direction. The root configuration of the various M^1 differs with that of the dP^4 in that both anterior roots are fused with the posterior rootmass just below the crown. The crown-base and the occlusal surface are slightly convex.

M^2: n = 5 (There are two pairs, one of which is complete and slightly worn M^2 (TT-4030 and TT-4031; Pl. 14, figs. 1-2). This pair fits to two worn M^1, all of the same individual as that of the holotype mandible. Of the other pair (TT-3814, sinistral and TT-3818, dextral; Pl. 12, figs. 4-5) only the first ridge of the dextral specimen is weakly abraded but damaged lingually; of TT-3814 the ridge 4 is damaged; one isolated specimen from the Sondaar collection (NNM F.BS 4.1) is half worn and incomplete anteriorly). The intact paired specimens both carry x7x ridges and have a length of 104 mm. The number of ridges in the other pair is x6x, or, if classifying the rather well developed posterior ridge as a full ridge, x7. The length of the sinistral specimen is 94 mm. That this pair represents M^2 and not M^1 follows from the wide and intact anterior contact facet of the sinistral specimen. This facet is much too wide to have been in contact with a dP^4. The lingual part of this contact facet is supported by the anterior half-ridge, which is located eccentric as is common in upper molars. The isolated specimen has -6x ridges over the posterior rootmass, indicating that at least one ridge is missing anteriorly on the broken anterior roots. The preserved length is 83 mm. If we add one ridge the total length would be c. 95e mm, suggesting that we deal with an M2 and not an M1 (Fig. 71).

Maximum width occurs at ridges 3 or 4 and varies between 41.8 mm and 46.9 mm amongst the four specimens. The M^2 are less curved in transverse direction as compared to the M_1, resulting in a less marked difference between the lingual and buccal lamellar frequency. The LF varies between 7.6 and 8.8, which is lower or equal as compared to the lower molars of the same rank. The h/w indices of individual unworn ridges vary between 67 and 85, overlapping with the ranges of the M^1 and M$_2$. The L/W ratios are only slightly larger or equal to those of the dP^4 or M^1, while in *Stegodon trigonocephalus* the relative length of the M^2 is considerably larger than the relative length of the M^1 and even more so than the dP^4 (L/W indices varying between 1.79 and 1.96 in the dP^4 and between 1.90 and 2.09 in the M^1; the L/W index in the single M$_2$ amounts to 2.48).

Individual ridges of the various M^2 bear 7-10 conules. The wear patterns show the two adaxial expansions slightly wider in antero-posterior direction than the abaxial portions. Valleys between the ridges are filled with cement leaving the flanks and conules free. The ET varies between 2.9 and 3.8 mm. In slightly worn ridges the enamel is folded with 3 to 5 folds per cm, but in ridges which are half worn or more, enamel folding is weak or absent on the medial and lateral sides of the wear patterns, while two folds or central expansions are well developed in the center of the wear patterns, both anteriorly and posteriorly of each ridge and corresponding with the adaxial conules. The amplitude of enamel folds is less than one third of the enamel thickness.

In the anteriorly worn specimens, the anterior portion of the roots consists of two parts, the smallest of which is developed medially and which points strongly transversely. The anterior portion of the roots carries x2 ridges. The posterior roots are only slightly fused near the crownbase, unlike the posterior roots of the M$_2$, where they are completely fused into a single posterior rootmass. Like in the M^1, the base of the crown as well as the occlusal surface is convex towards the crown, as is characteristic for upper molars in general.

M^3: n = 1 (This is a worn posterior fragment (TT-3856; Pl. 15, fig. 1)). The only M^3 fragment represented in the collection shows the characteristic posterior tapering of the last molar. There are -$^1/_2$5x ridges preserved, of which only the posterior half-ridge, consisting of one conule, is unworn and covered with cement. This M^3 fragment was found broken into several pieces in the sediment. The base of the crown is damaged in most ridges but the width of the ridges can be estimated. The fourth ridge from behind is the most anterior ridge of which the width could be estimated. It is c. 44e mm wide. This estimate is probably a few millimeters less than the original W value of the tooth. The lamellar frequencies measured at ridges IV and V are 6.5 buccally and 7.1 lingually, giving a LF of 6.8, which is the lowest observed value of all teeth examined. The enamel is rather thick, varying between 3.7 and 4.3 mm. The scalloped enamel is double-layered with the inner layer delicately wrinkled with up to 5 folds in 10 mm. The amplitude of these folds is 0.3 mm or less, which is far less than the enamel thickness itself.

Besides the above mentioned identifiable material there are 14 molar fragments of uncertain rank. Most consist of isolated ridges, but 2 represent larger fragments. One is an anterior fragment of a lower molar with all x5- ridges worn (TT-3839). The maximum width of 42 mm occurs at ridge 5. The enamel thickness varies between 3.8 and 4.1 mm. As there is overlap between the width and ET ranges of the last three lower molars, it can represent either of them. Another posterior fragment (TT-3813) is of an upper molar with -$^1/_2$4x ridges, all worn except the posterior half-ridge. Ridge III has a width of 41.8 mm, but the maximum width might have been slightly larger. The enamel thickness varies between 3.2 and 4.1 mm. The relatively low value of the LF (7.2) speaks in favour of an M^3, though the tooth is not markedly tapering.

As follows from the descriptions of the *Stegodon sondaari* sp. nov. molars presented above, the W of the successive molars, M1, M2 and M3, does not increase markedly with increasing molar number. The W of the M_3 in the type mandible is the same as that of the M_2 and only 3% wider than the M_1 in the same mandible. It can be concluded that growth in this pygmy stegodont stopped at an earlier ontogenetic stage as compared to large-sized Elephantoidea, where the average W of the M2 is larger than that of the M1, and where the average W of the M3 is commonly larger than the average W of the M2 (e.g. Tables 31-32). In large-sized stegodonts the jaws continued to grow until very old age, so that molars with successively increasing widths could be allocated.

From the upper dentition associated with the *S. sondaari* holotype mandible it can be observed that upper molars of the same rank as the lowers have approximately the same length as the lowers, but slightly higher W values. The W of the lowers is approximately 90% of the W of uppers. This leads to slightly higher hypsodonty indices and higher L/W indices for the lower molars, a common development in *Stegodon*.

Tusks — There are two more or less complete tusks in the Tangi Talo collection (TT-3887/88 and TT-3819). Further there is a proximal fragment on which the diameter could be measured (TT-3812) and 6 smaller tusk fragments. The most complete tusk, though not the largest one, is preserved from the worn tip to the pulpa cavity (TT-3887/88; Pl. 15, fig. 2). It is considerably curved upward. It measures 180 mm in straight length, while the length measured along the convex ventral surface amounts 201 mm. The tusk is only very slightly tapering and the dorso-ventral diameter near the pulpa cavity (27.1 mm) differs only slightly from the dorso-ventral diameter 10 cm more distally (26.3 mm = 97% of the proximal value). The transverse diameter decreases even less so (25.3 mm proximally versus 25.0 mm halfway the length of the tusk). Only the distal 3 cm are strongly tapering due to the fact that the tip is heavily worn, the ventral surface more so than the dorsal surface, creating an asymmetrical wedge. Of two tusks of *S. trigonocephalus* present in the skull figured by Hooijer (1955b: pl. VI, figs. 1-2), the left one is almost completely preserved. Hooijer (1955b: 53) noted that: ‘it measures 16 by $16^1/_2$ cm in cross section at the alveolar border, and for a length of about 150 cm it projects forward in a gentle upward curve, then it begins to turn outward on its line of projection’. Further he notes that: ‘at 200 cm the cross section is dorso-ventrally compressed, $12^1/_2$ cm horizontally, and 10 cm vertically. At the broken tip, which is 240 cm from the alveolar border, the diameters are 10 cm horizontally, and 7 cm vertically’. Examination of this specimen, housed in the NNM, revealed that the ovally shaped cross section of the distal tip is not compressed, but worn ventrally. This is easily visible at the cross-sectional pattern in broken surfaces, which shows that the successive dentine cones that make up a elephantoid tusk, are cut off by a smooth convex wear surface ventrally, making a V-shaped pattern. The wear surface is not exactly ventrally, but tends towards the external side. Assuming a similar combination of curvature and wear pattern in the *S. sondaari* sp. nov. tusk, this specimen can be regarded as being of the left side.

The most interesting aspect of these *S. sondaari* tusks are a number of constrictions most markedly visible on the ventral and medial surfaces. In addition to these constrictions, the unworn part of the tusk is marked by parallel longitudinal striations, which follow the curvature of the tusk. Furthermore, at regular longitudinal distances of 9 to 16 mm, there are delicate but irregular ribbons of dentine visible, usually more than one and closely spaced, which make sharp angles of c. 80 with the longitudinal striations and which can be traced around the circumference of the tusk. The constrictions, less than half a millimeter deep, correspond with the ribbon marked intervals. The constrictions are only occurring in the middle portion of the tusk, while the spaced ribbon-marked intervals are present from the onset of the worn tip of the tusk to the most proximal part at the pulpa cavity. There is no cementum present on the dentine surface, it was either not deposited or has not been preserved.

Similar topographic expressions on the dentine surface of proboscidean tusks were already observed by Osborn (1910). They are explained as being the surface expressions of growth increments of the successively formed dentine cones deposited in the inner surface of the pulpa cavity (Fisher, 1996). The constrictions on the tusk mark first-order, annual growth increments and are caused by seasonal variations in the rate of dentine deposition. The ring-like ribbons (perikymata) mark second-order (generally fortnightly) increments caused by cyclic physiological depositional cycles.

Annual growth rings are often found in teeth of ectothermic vertebrates, but in endothermic vertebrates annular growth structures are rare except in species living under severe climatic conditions. For example, canines of *Odobenus* are made up of a successive number of dentine cones, which intermittently grow in an annual rhythm (Fay, 1982; Harington et al., 1993). In *Odobenus* the annual growth structures are better developed in males than in females. First order cyclic growth patterns have been found on tusks of *Mammuthus primigenius* (Lister & Bahn, 1994) and *Mammut americanum* (Fisher, 1996), and are thought to correlate with nutritional status and with somatic growth rate: low during winter and higher during spring-autumn.

If such annual incremental structures occur in tusks of tropical elephantoids, such as is the case with the dwarf *S. sondaari* sp. nov., low growth rates are expected to correlate with the dry season corresponding with low food availability and high growth rates with the rainy season, when there is a relative abundance of food. The present-day climate of Flores is strongly seasonal with an extended period of drought during the southeast monsoon. The climate was probably even more seasonal during large parts of the Quaternary when the Sunda and Sahul shelves were exposed at times of low sea level. At least for the last glacial episode there is substantial evidence from pollen records that the region experienced an increased aridity (van der Kaars, 1991). Extreme climatic conditions in combination with habitat destruction on the overpopulated island could have provoked seasonal periods of slow growth during adverse times in the pygmy stegodonts, leading to the above mentioned tusk growth rings. Such seasonal variations in growth have also been noted by Malpas (in: Eltringham, 1982) in African elephants living under stressed conditions. Malpas made a comparative study on diet and physiological condition of three elephant populations in relation to various ecological factors. One of the studied populations in the Kabalega Falls Park had an history of overpopulation and general habitat destruction. Amongst other factors he measured the hydroxyproline-creatinine ratio to determine the instantaneous growth rate during various times of the year. It followed that growth rates were higher in the wet season than in the dry season in the Kabalega elephants, whereas in the population from Rwenzori National Park, where the general conditions were much better, there was no seasonal difference in growth rate.

Thus assuming that the cross-striated intervals on the tusk of the Flores pygmy *Stegodon* mark seasonal growth variations, then theoretically the individual age at death could be estimated. There happen to be 14 intervals marked by striations. The average distance at which these intervals occur along the internal surface of the more distal tusk portion is 11 mm, while proximally the average distance increases to 13 mm. From the most distally visible ribbon ring to the tip of the worn tusk there is 35 mm left in longitudinal direction, which would be equivalent with another $3^1/_2$ years using the average distance of 11 mm. Judging from the distal tapering, probably 1-3 cm of tusk have been completely abraded by wear, so maximally the growth rings of 4 to 6 years would have been lost by wear or abrasion. This gives us an estimated minimum age of 18 to 20 years for this individual. Unfortunately we don't know which molar wear stage corresponds with this tusk, as it was found isolated. The tusk might not belong to a full-grown individual, as there are fragments with a larger diameter present in the collection.

One of these fragments of a larger tusk is a broken proximal fragment (TT-3812) including the pulpa cavity. It has a preserved length of 82 mm and a proximal diameter of 45 mm. This larger proximal fragment is very eroded and does not allow an examination of its surface structures. The other is a tusk preserved over a straight length of 244 mm including the worn tip but lacking the basal portion with pulpa cavity (TT-3819; Pl. 15, figs. 3-4). It is also rather eroded and broken. It was excavated from the topsoil and several fragments are missing. Longitudinal striations are visible on this tusk, but no constrictions or transverse ribbons can be seen macroscopically. While the straight preserved length amounts to 244 mm, the curved length measured along the inferior convex surface is 258 mm. The curvature is oriented in a single plane and in ventral view (Pl. 15, fig. 4) the tusk appears tapering but straight. The transverse diameter most proximally measures 34.2 mm, while 10 cm more distally and halfway the tusk it amounts 28.3 mm, which is only 83% of the more proximal value. Similarly, the dorso-ventral diameter decreases from 34.9 mm proximally to 30.7 mm (= 88% of proximal value) halfway the tusk fragment. So this tusk tapers markedly stronger than specimen TT-3887/88. Though there is no fit, perhaps the eroded proximal fragment with pulpa cavity belongs to the same tusk as they were found close together. If so, the original length of the tusk might have been between 15 and 20 cm longer, giving a total curved length of 40e to 45e cm. Also in this tusk the tip is abraded by wear, over a longer distance ventro-laterally than at the dorso-medial surface, leaving the tip asymmetrical in ventral view (Pl. 15, fig. 4). It therefore represents a sinistral tusk. The remaining tusk fragments are small fragments on which no measurements could be taken.

There are several possibilities to explain the size variation in the Flores tusks: 1) the smaller tusk with well-marked growth rings either belonged to a subadult individual while the larger ones belonged to full-grown animals; 2) the smaller tusk represents a female individual while the larger tusk fragments belonged to males. Sexual dimorphism in tusk size was also found in the pygmy elephant from Sicily, *Mammuthus falconeri* (Ambrosetti, 1968) and is common amongst the Elephantoidea in general; or 3) there was considerable variation in tusk size amongst the pygmy stegodonts due to release of evolutionary constraints on the island. The latter possibility is less probable because all tusks show considerable wear indicating that they were highly functional.

Enamel microstructure — Two molar fragments of *S. sondaari* sp. nov. were cut and various sections were studied under the polarizing light microscope and SEM. One is an upper molar fragment (TT-3813, which represents either an M^1, an M^2, or an M^3). The other specimen examined is an isolated lamella from the 1980 collection. In this specimen the enamel was not yet fully completed near the base. The basal width amounts to 32.7 mm, suggesting that it belonged to either a dP4 or an M1.

In molar enamel of Stegodontidae the outer enamel adjacent to the coronal cementum has a simple structure, in which the enamel prisms are all aligned parallel to each other and perpendicular to the outer surface or slightly directed towards the crownbase. The inner enamel layer is more complex. Here the enamel prisms are inclined towards the occlusal surface, but groups of prisms alternately point in lingual and buccal direction. This decussation of the enamel prisms is visible as the so-called Hunter-Schreger Bands (HSB) under the polarizing light microscope. Prisms of alternating HSB (the so called diazones and parazones) tend to become aligned in one direction towards the boundary between inner and outer enamel, but this direction is still inclined towards the occlusal surface, only changing to a horizontal direction when passing this boundary to the outer enamel layer.

Near the enamel-dentine junction (EDJ), where originally the formation of the prisms started by the outward moving ameloblasts, groups of prisms are interwoven in a more complex way, and HSB cannot be distinguished clearly. This is the 3 dimensional enamel (3D), in which groups of enamel prisms are oriented in all directions away from the EDJ. The transition between the 3D enamel and the HSB enamel sublayers of the inner enamel is irregular. Locally ‘flame-structures’ of the 3D enamel invade the HSB enamel, while in between these ‘flames’ the 3D enamel merges into the HSB enamel over a much shorter distance from the EDJ.

The evolution of the proboscidean enamel structure is characterized by an overall increase in complexity (Kozawa et al., 1986). In *Moeritherium* and *Paleomastodon* the HSB are regular and slightly curved, and occupy c. 65% of the total enamel thickness (Bertrand, 1986). Decussation in this inner enamel layer is horizontal, while in the outer enamel no decussation is developed. In the gomphotheres prism decussation also has a vertical component besides the horizontal component and this 3D enamel is developed close to the EDJ. In the outer part of the inner enamel layer regular HSB are developed. Outer enamel with no decussation occupies 55-60% of the total ET. In the elephants (sensu stricto) the total thickness of the enamel is greatly reduced. However, the 3D layer is comparatively thick, while above all the outer radial enamel layer has been greatly reduced. The complex enamel with a high degree of horizontally and vertically crossing prism directions gives a greater resistance to tensile stresses and cracking in these large grinding herbivores (Pfretzschner, 1992). The Stegodontidae possess an intermediate enamel structure in which the 3D enamel layer has a proportionate thickness intermediate between gomphotheres and elephants, while the outer enamel layer still occupies c. 50% of the ET.

The enamel of *Stegodon sondaari* consists of two macroscopically visible layers of approximate equal thickness, which is generally the case in stegodonts. The enamel in both studied samples of this dwarf is very weakly folded, merely undulating, which is a primitive character. In individual ridges the total enamel thickness is more or less constant in the upper half, but decreases considerably near the crownbase: in the upper molar fragment the enamel thickness (ET) varies between 2.8 and 4.1 mm in the upper half of the lamellae, decreasing to between 2.3 and 2.6 mm near the crownbase. In the isolated ridge studied, the ET near the fully developed upper part lies between 3.2 and 3.4 mm, while near the base the outer enamel layer has not yet been formed completely. Compared to other stegodonts of which the enamel has been examined (*S. trigonocephalus*, *S. sompoensis*, *S. orientalis*, *S. aurorae*), the enamel of *S. sondaari* is characterized by a very weakly developed 3D enamel sublayer, which maximally constitutes 17% of the total enamel thickness. However, over large tracks along the EDJ the 3D enamel is not developed at all in both samples studied, and the average percentage of the ET occupied by the 3D enamel is only 7.9% (15 measurements). At these places prism decussation is also weakly developed and the prisms run regularly from the EDJ towards the boundary with the outer enamel (Pl. 16, fig. 5). The OEL occupies 39% to 56% of the ET (average 48.4%; n = 15). Overall, the enamel is very regular in *S. sondaari*, much more so than the complex IEL structure of *S. trigonocephalus* or *S. sompoensis* (Pl. 16, fig. 6). In *S. trigonocephalus* the OEL occupies 34% to 69% of the ET (average 49.8%; n = 16), similar to that of *S. sondaari*, but the 3D enamel of the IEL is relatively thicker, occupying 7% to 31% of the total ET with an average of 19.4% of the ET (n = 16). Also *S. sompoensis* has a better developed 3D enamel sublayer, which occupies 11% to 43% of the ET with an average of 23.6% (n = 15). In the specimen examined, the OEL is rather thin, occupying only 21% to 47% of the total ET, with an average of 33.1%. Also *S. aurorae* and *S. elephantoides* have a better developed 3D enamel sublayer as compared with *S. sondaari* (qualitative observation only). Of the *Stegodon* species examined, *S. sondaari* appears the most primitive with its very weakly developed 3D sublayer. Also in the relatively weak enamel folding, the enamel of this dwarf appears intermediate between that of the gomphotheres and the stegodonts.

Mandible — The molars of the holotype mandible TT-3837 (Pl. 13, figs. 1-3) were already described above. Here this mandible will be treated in more detail. In addition, there is also a juvenile dextral mandible fragment lacking dentition (TT-4069) in the Tangi Talo collection, and two isolated mandibular symphysis fragments.

Of the mandible TT-3837 the sinistral ramus and corpus are the most complete, including the intact condyle and coronoid process. The medio-ventral part of the ascending ramus is broken away from the base of the horizontal ramus to the mandibular foramen. This leaves the incompletely mineralized M_3 in the half-opened alveole exposed. The symphysis is also completely preserved, but of the dextral corpus only an anterior fragment of the horizontal ramus remains, carrying the worn M_1 and the anterior part of the M_2. Measurements of TT-3837 and some other *Stegodon* mandibles are given in Table 15.

As the dental stage indicates, this mandible belonged to a subadult to adult individual. The M_2s were in a beginning stage of wear, having the three anterior ridges worn, while the anterior part of the completely worn M_1 had already been shed. This dental stage corresponds with stage M1/M2 B in the dental wear age classification of

Beden (1979; see also chapter 8), or with dental age group XIII according to Laws' (1965) scale, both elaborated for the African elephant, *Loxodonta africana*. Of course, when applied to the Flores pygmy *Stegodon*, these dental ages represent relative ages and by no means could the dental age class be tied to a real age as was done for the living *L. africana*. The lifespan of a dwarf stegodont was possibly, but not necessarily, shorter than that of its large-sized ancestor.

The total length of the occlusal wear surface of TT-3837 (developed on both the M_1 and M_2) amounts to 103 mm in the sinistral ramus (in the dextral ramus the anterior part of the M_1 has suffered postmortem damage and the total length of the wear surface cannot be given). The length and also the maximum width of the occlusal wear surface are comparatively large in relation to the other mandibular dimensions, as has been visualized in a log-ratio diagram (Fig. 72) of the measurements presented in Table 15. Besides, there are some characteristics of the mandible that are not encountered in other *Stegodon* mandibles. The anterior region of the horizontal ramii is relatively enlarged. The rounded crista interalveolaris of the ramii descends downward vertically from the anterior border of the alveole to the symphysis, and does not protrude forward as is usual in *Stegodon* mandibles. There is also no forward protruding symphysal rostrum. Instead, the anterior border of the symphysis is situated right in between the anterior borders of the alveoles. The total length of the symphysis (M21) is relatively short as compared to *S. trigonocephalus* (Fig. 72). On the other hand, the anterior portion of the horizontal ramus is relatively stronger built and broader compared to *S. trigonocephalus* as expressed by the relatively large value of measurement M20 (Fig. 72). In this figure it can be noticed that when comparing all measurements of TT-3837 amongst each other, the length (M24) and the width (M25) of the occlusal wear surface are also relatively large. The large size of the teeth and their wear surface seems to be correlated with the widening of the anterior ramus, thus creating more space for supporting the comparatively large teeth. It is well possible that the forward shift of the molars with their roots also caused the forward displacement of the posterior border of the symphysis, which consequently became relatively shorter. The latter tendency of a shortening symphysis is also expressed in the mandible of the dwarfed *S. timorensis* (M21: Fig. 72), though here the symphysis is still placed well in front of the anterior alveolar border.

The changes in mandibular shape encountered in *S. sondaari* sp. nov. may be an adaptation to accommodate these relatively large molars and thus facilitate enlargement of the occlusal wear surface. The alveoles are relatively wider and the width of the molar crowns occupies a relatively broader area of the horizontal ramus. The latter can be easily noted when comparing the occlusal view of mandible TT-3837 (Pl. 13, fig. 1) with large-sized *Stegodon* mandibles in similar aspect (e.g. the *S. trigonocephalus* mandible figured by Hooijer, 1955b: pl. III, figs. 3, 6). Also in *Mammuthus falconeri*, the smallest dwarf elephantoid known to date, the dimensional reduction of the molars was less than for the other skeletal parts (Ambrosetti, 1968; he places '*falconeri*' in the genus *Elephas*). In *M. falconeri* it is even so that the M_2, and particularly the M_3, have such large dimensions that they surpass the receptive capacity of the mandible. The posterior part of the last two molars is still being formed while the anterior laminae are already worn down. In the *S. sondaari* the situation seems less extreme, and the M_3 is already under formation (4 ridges being fused, 4 more having

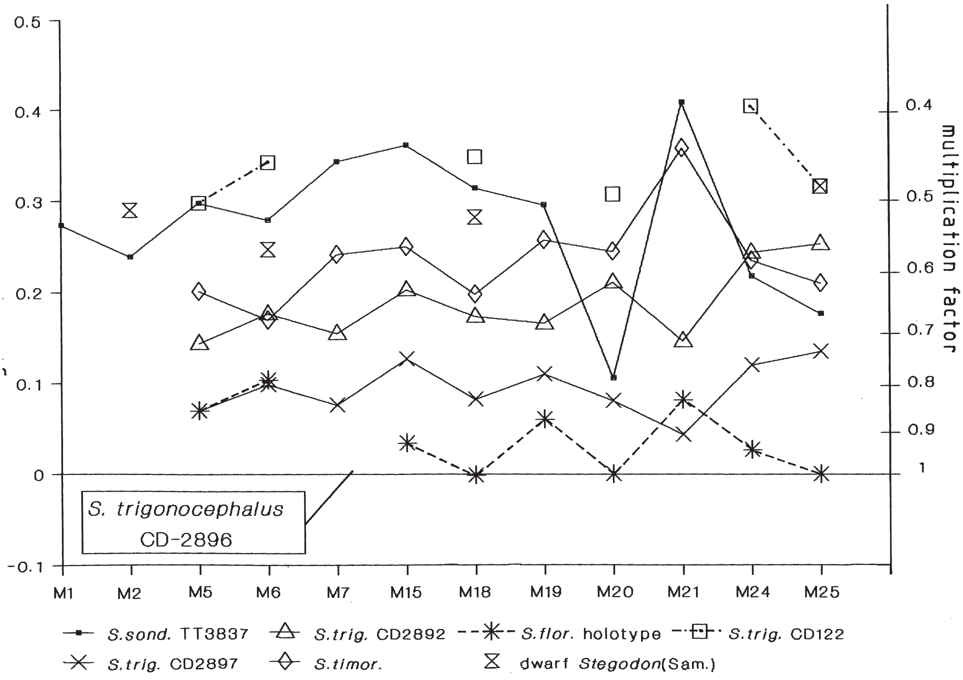


Fig. 72. Comparative log-ratio diagram of measurements taken on the holotype mandible of *Stegodon sondaari* (TT-3837) as compared to several mandibles of *S. t. trigonocephalus* in various ontogenetic stages (with numbers starting with CD), the *S. florensis* holotype mandible from Ola Bula, Flores, the *S. timorensis* mandible from Weaiwe, Timor (this specimen was figured by Hooijer, 1969a: pl. 1), and the dwarf *Stegodon* mandible from Sambungmacan (this specimen was figured by Aziz & van den Bergh, 1995: pl. I). See Table 15 for the original measurements. The zero reference level is represented by *S. t. trigonocephalus* mandible CD-2896 from Trinil, which has the first 2 ridges of the M_3 worn. Dental wear stages of the other mandibles are as follows: TT-3837: first 2 ridges of M_2 worn; CD-2892 (Trinil): first 5 ridges of dP_4 worn; *S. florensis* holotype mandible: first 6/7 ridges of M_3s worn; CD-122 (Trinil?): first 6 ridges of dP_3 worn; CD-2897 (Trinil): first 3 ridges of M_1 worn; *S. timorensis* mandible: first 0/3 ridges of M_3s worn; Sambungmacan dwarf *Stegodon* mandible: first 3 ridges of M_1 (or M_2?) worn.

been partly formed but not yet fused at the base) at the time when the anterior part of the M_2 is being worn (3 ridges being worn). This can be explained by the fact that the total amount of ridges is less than in equivalent molars of *M. falconeri* (x8 to x8x ridges versus x11 to 13x lamellae respectively in the M_2). Besides, in *M. falconeri* the forward extension of the alveoles is less developed than in the Flores pygmy *Stegodon*, thus not using all the potentially available space at the anterior end of the horizontal ramus. The only *Stegodon* species which seems to have a similar enlargement of the anterior part of the horizontal ramus and reduced symphysis is *S. aurorae* Matsumoto, 1918 (Konishi, 1995). This Late Pliocene to Early Pleistocene insular dwarfed species from Japan (shoulder height less than 2.0 m) possessed subhypsodont molars (Taruno, 1991) and like *S. sondaari* also possessed relatively large mandibular molars as compared to the size of its mandible in adult individuals. *S. aurorae* shows a very diagnostic characteristic on the skull, namely the development of an epifrontalonasal fossa, which relate it to the Early Pliocene *S. huanghoensis* Zheng et al., 1975, from China. The latter mentioned is synonymous to *S. zdansky* Hopwood, 1935 according to Saegusa (1987). *S. aurorae* has more ridges (x11x to x13x in the M^3, and x12x to x13x in the M_3) than the Flores pygmy (Taruno, 1991).

The other mandible fragment from Tangi Talo, specimen TT-4069, is a juvenile dextral horizontal ramus with three distinct alveoles but lacking the teeth and damaged laterally. The ramus measures 107 mm as far as preserved. The most anterior alveole is subrounded in shape with a diameter of 6.8-7.7 mm. It must have been of the dP_2 with a single root. The alveole behind it is 25 mm long and 7.6 mm wide in front and widens in posterior direction though the posterior width could not be taken due to the fact that the lateral margin has broken away. The size of this alveole would fit well with the root of the isolated dP_3 described earlier (TT-4044). The margins of the posterior alveole are only preserved anteriorly and partly medially. The anterior width would be at least 16 mm. The minimum transverse thickness of the ramus in front of the anterior alveolar margin (M20) is 16.7 mm. Considering what is left of the symphysis, it can observed that the anterior border of the the most anterior alveole, that of the dP_2, is located well behind the posterior rim of the symphysis, unlike in the holotype mandible. Juvenile elephantoid mandibles generally have a more elongated ramus, which could explain this difference. Though the exact dental wear stage can not be determined, the mandible under consideration would be equivalent with one of the stages I to IV of Laws (1965) as the alveole of the dP_2 is still present in front.

There remain two isolated symphysis fragments on which no measurements could be taken. Their dimensions are similar to that of mandible TT-3837.

Cranial fragments — The only two identifiable skull fragments in the Tangi Talo collection are maxilla fragments. One (TT-3836; Pl. 12, figs. 1-2) is a juvenile dextral maxilla with the dP^4 still in place. The other is a larger but more incomplete sinistral fragment (TT-3817) bearing only the alveole of the antero-lateral root of what was probably an M^1 or M^2 judging from the size of it.

The juvenile maxilla carries a dP^4, which has shifted forward and is half worn. Nothing of the dP^3 nor its alveole remains, while the posterior part of the maxilla fragment is represented by the anterior part of the empty alveole for the M^1. The M^1 had not yet erupted. The maxillary portion of the orbit is broken at the base. The upper termination of the fragment corresponds roughly with the maxilla/frontal suture. The palatin process of the maxillary and the maxillary portion of the tusk sockets are preserved for a large part. Of the dP^4 4 in a total of x6x ridges are worn. The total length of the occlusal wear surface is 38.5 mm. The dental progression would correspond with upper molar stages D3/D4 C or D4 A of Beden (1979). The maxillary portion of the tusk socket has its ventral surface pointing in anterior direction, making a sharp angle of 27 with the occlusal wear surface. This configuration represents the juvenile stage of development, while with aging the tusk sockets normally rotate downwards relatively to the occlusal wear surface, similar as in *Loxodonta africana* (Beden, 1979). Judging from the basal outline of the broken orbit, the latter was dorso-ventrally compressed. In antero-posterior direction the basal outline of the orbit measures approximately 37 mm from the infra-orbital foramen in front to the weak crest merging from the basal orbit in posterior direction, while the dorso-ventral diameter measures only 12.5 mm.

A juvenile skull of *S. trigonocephalus* from Trinil has been figured, in which the dental wear stage is similar as in specimen TT-3836. It is skull No. 203 excavated during the Selenka expedition and figured by Janensch (1911: pl. XXI figs. 1-2) under the name *S. airawana*, a junior synonym for *S. trigonocephalus* (Hooijer, 1955b). From the figure of the dentition (Janensch, 1911: pl. XXII, fig. 1) it follows that of the dP^3 -$^1/_2$4 worn ridges remain and that of the dP^4 the anterior x5- ridges of a total of x7x ridges are worn. The length of the dP^4 in the Trinil and Flores specimens under consideration amounts to 101 mm and 59.2 mm, respectively, the latter having a length which is 59% of the length in the Trinil dP^4. The W measurements of the dP^{4}s are 52.5 mm and 29.0 mm, respectively, the latter representing 55% of the width in the Trinil specimen. The maxilla of the Flores pygmy seems relatively small as it can accommodate only one milkmolar (the dP^4), whereas the maxilla of the Trinil individual accommodates one and a half milkmolars (posterior portion of the dP^3 + dP^4). Like the holotype mandible, the present maxilla again indicates that *S. sondaari* possessed relatively large molars compared to its jaws.

The second maxilla fragment of the Flores pygmy Stegodon (TT-3817) does not provide additional clues with regard to the relative size of the molars. It belonged to a subadult or adult individual, because the anterior width of the alveole was 28 mm or more, too big for the anterior root of a milkmolar. The basal part of the orbit is somewhat further preserved as in the juvenile specimen but in all other aspects this maxilla is much more fragmentary. In antero-posterior direction the basal orbit outline, measured at a similar level as in specimen TT-3836, is c. 60 mm, while the dorso-ventral diameter measures 43 mm. The maxillary portion of the orbit is more robust and less compressed dorso-ventrally as in the juvenile specimen.

Postcranial elements, description and comparison — Postcranial elements of *S. sondaari* are relatively scarce at the locality Tangi Talo. The postcranial material recovered consists of a femur fragment (TT-4083), a phalanx (TT-4065), three vertebrae thoracales (TT-4086, TT-4082 and TT-4115), a processus spinosus of a vertebra thoracale (TT-4078), an atlas fragment (TT-3844) and 13 costa fragments. In addition, the Sondaar collection contains an almost complete atlas (F/BS-3.1), which was mentioned in a previous paper under *Stegodon* sp. C (van den Bergh et al., 1992), and two fragmentary vertebrae thoracales (F/BS-3.2 and F/BS-3.3), 4 isolated processus spinosus fragments and 2 proximal costa fragments.

Atlas: The atlas mentioned in van den Bergh et al. (1992) is almost complete, only lacking the sinistral processus transversalis and part of the ventral margin including the ventral tubercle (F/BS 3.1; Pl. 16, figs. 1-2). It is about two times smaller in linear dimensions as compared to the most complete atlas of *S. trigonocephalus* (CD-3726; Table 19) and also smaller than a fragmentary atlas from Timor, which has been attributed to *S. timorensis* (Hooijer, 1969a: 208). F/BS-3.1 is quite robust, with the lateral margins of the facies articularis cranialis thick and rounded. The lateral tuberosities of the arcus and tip of the dextral processus transversalis are covered with rugosities. The atlas is of a full-grown individual. The total height (measurement A1) as far as preserved is 88+ mm (the ventral margin is damaged), but the total height must have been less than 100 mm. A1 is 168 mm in the most complete atlas of *S. trigonocephalus* (CD-3726), and varies between 155 and 180 mm in other fragments attributed to this species (Hooijer, 1955b). In F/BS-3.1 the total transverse diameter (A2) cannot be measured directly, but half this distance measured over the dextral processus transversalis = 85 mm, which would give a total of c. 170e mm. In CD-3726 half the transverse diameter amounts 142 mm over the intact sinistral processus transversalis, giving a total of c. 284e mm.

Of the atlas fragment collected more recently at Tangi Talo (TT-3844) only the dextral side is preserved, though rather damaged. The total height as far as preserved is 95+ mm. This specimen has slightly larger dimensions than F/BS-3.1, but is still smaller than the *S. timorensis* atlas.

Compared to *S. trigonocephalus*, the atlas of *S. sondaari* is more dorso-ventrally compressed, as follows from the different indices RA2 and RA4 (Table 19). The corpus of the latter is also markedly shorter relative to the width as indicated by the smaller indices RA6 and RA7 (Table 19) compared to *S. trigonocephalus*. The *S. timorensis* atlas resembles more *S. trigonocephalus* in these aspects. Another difference is that in the Flores pygmy the dorsal margin of the processus transversalis points slightly upward, while in the Java stegodont it is inclined downwards. In the Timor specimen the processus transversalis is broken.

Vertebrae thoracales: Measurements of the vertebrae are given in Table 20. Three specimens in which the corpus is more or less complete were collected recently, while there are two more in the collection made by Sondaar in 1980. In all specimens the epiphyses are fused completely, thus representing full-grown individuals. Specimen TT-4086 (Pl. 16, figs. 3-4) is a vertebra thoracale of which the right side including the processus transversalis and the tip of the processus spinosus are broken. On the left side the extremity of the transverse process is superficially damaged. The processus spinosus is inclined backward and, as far as preserved, it is longer than the total height of the corpus. The articulation facets of the processi articulares caudales are placed parallel to the length axis of the processus spinosus, as in the more anterior vertebrae thoracales of *S. trigonocephalus* figured by Hooijer (1955b: pl. VIII, fig. 1). In the more posterior vertebrae thoracales of *S. trigonocephalus* these facets tend to be more horizontally oriented and make an angle with the length axis of the processus spinosus. In our specimen the left transverse process points slightly upward, in the same way as in the vertebra thoracale IV described by Hooijer (1955b: 66). In the first three thoracales these processes are inclined downwards. By comparison, TT-4086 most likely represents a thoracale IV or V. A less well-preserved vertebra thoracale of the anterior region of the vertebral column (F/SB-3.2) has only the corpus and part of the sinistral transverse process preserved.

Specimens TT-4082 (Pl. 17, figs. 1-2) and F/SB-3.3 represent vertebrae thoracales of the posterior part of the column, characterized by a single costal facet on each side of the corpus. Of TT-4082 the ventral and caudal side of the corpus are considerably abraded, so that no dimensions of the corpus can be given, but in F/SB-3.3 the corpus is intact. In TT-4082 the arch and the basal part of the processus spinosus is preserved, while in F/SB-3.3 only the basal part of the arch is preserved. In TT-4082 the facets of the processus articulares caudales are horizontally oriented and placed behind the caudal articulation surface of the corpus. Comparison with the lectotype skeleton of *Elephas maximus sumatranus* in the NNM and the six last thoracales figured by Hooijer (1955b: pl. VIII, fig. 2) indicates that TT-4082 represent one of the five most posterior thoracales.

Specimen TT-4115 can be identified as a vertebra thoracale with an intermediate position. The tip of the processus spinosus and the right processus transversalis are broken, while there is much superficial damage on the left processus transversalis. The processus spinosus as far as preserved was longer than the height of the corpus. It is strongly inclined backward, making an angle of 115 with the vertical axis of the corpus. The processus articulares caudales are placed far backward behind the caudal surface of the corpus. The anterior costal facets are damaged. The caudal costal facets are placed above the corpus on the ventral side of the caudal portion of the transverse processes.

Specimen TT-4078 is an isolated processus spinosus, of which the tip is broken. Its length as far as preserved is 80 mm. The inferior portion is perforated, a characteristic also recorded by Pohlig (1911) and Hooijer (1955b) in the processus spinosus of some vertebrae thoracales and cervicales of *S. trigonocephalus*. There are 4 more isolated processus spinosus fragments in the Sondaar collection. The best preserved specimen (F/SB-3.4) is strongly built and of the anterior part of the vertebra column. It has a preserved length of 150 mm. It is rapidly widening distally but the tip is abraded. Proximally the widening is more gradual, with the base strongly built. A vertical groove runs along the basal part of the posterior surface. The minimum transverse diameter is 13.5 mm, the minimum antero-posterior diameter is 14.3 mm.

As follows from the measurements presented in Table 20, all above described specimens, in which the epiphyses are fused, are of small size compared to *S. florensis* vertebrae. Therefore, they can be safely attributed to *S. sondaari*.

Femur: The only long bone in the collection from Tangi Talo consists of a sinistral femur diaphysis of a supposedly adult individual (TT-4083; Pl. 17, figs. 3-4). Both the distal and proximal epiphyses are gone, and parts of the diaphysis at both ends are broken away as well. Measurements that could be taken are given in Table 26. As follows from this Table, specimen TT-4083 is clearly of small size, smaller than femurs of *S. florensis* and *S. trigonocephalus*. The length as far as preserved is 243+ mm. The supposedly adult stage of this specimen can not be directly deduced from observations on the epiphysal fusion, because the extremities have been broken away further than the epiphysal junctions. However, the disto-lateral edge of the diaphysis is covered with well-developed tuberosities for attachment of the biceps femoralis. Comparison with *S. trigonocephalus* femurs of both juvenile and adult individuals present in the Dubois Collection, reveals that these tuberosities are only developed in full-grown specimens in which the epiphyses were fused. In both the *S. trigonocephalus* femurs and TT-4083 there is a marked bend along the disto-lateral edge of the diaphysis near the onset of these tuberosities. This character is not encountered in femurs of *Loxodonta*, *Elephas* and *Mammuthus*, where the shaft has a more straight course. A difference between adult femurs of *S. trigonocephalus* and the small femur fragment from Tangi Talo, is that in the latter these tuberosities arise above the lateral bend of the femur shaft extending downward along the lateral edge of the shaft, while in adult *S. trigonocephalus* femurs they start right at this bend extending downward only. In the

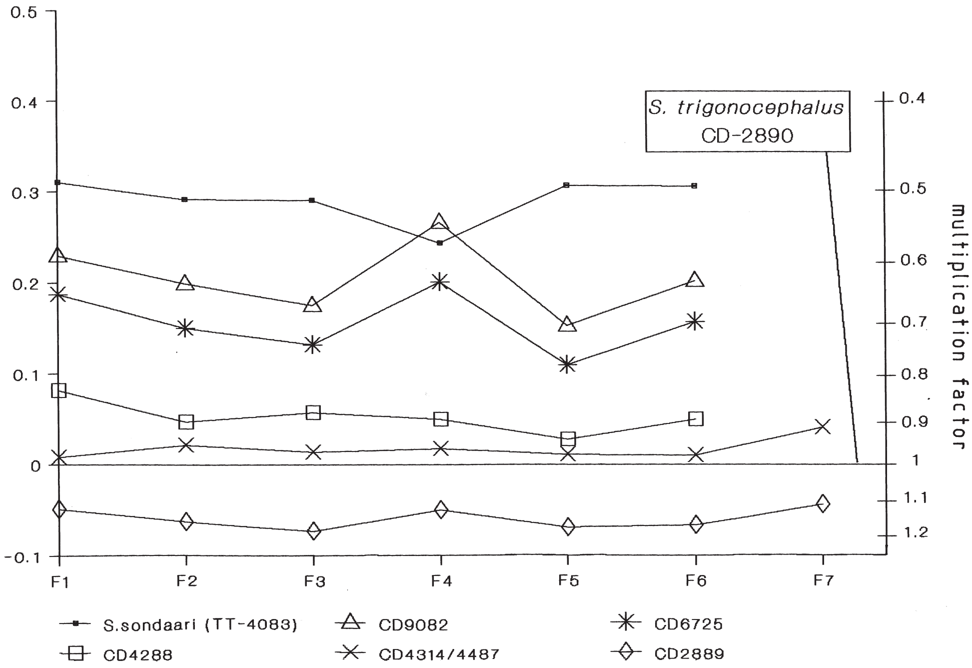


Fig. 73. Comparative log-ratio diagram of the measurements taken on the femur diaphysis of *Stegodon sondaari* (TT-4083) as compared to several femurs of *S. trigonocephalus* from Trinil in various ontogenetic stages. The zero reference level represents a fullgrown femur (CD-2890) with fully fused epiphyses. In specimens CD-2889 and CD-4314/4487 the epiphyses are also fused. Specimens CD-9082, CD-6725, and CD-4288 are immature specimens.

small femur from Flores the transverse diameter of the diaphysis below this bend (measurement F4 in Table 26) is relatively larger to the other measurements that could be taken, when compared with several *S. trigonocephalus* femurs from Trinil (Java) in various ontogenetic stages. This can be easily seen in a log ratio diagram (Fig. 73). Other proportions of size measurements taken on specimen TT-4083 are similar to adult *S. trigonocephalus* femurs in which the epiphyses have been fused, while juvenile femurs of the latter species have relatively small antero-posterior diameters (measurements F2, F3 and F5) as compared to the transverse diameters (measurements F1 and F4). These observations also point in the direction that TT-4083 represents an adult individual, with disregard of its small overall size. It is therefore attributed to the dwarf *S. sondaari*. In the adult femur of this dwarf species the disto-lateral tuberosities on the diaphysis are even more robust as compared to adult femurs of *S. trigonocephalus*.

From Fig. 73 we can also deduce a rough estimation of the original total length (F7) of the *S. sondaari* femur, assuming that the ratio between F7 and other measurements was about the same in this femur and the *S. trigonocephalus* reference femur in the diagram. If so than the following equation should be valid: $\log(F7_{ref.}) - \log(F7_{TT4083}) = 0.3$, in which $F7_{ref.}$ represents the total length (in mm) of the reference femur CD-2890 and $F7_{TT4083}$ represents the estimated total length of specimen TT-4083. The value 0.3 is based on the assumption that the length/width proportions of the *S. sondaari* femur were similar to adult *S. trigonocephalus* femurs. In that case the all log ratio values in Fig. 73 should ideally lay on a horizontal line with the other log ratio values of the *S. sondaari* femur, which cluster around the value 0.3. Measurement F7 of the reference specimen, CD-2890, amounts to 922 mm. Therefore: $\log(922) - \log(F7_{TT4083}) = 0.3$ and thus: $F7_{TT4083} = 460$ mm.

It must be stressed that this value of 460e mm should only be used as a very rough estimation for the size of the dwarf stegodont individual. After all the possibility exists that the pygmy had different femur proportions as compared to *S. trigonocephalus* adults. An error of 460 ± 50 mm seems reasonable. This length estimate can in turn be used for calculating an estimate of the bodyweight of the Flores pygmy *Stegodon* (chapter 8).

Phalanx: There is one first phalanx present in the Tangi Talo Collection (TT-4065; Pl. 17, figs. 5-6). The epiphyses are fused. It is almost symmetrical in shape indicating that we deal with a phalanx of a third or fourth digit of either a fore or hind leg. The phalanx is 27 mm long. The proximal diameter is 26.6 × 18.6 mm, the distal diameter is 21.2 × 15.7 mm, while the minimum diameter of the diaphysis is 20.0 × 8.3 mm.

Phalanges of fossil elephantoids are relatively rare, and of *S. trigonocephalus* none has been described so far. The proximal transverse diameters of the 3rd and 4th phalanges I in a modern *E. maximus* carpus are both 62 mm, while the distal transverse diameters are 55 and 54 mm, respectively. These measurements are more than twice those of the fossil phalanx from Tangi Talo. Based on its small size it can be attributed to *S. sondaari* sp. nov.

Costae: Finally, there are 15 costa fragments from Tangi Talo, all in a fragmentary state of preservation but clearly of small size. They are not discussed further.

Discussion

The stegodontine molars and skeletal elements from Tangi Talo constitute a homogeneous assemblage and all elements can be ascribed to a single species of a pygmy stegodont, *Stegodon sondaari* sp. nov. Its molars and mandible are the smallest of all pygmy stegodonts recorded to date. Adult individuals were approximately half the size in linear dimensions as compared to adults of *S. trigonocephalus* (Fig. 74). In Table 38 the ridge-crest formulas of *S. sondaari* and various other *Stegodon* species can be compared. The numbers of ridges in the last three molars are lower than the lowest amount observed in homologue teeth of *S. t. trigonocephalus*. For the M_3 of *S. sondaari* the difference is significant (x8 versus x13x or x13 in *S. t. trigonocephalus;* the minimum recorded amount of ridges in the M_3 of *S. trigonocephalus* is x11x as recorded by Hooijer (1955b). This low amount has been shown in this thesis to correspond with the more primitive subspecies *S. t. praecursor*. When comparing the plate formula of the M_3 of *S. sondaari* with those of other large-sized *Stegodon* species, it corresponds best with that of some primitive Pliocene species, such as *S. zdanskyi* from China, *S. shinshuensis* from Japan (by some authors believed to be synonymous with *S. zdanskyi*, e.g. Saegusa, 1996) and *S. bombifrons* from the Indian Subcontinent (Table 38). However, in the Japanese and Chinese species the number of ridges in the milk-molars and/or the M1 is lower than in those of the Flores pygmy. *S. bombifrons* comes

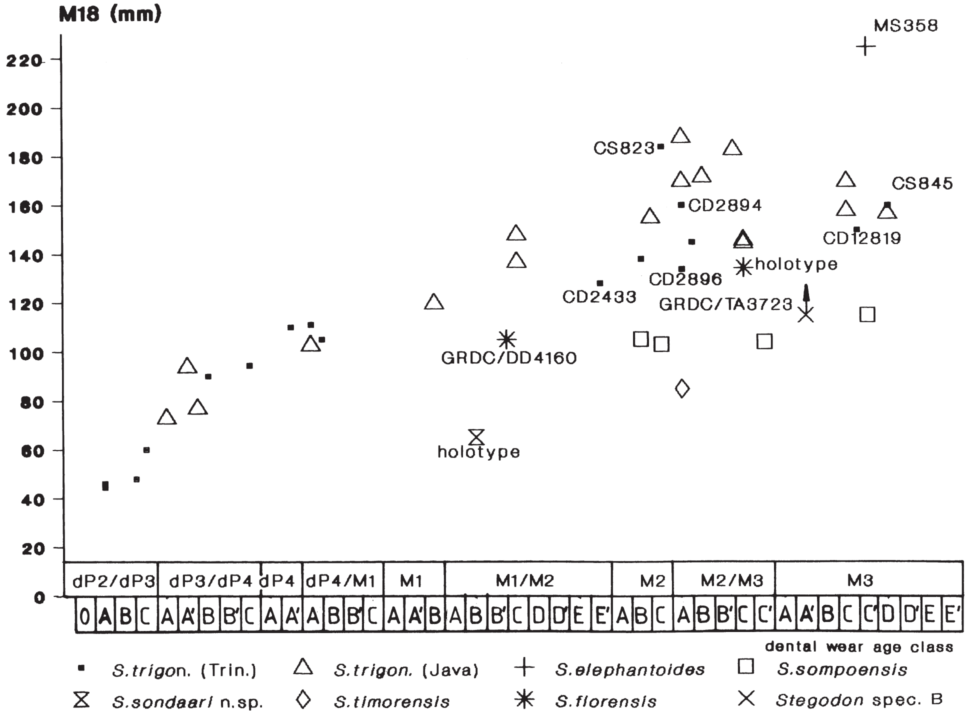


Fig. 74. Mandible size parameter M18 (= transverse width of the horizontal ramus at the widest point near the onset of the ascending ramus) as a function of dental wear age class, for various *Stegodon* species (See also Figs. 57-58 for comparable figures on other mandible size parameters). Measurements are taken on mandibles and mandible fragments in the NNM and GRDC collections, and from a few Selenka expedition specimens as given by Janensch (1911). Successive dental wear age classes are after Beden (1979) as defined for *Loxodonta africana* (see also Fig. 75). *S. t. trigonocephalus* mandibles from the loc. Trinil and from other Javanese localities are represented by different symbols. Note that the Trinil mandibles are smaller on average than those from the combined other Javanese localities. The largest Trinil mandible (Coll. Selenka no. 823) does not originate from the 'Hauptknochenschicht', but was excavated 5 m above the main fossiliferous layer at Trinil (Oppenoorth, 1911). Other mandibles from Trinil are supposedly originating from the 'Haupt-knochenschicht', either based on labels, or, if lacking, based on data from the register of the Dubois Collection and the type of fossilization and matrix. Other *Stegodon* species shown are: *S. elephantoides*, *S. florensis*, *S. sondaari*, *S. sompoensis*, *S.* sp. B, and *S. timorensis*. The reference numbers of some specimens mentioned in the text are added to some of the data points. The M18 value of *Stegodon* sp. B mandible TA-3723 represents a minimum value, as the ramus is rather damaged. The actual width must have been larger, as indicated by the vertical arrow.

closest to the Flores pygmy in its plate formula. Comparison with other fully or partly dwarfed *Stegodon* species, such as *S. timorensis*, *S. sompoensis*, *S. aurorae*, and *S. florensis*, reveals that *S. sondaari* has the lowest number of ridges in all homologue molars of which material has been described from the other species and which can be used for comparison.

An important question is: do these observations tell us something about phylogenetic relationships? If we would assume that in the coarse of evolution the amount of molar ridges has only increased, we could skip a number of species as the possible ancestors of *S. sondaari*, namely all those with higher plate formulas. However, it has been inferred that the number of molar ridges in pygmy elephantoids was reduced as a functional necessity resulting from the size reduction (Maglio, 1973). It was argued that if the molars, including the enamel, would scale down isometrically, the enamel would become too thin to maintain its durability. It was thus thought that the ET had to scale down to a lesser degree than the overall body-size reduction. If under these circumstances the number of lamellae would remain constant, space problems would occur in the mandible, and therefore the amount of ridges had to be adjusted. This interpretation was based on the assumption that the dwarf elephant of Sicily, *Elephas falconeri* had descended from *E. namadicus*. This hypothesis is generally accepted by most specialists.

However, Mol et al. (1996) do not agree with this view. Absolute datings (Belluomini & Bada, 1985; Reese et al., 1996) indicate that dwarfs such as *Elephas falconeri* and *E. creticus* were not derived from *E. antiquus/namadicus* but from older representatives of the *Mammuthus* lineage, which had a lower amount of lamellae than *E. antiquus/namadicus*. They argue that *E. falconeri* and *E. creticus* are pygmy derivatives of the early mammoth stock, from either *M. meridionalis* or *M. trogontherii*. This hypothesis was also advanced by Lister & Bahn (1994), who stated that the strongly curved tusks and the single-domed skull of the dwarf elephant from Sicily better fit with a *Mammuthus* ancestry. Also the molar morphology of the Mediterranean dwarfs agrees better with early *Mammuthus*, as already noted in the first description of *E. creticus* by Bate (1907). She felt that molars of *E. creticus* resembled those of *E. meridionalis* more than any other of the larger elephants from the Mediterranean region, but because remains of *E. antiquus* were known to occur on the same island, she concluded that *E. creticus* had descended from this species.

Assuming that the Mediterranean dwarfs descended from early mammoths, as done by Mol et al. (1996), the pygmy elephants from Crete and Sicily should be allocated to the genus *Mammuthus*, a view followed in this thesis. An implication of such a phylogenetic relationship would be that a reduction in molar lamellae in the coarse of dwarfing of these island mammoths has not necessarily taken place. The amount of lamellae in the M3 of *Mammuthus meridionalis* varies between 10 and 14, whereas *M. falconeri* has 15 lamellae and *M. creticus* has 13 lamellae in the same element. Mol et al. (1996) also note that the enamel thickness is not disproportionally reduced in the Mediterranean pygmies when *M. meridionalis* is considered the ancestor.

Nevertheless, there may be some truth in the hypothesis of Maglio (1973). It can't be excluded that reduction of the amount of molar lamellae may have taken place in cases when the original amount of lamellae was high. Lister & Joysey (1992) presented an observation in line with this. They found that in a sample of *Mammuthus trogontherii* M^3s from Süssenborn (Germany) LF showed an inverse correlation with tooth length and with tooth width (regression exponents -0.646 and -0.605, respectively). Smaller tooth had higher LF as expected, but the fact that scaling was allometrically suggested that as tooth size decreased there was some tendency for the number of lamellae to decrease as well, rather than a purely isometric scaling down.

On the other hand there are examples of dwarfed stegodonts which have an increased number of molar ridges as compared to their large-sized ancestors. The small-sized but not yet completely dwarfed *S. aurorae* from Japan has 2-4 ridges more in its lower and upper M3s than its direct ancestor *S. shinsuensis* from Japan, which in turn is very closely related or even synonymous with *S. zdanskyi* from China. Of all known *Stegodon* species, *S. florensis*, with comparable size as *S. aurorae*, has the largest number of ridges (14) in its M_3. As pointed out by Roth (1989), the number of lamellae and the linear dimensions of an elephant tooth could be genetically predetermined. Alternatively, they could reflect the amount of space available for a certain tooth in the growing jaw, but likely the situation lies somewhere in between these two extremes.

A common observation in dwarfed mammals is that they possess relatively large teeth (Gould, 1975). *S. sondaari* sp. nov. follows this trend, as do some other dwarfed elephantoids (Ambrosetti, 1968; Roth, 1982). This suggests that the size-reduced jaw is able to accommodate tooth that are disproportionally large, to a certain limit. In the case of dwarfed island stegodonts there is also a trend of increased hypsodonty, whereas large-sized mainland stegodonts are very conservative in their brachiodonty.

The adjustments that took place in the molars of dwarfing lineages of island elephantoids may have followed different paths depending on the starting-point (e.g. elephant versus stegodont) and on an interplay of environmental factors (e.g. does island life enforce a different type of food to be consumed than was consumed by the ancestral stock), mechanical and physiological constraints (e.g. critical values of enamel strength), and the degree of complexity of the morphological adjustments themselves (fenotypic versus genotypic; e.g it may be easier for the mandible to adjust the size of the alveoles in response to relatively larger growing molars than the molars decreasing their number of lamellae during ontogenetic development, which in turn may be easier than to change the complexity of enamel microstructure).

Returning to *S. sondaari* sp. nov., it appears to be the only species within the genus in which the number of ridges in the M_3 does not exceed that of the M_2 (though the evidence is poor, based only on a single M_3 still in the alveole). This suggests that reduction of the number of ridges in the M_3 did take place during the dwarfing process. *S. timorensis*, of only slightly larger proportions than *S. sondaari*, has 10 fully developed ridges in the M_3 and 9 in the M_2. Its M_3 and M_2 have thus 2 and 1 ridges more compared to homologue molars of *S. sondaari*. The lower number of ridges encountered in *S. sondaari*, may be mainly reminiscent of a more primitive ancestor with lower ridge numbers as compared to the ancestor of *S. timorensis*. Still, in both lineages the total amount of ridges may have been reduced in the coarse of dwarfing. A more primitive ancestor for *S. sondaari* is corroborated by the fact that it has relatively thicker enamel, varying between 2.9 and 4.3 mm in the last two molars, both upper and lower (Table 35), than *S. timorensis*, which has the ET in the M2 and M3 varying between 2.2 and 2.9 mm (Table 36). The relatively thick enamel of the Flores pygmy may be imposed by a comparatively simple (and weaker) enamel microstructure. Though the enamel microstructure of *S. timorensis* was not examined during this study, the 3-D layer of the inner enamel in *S. sondaari* was found only weakly developed as compared to *S. trigonocephalus* and *S. sompoensis* (on average 7.9% only of the total ET in the Flores versus 19.4% and 23.6% in the other two stegodonts respectively). The enamel of the Flores pygmy may have simply not yet developed enough internal strength as to enable further reduction of the total enamel thickness, and consequently, the development of more but thinner molar ridges. In addition, the enamel of the Flores pygmy is less delicately folded as compared to *S. timorensis*, though there is some overlap (compare Tables 35 & 36).

The hypsodonty indices of both *S. sondaari* sp. nov. and *S. timorensis* are similar (Tables 35-36), together having the highest recorded hypsodonty indices amongst the Stegodontidae. The h/w indices of the M^2 vary between 61 and 85 in the Flores, and between 79 and 98 in the M^2 and M^3 of the Timor pygmy. For the two last lower molars of the two species the h/w indices vary between 70 and 89, and between 70 and 88, respectively (Tables 35 & 36). *S. sompoensis*, the dwarf stegodont from Sulawesi, has larger molars (both L and W: compare Tables 33 & 35) and larger mandible dimensions than the Flores pygmy (Fig. 74). The M_3 of *S. sompoensis* has also more ridges (9-10). The range of variation of its ET (2.2-4.6 mm for the last two molars, upper and lower, Table 33) includes the range observed in *S. sondaari* molars of the same rank (2.9-4.3 mm, Table 35), even though in absolute size the molars of *S. sompoensis* are c. 40% larger. In ET and EF *S. sompoensis* is rather variable, presumably reflecting evolutionary changes during its relatively long presence on South Sulawesi. The scanty material suggests that *S. sompoensis* became more hypsodont through time (van den Bergh et al., 1994).

The above mentioned characteristics of the Tangi Talo dwarf stegodont show it to be sufficiently differentiated from the other dwarf stegodonts of the region, to justify the erection of a new species. On theoretical grounds the erection of a separate species for the pygmy stegodont from Flores seems also justified, as it is highly likely that it evolved in isolation from stegodont populations on the other islands. Its ancestry remains obscure, the more so as no skull material has been found to date. Likely, it did not descend from *S. trigonocephalus* nor from *S. sompoensis*. Also *Stegodon* sp. B from Sulawesi is unlikely to have given rise to *S. sondaari* sp. nov., because it is already quite advanced in molar structure and plate formula. *S. bombifrons* or *S. elephantoides*, the latter now also recorded from the Lower Pleistocene of Java, seem to be the best candidates for the time being.

Stegodon cf. *sondaari* sp. nov.

Description of the material

Specimen OB3 from the collection made by Hartono in 1960, is an unworn posterior fragment of a sinistral molar, identified by Hooijer (1967a, p.156) as a dP_4 of *S. trigonocephalus florensis*. The fragment consists of $-{}^{1}/{}_{2}4x$ ridges. The maximum width occurs at ridge IV, which is quite unusual for stegodont dP_4s. The outer enamel layer of the posterior ridges was not yet fully mineralized when the animal died, though the ridges are already connected at their bases. Cementum was not yet deposited. The widths and heights of individual ridges can be given as follows: posterior halfridge: w = 12e mm, h = 18e mm; I: w = 32 mm, h = 27 mm; II: w = 38.5 mm, h = 31 mm; III: w = 42.5 mm, h = 33 mm; IV: w = 44.5 mm, h = 33 mm. The h/w indices of individual ridges (excluding the posterior ridge and halfridge) can be given as varying between 74 and 80. The length as far as preserved is 65+ mm. The ET at the broken anterior ridge varies between 3.9 and 4.7 mm. The number of digitations varies between 6 and 8. The LF is 7.8.

The relatively thick enamel and the posterior tapering suggest that this fragment does not represent a dP_4 of *S. florensis*. The fragment also seems too small and the LF too high for an M_3 of *S. florensis* (compare Table 37). Therefore, Hartono (1961) determined the specimen as an M_3 fragment of the dwarfed *S. hypsilophus* Hooijer, known from Java (Hooijer, 1955b). The pair of very small milkmolars from the same collection, also reportedly originating from the surroundings of Ola Bula, were attributed by Hooijer (1964b) to a pygmy *Stegodon*, and are designated as dP_3s of *Stegodon sondaari* sp. nov. in this thesis.

The dimensions of specimen OB3 slightly exceed those of the uncompleted M_3 in the alveole of the type mandible *S. sondaari* sp. nov. Therefore, OB3 is referred to here as a posterior M_3 fragment of *Stegodon* cf. *sondaari* sp. nov. It is not known for sure whether this molar fragment originates from the same stratigraphic level as the other *S. sondaari* remains treated in this chapter.

Stegodon florensis Hooijer, 1957

Stegodon trigonocephalus florensis nov. subsp.; Hooijer, 1957a: 120-125, pl. II, figs. 1-2; pl. III, figs.1-5.
Stegodon trigonocephalus florensis; Hartono, 1961: 24-27, 37-38.
Stegodon hypsilophus; Hartono, 1961: 28-31.
Stegodon trigonocephalus florensis; Hooijer, 1967a: 157.
Stegodon trigonocephalus florensis; Hooijer, 1972a: 14-24, pl. 1, figs. 1-4, pl. 2, figs. 1-3, pl. 3, figs. 4, 6.
Stegodon trigonocephalus; Sondaar, 1987: 162.
Stegodon trigonocephalus florensis; van den Bergh et al., 1992: 38.
Stegodon trigonocephalus florensis; Aziz, 1993: 3, pl. 2, lower figure.
large sized proboscidean; Sondaar et al., 1994: 1257.
Stegodon trigonocephalus florensis; van den Bergh et al., 1996: 31.
Stegodon trigonocephalus florensis; Mol et al., 1996: 91.

Holotype — The mandible fragment with a large portion of the dex. M_3 and the anterior half of the sin. M_3, originating from Ola Bula and described and figured by Hooijer (1957a: 120-122, pl. II, figs. 1-2).

Hypodigm — Amongst the material collected in Flores by Verhoeven between 1956 and 1968 there is a complete upper and lower dentition of a single adult individual consisting of the M3s and both tusks (Hooijer, 1972a: pl. 1, figs. 1-4). In addition, there are an almost complete sin. M^3 (Hooijer, 1972a: pl. 2, fig. 2) and sin. M_3 (Hooijer, 1972a: pl. 2, fig.1), a dex. half-mandible fragment with dP_4 and M_1 (Hooijer, 1972a: pl. 2, fig. 3) and a complete isolated M^1 or M^2 (Hooijer, 1972a: pl. 3, fig. 4). In addition there are a number of smaller molar fragments and postcranial elements represented in the Verhoeven Collection, some of which have been described by Hooijer (1967a: 156-157). In 1960 Hartono collected some molar fragments in the Soa Basin, all referred to as originating from Ola Bula (numbers starting with prefix OB), but actually collected at various sites, except for specimen OB3, which was given to Hartono by Verhoeven and reportedly originated from the surroundings of Ola Bula. In the NNM collection there is a dextral metatarsus IV collected by Hooijer in 1970 (Hooijer, 1972a: 24). Further, there are an undescribed pair of M^3s (NNM F.BL-10.2 and F.BL-10.3) and an isolated dex. M^3 fragment (NNM F.BL-10.1), collected by Sondaar in 1980.

The 1991-1994 GRDC-NNM expeditions have yielded a number of dental and skeletal elements, notably a mandible excavated at the locality Dozo Dhalu with both M_1 remnants and complete M_2s (GRDC DD-4160), a large portion of an sin. M^3 (GRDC F-OB3800) and the posterior portion of a dex. M^3 (GRDC MM-4118).

There are a number of large-sized *Stegodon* molar remains originating from Timor, which were attributed by Hooijer (1972a) to *S. trigonocephalus florensis*. The specimens that could be examined at the NNM are very fragmentary, and the stratigraphic position of the Timor remains is not known. The Timor specimens are not included here in *S. florensis*. All known specimens from Flores that are here attributed to *S. florensis* are listed in Table 8. The holotype and a small number of postcranial remains from the Verhoeven collection are stored in the NNM, besides the specimens from the Sondaar collection and various casts of molars from the Verhoeven collection. Material collected during the 1991-1994 expeditions is housed in the GRDC. The whereabouts of other specimens described by Hooijer (1972a) are unknown.

Type locality — The holotype mandible was excavated in 1956 by Verhoeven from a fluvial sandstone layer on the flat-topped hill of Ola Bula (8°41′S and 121°7′E), Ngada District, west Central Flores, Indonesia. This level corresponds with the upper part of Member B of the Ola Bula Formation.

Age and localities — Besides Ola Bula, *S. florensis* remains have been found at the localities Boa Leza, Mata Menge and Dozo Dhalu, in fluvial sandstone-siltstone layers pertaining to Member B of the Ola Bula Formation in the Soa Basin. The age is early Middle Pleistocene. Based on palaeomagnetic sampling of the sections near Mata Menge and Tangi Talo/Ola Bula, the fossiliferous horizons can be correlated with the earliest part of the Brunhes epoch (Sondaar et al., 1994). The locality Menge Ruda, a still inhabited village, was also mentioned by Hooijer (1972a: 20). Two M3 fragments originate from this locality, but the exact site could not be relocated.

Original diagnosis — See Hooijer (1957a: 120).

Revised diagnosis — A *Stegodon* with slightly reduced dimensions compared to *S. trigonocephalus trigonocephalus* from Java, but not completely dwarfed. The number of ridges per molar is high:

$$\text{dP4:}\frac{\text{—}}{\text{-7x}}\quad \text{M1:}\frac{\text{x7x/-8x}}{\text{x9x}}\quad \text{M2:}\frac{\text{—}}{\text{x10x}}\quad \text{M3:}\frac{\text{x12x}}{\text{x14x}}$$

Molars subhypsodont, with h/w indices of upper molar ridges varying between 60 and 85 and of lower molar ridges varying between 68 and 81. Molars are comparatively narrow and elongated. Molar W and H slightly increasing in successive molars; width of the M^3s ranging from 78 to 87 mm and of M_3s from 68 to 78 mm. Largest width of the ridges occurs near their base, lingual and buccal borders weakly converging in apical direction. Amount of digitations per ridge variable between 6 and 11, digitations of subequal size. Median cleft may be developed only in the anterior two ridges, and more frequently in lower than in upper molars. Wear pattern of the ridges usually without median expansions, except for the anterior one or two ridges. Enamel is regularly and delicately wrinkled with 2-5 folds per 10 mm and an amplitude smaller or equaling the thickness of the enamel. The ET in the M3s varies between 3.2 and 5 mm. The enamel is double-layered, with the outer enamel layer comprising c. 50% of the total ET. Scalloped folding of the enamel. Stepwise wear of the two enamel layers. The innermost 3D enamel is well developed, showing complex decussation of the prism bundles. Cement well developed, frequently covering the ridge flanks and digitations of unworn ridges. Mandibular symphysis short, with small anteriorly protruding rostrum. Weakly outward curved stegodontine tusks with an (unworn) almost circular cross section.

Differential diagnosis — *S. florensis* differs from all other *Stegodon* species in having a superior number of molar ridges in the M_3 (14 ridges). The number of ridges of the M^3 (12 ridges) overlaps with the following species: *S. aurorae*, *S. orientalis* and probably *S. trigonocephalus ngandongensis* (Table 38). It generally has a higher degree of hypsodonty compared to most other stegodonts, only surpassed by the subhypsodont molars of the various pygmy stegodonts from SE Asia, which are however, of inferior size. Molars of *S. florensis* are 1.5 to 1.9 times longer and 1.2 to 1.9 times wider than homologue molars of the pygmy *S. sondaari* sp. nov., also known from Flores. *S. florensis* further differs from this pygmy stegodont in having relatively thinner and more wrinkled enamel, showing a more complex decussation of the 3D inner enamel layer. Further the digitations are of subequal size whereas those of *S. sondaari* tend to have larger adaxial digitations compared to the abaxial ones. *S. florensis* differs from *S. t. trigonocephalus* in being slightly smaller (molars, mandibles and postcranials are usually below the size ranges observed in the Javanese species or corresponding with the smallest specimens of the Javanese species) and having more hypsodont and relatively narrower molars (L/W ratios of molars beyond or corresponding with the upper limit of the range of variation in homologues of *S. t. trigonocephalus*). *S. trigonocephalus ngandongensis* is even larger than *S. t. trigonocephalus*. Its molars ridges tend to have smaller h/w indices than in *S. florensis*. Molar morphology of *S. florensis* comes closest to that of the poorly known *Stegodon* sp. B from South Sulawesi and Sangihe. This species may eventually turn out to be a subspecies of *S. florensis* when more fossil material will become available. *Stegodon* sp. B has a slightly larger size, both of the mandible and known molars, but similar h/w and L/W indices in the M^1.

Description and comparison of the material

Unfortunately no skull material of *Stegodon florensis* has been found so far, but there is now a fair number of complete molars from the various localities of Member B of the Ola Bula Formation. All the complete molars and larger molar fragments from the Verhoeven collection were described by Hooijer (1957a, 1967a, 1972a). A number of molar and postcranial specimens collected by Sondaar in 1980, and the material collected during the 1991-1994 GRDC/NNM campaigns remained undescribed so far, and will be treated below. The dental material will be described first, followed by mandible material and finally the postcranial remains. All the identifiable material is listed in Table 8 with the collection numbers, and, of the specimens excavated at Mata Menge, with the excavation coordinates.

Dental elements — In addition to the various dental remains described by Hooijer (1957a, 1967a, 1972a), 13 molars and molar fragments are contained in the 1980 collection, and the 1991-1994 GRDC/NNM collection. Of these 13 molars there are 6 that constitute 3 pairs. There is one large tusk portion from Mata Menge besides a number of smaller tusk fragments from this locality. Two larger tusk portions of the same tusk were damaged during an inspection of local officials and have not been taken to Bandung. Amongst all molar material collected so far, milkmolars are very rare.

dP$_3$: n = 1 (Hooijer 1967a: 156) The sinistral anterior fragment consists of 3- ridges, of which the posterior one is heavily damaged. The width of the anterior ridge is 16.4 mm, that of the second ridge 19.4, while of the third ridge no measurements could be taken. The length as far as preserved is 35.5+ mm. The ridges are worn down into single enamel loops. The enamel is very thin (ET = 1.0-1.1 mm) and delicately wrinkled with c. 7 folds per cm and an amplitude of 0.5-1 mm. The occlusal surface is plane. There is little cement between the ridges. The enamel on the ridge flanks is wrinkled with vertical grooves as characteristic for milkmolars. The LF is c. 12.5. As noted correctly by Hooijer (1967a), the peculiar outward twist of the anterior ridges clearly shows that the fragment represents a sinistral dP$_3$.

dP$_4$: n = 2 (Hooijer 1972a: 19, pl. 2, fig. 3) The most complete dP$_4$ is the worn one in a dextral halfmandible from Boa Leza (Hooijer 1972a: pl. 2, fig. 3). It has -7x ridges preserved and a maximum width of 41 mm at ridge II. The other posterior fragment from Mata Menge reportedly has a greatest width of 44 mm (Hooijer 1972a: 19).

M$_1$: n = 5 (Hooijer 1972a: pl. 2, fig. 3; Hooijer 1967a: 157. GRDC: F/OB-3802, DD-4160 = a pair of M$_1$ remnants in a mandible from Dozo Dhalu) The only complete specimen known so far is the M$_1$ from the Boa Leza dextral halfmandible figured by Hooijer (1972a: pl. 2, fig. 3). It carries x9x ridges, is 134 mm long and the W at ridge II is 48 mm. The h/w index of ridge II is 77 and the LF as given by Hooijer amounts to 7.5.

The isolated sinistral specimen from Boa Leza mentioned by Hooijer (1967a: 157) has -$^1/_2$6x ridges preserved and has a maximum width of 55 mm at ridge IV. The h/w indices of the unworn ridges II and III are 69 and 70, respectively. The ridges bear 7 to 8 digitations of subequal size. The LF is 6.0. The ET varies between 3.2 and 3.3 mm. The double-layered enamel shows 2 to 3 folds per cm with an amplitude of up to 1.3 mm. Vertical grooves in the enamel surface on the ridge flanks are weakly developed.

Specimen F/OB-3802 is a sinistral posterior M$_1$ fragment with -3x, unworn ridges preserved. The measurements taken on these ridges are: posterior halfridge: w = 44 mm, h = 29.5 mm; I: w = 49(c) mm, h = 39(c) mm; II: w = 52(c) mm, h = 46(c) mm; III: w = 55 mm, h = 43 mm. The h/w indices of individual ridges varies between 78 and 88. The LF amounts to 6.2 and the ET, which could be measured at a broken basal termination of the most anterior ridge, is 3.3 mm. The anterior ridge has 9 digitations.

The two paired specimens in the Dozo Dhalu mandible are nothing more than completely worn remnants that were about to be shed. Only along the posterior margins remains a bit of enamel, but the central occlusal areas are formed by a single, concave dentine surface. Both remnants are preserved over a length of c. 66+ mm and have a preserved width of 44+ mm.

M$_2$: n = 3 (Hooijer 1972a: 18; GRDC: DD-4160 = pair of M$_2$s in mandible). Hooijer (1972a: 18) mentioned a posterior remnant of an M$_2$ in a dextral mandibular ramus from Boa Leza. The fragment has -6x ridges preserved, with a LF of 5.1 and a width of 63 mm at ridge V. The W cannot be measured on this fragment. The dextral M$_2$ in the Dozo Dhalu mandible (DD-4160; Pl. 18, figs. 1-2) is the first recorded complete molar of this rank of *S. florensis*. In its sinistral counterpart ridges 7 and 8 are lacking. The dextral M_2 carries x10x ridges. Of the posterior -5x ridges the lateral side is embedded still in the alveole, so that the exact widths of these ridges and the total length cannot be given. The estimated length is 187e mm. Only the anterior three ridges are worn. The widths and heights of the successive ridges in the dextral molar are as follows: anterior halfridge w = 43 mm; 1: w = 51 mm; 2: w = 52 mm; 3: w = 54 mm, h = 40+ mm; 4: w = 56 mm, h = 42e mm; 5: w = 57.5 mm, h = 42e mm; 6: w = 58e mm, h = 42e mm. In the sinistral M_2 the widths and heights of the successive ridges are as follows: anterior halfridge w = 41 mm; 1: w = 50 mm; 2: w = 52 mm; 3: w = 54e mm; 4: w = 56 mm, h = 42 mm; 5: w = 58.5 mm, h = 42.5 mm; 6: w = 59.5 mm, h = 42 mm; 7 & 8 missing; 9: w = 60.5 mm, h = 44 mm; 10: w = 50.5 mm, h = 43 mm; posterior halfridge: w = 29 mm, h = 35 mm. The h/w indices vary between 71 and 75. The LF is 5.9 and the ET is c. 3 mm. The scalloped enamel shows stepwise wear. The ridges carry 8 to 9 digitations of subequal size. The antero-medial hook of the root carries x2- ridges in both specimens.

M_3: n = 17 (one pair of incomplete M_3 in the holotype mandible figured by Hooijer, 1957a: pl. II, figs. 1-2; one pair of M_3 of which the complete sinistral one is figured by Hooijer, 1972a: pl. 1, figs. 3-4; one pair of posterior M_3 fragments described by Hooijer, 1957a: 124; an isolated sinistral M_3 from Mata Menge figured by Hooijer, 1972a: pl. 2, fig. 1; an isolated posterior fragment of sinistral M_3 figured by Hooijer, 1972a: pl. 3, fig. 6; an intermediate portion of a dextral M_3 Hooijer, 1972a: 20; 8 small posterior M_3 fragments from various localities described by Hooijer, 1972a: 21-22, specimens c-i, k).

The molars in the holotype mandible from Ola Bula are both incomplete. The dextral one has the most ridges preserved (x11-) and is slightly damaged in front. The length as far as preserved is 230+ mm. The LF is 4.7 and the ET varies between 3.8 and 4.5 mm. The enamel is folded with 2.5 to 5 folds per cm and an amplitude between 0.4 and 1.4 mm. Further details are given in Hooijer (1957a: 120-123), though the estimated original total length of 250e mm given by him seems rather too low and a value of between 290e and 300e mm is more appropriate assuming that 3 ridges are missing behind.

The complete sinistral M_3 from Boa Leza (Hooijer, 1972a: pl. 1, figs. 3-4) carries x14x ridges. Only the two anterior ridges are worn. The total length reportedly amounts to 300 mm and the maximum width (at ridge 7) is 78 mm. The LF, measured on a cast of this molar, is 4.9. The ridges carry 8-10 digitations.

The other lower M_3 specimens dealt with by Hooijer (1957a, 1972) will not be treated again here but where possible, Hooijer's measurements have been included in Table 37, presenting the summary measurements of the *S. florensis* molar series.

M^1: n = 3 (Hooijer, 1972a: pl. 3, fig. 4; GRDC: F/OB-3801 and F/OB-3803) There is one complete dextral M^1 of *S. florensis* (Hooijer, 1972a: pl. 3, fig. 4). It originates from Mata Menge and carries x7x ridges in a total length of 126 mm. Five ridges are worn. The largest width (W) of 57 mm occurs at ridge I. Ridge II has a h/w index of 64. The LF as given by Hooijer is 6.5.

Specimen F/OB-3803 is a posterior M1 fragment, of which -4x ridges remain. Judging from the in apical direction concave crownbase, it represents an upper one. The LF is 6.9, slightly higher than in the foregoing M^1. The two anterior ridges are slightly worn. The ridge measurements are: posterior halfridge: w = 36(c) mm, h =

29(c) mm; I: w = 55 mm, h = 40(c) mm; II: w = 59(c) mm, h = 41(c) mm; III: w = 60(c) mm; IV: w = 59(c) mm. The h/w index of ridge II is 69. Ridge III, of which the digitations are just abraded, has 9 or 10 digitations of subequal size. The enamel wear on the occlusal surface is stepwise and the ET lies at c. 3.5 mm. Cement is abundantly developed.

M^3: n = 10 (Hooijer, 1957a: 124, pl. III, figs. 1-2; a pair of upper M^3s from Boa Leza, of which the dextral one is figured by Hooijer, 1972a, pl. 1, figs. 1-2; an isolated sinistral M^3 from Boa Leza figured by Hooijer, 1972a, pl. 2, fig. 2; an isolated fragment from Menge Ruda described by Hooijer, 1972a, p. 20; further there are three M^3 fragments collected by Sondaar: one pair of posterior M^3 remnants from Ola Bula (NNM F/BL-10.2 (sin.) and F-BL-10.3 (dex.)) and an isolated anterior fragment of a dextral M^3 from Ola Bula (NNM F/BL-10.1); one posterior fragment of an M^3 sin. found south of Ola Bula and a posterior fragment of an M^3 dex. excavated at Mata Menge in 1994: GRDC F/OB-3800 and MM-4118, respectively).

The number of ridges in the two complete M^3s recorded by Hooijer (1972a: pl. 1, figs. 1-2; pl. 2, fig. 2) are in both specimens x12x. The L is 270 mm and 140 mm and the W is 86 mm and 82 mm, respectively. The h/w indices of intermediate, unworn ridges in these two molars vary between 64 and 81. Where possible, Hooijer's measurements on the various M^3s have been included in the summary measurements (Table 37).

Specimens that have not yet been described previously will now be treated. One is specimen F-BL-10.1, an anterior portion of a dextral M^3. It has x8$^1/_2$- ridges preserved, of which the anterior 4 ridges are worn. The anterior halfridge and ridge 1 are broken on the lingual side. An inward curved enamel loop marks the presence of a median cleft in the halfworn anterior ridge, but lacks in the more posterior ridges. The successive widths and heigths that can be given are as follows: 2: w = 80 mm; 3: w = 83.5 mm; 4: w = 83(c) mm, h = 52.5 mm; 5: w = 86(c) mm, h = 51.5 mm; 6: w = 87(c) mm, h = 55 mm; 7: w = 82(c) mm, h = 54.5 mm; 8: w = 75.5 mm, h = 58 mm. The h/w indices of unworn ridges vary between 60 and 77. The molar has very thick cement. The LF is 4.5. The ridges contain 9 to 10 digitations.

In a pair of M^3 remnants (F/BL-10.2 and F/BL-10.3) -$^1/_2$8x ridges remain on both sides. The anterior ridges are worn down to the crownbase. All the ridges are worn except for the posterior halfridges. Of the dextral M^3 the widths of the ridges can be given as follows: posterior halfridge: w = 37(c) mm, h = 37(c) mm; I: w = 55(c) mm, h = 42.5+; II: w = 65(c) mm; III: w = 68(c) mm; IV: w = 72.5(c) mm; V: w = 78.5 mm; VI: w = 79 mm; VII: w = 82.5 mm; VIII: w = 76e mm. The posterior tapering and the in apical direction concave crownbase clearly indicates that M^3s are concerned here. The ridges are widest near their bases and are apically bended in anterior direction. The LF is 4.6 in the dextral and 4.5 in the sinistral specimen. The enamel is scalloped with stepwise wear. The ET varies between 4.0 and 5.3 mm. The enamel is folded with 3 to 5 folds per cm and an amplitude of 1-2 mm. The posterior unworn ridge carries 10 digitations. The occlusal wear surface is convex in antero-posterior direction in the sinistral M^3, but concavo-convex in the dextral one. Both molars have the peculiarity of possessing a number of accessory intravalley conules on the lingual side. In the dextral molar these conules are present between the ridges IV to IX. The largest intravalley conule is the most posterior one, which is 23.5 mm high and has a diameter of 12 mm. In the sinistral molar these conules are smaller and developed only between ridges V to IX. The largest conule here is also the most posterior one, with an height of 16 mm and a diameter of 7.5 mm. In anterior direction the conules become gradually smaller in both specimens. Though the deposition of cementum is strong, covering the flanks of most ridges, the intravalley conules are emerging from the cementum. The enamel wearpatterns do not show any irregularities and those of the more worn ridges have a rectangular shape without median expansions.

Specimen MM-4118 (Pl. 18, fig. 3) was excavated from the base of the siltstone interval of Unit 1 at Mata Menge (Fig. 69). It is a posterior M^3 fragment, with $-^1/_2 8x$ ridges remaining, all worn except for the posterior halfridge. The specimen has a preserved length of 200+ mm. Of ridges IV to VIII the lingual side is damaged. The ridge measurements are as follows: posterior halfridge: w = 43 mm, h = 42 mm; I: w = 53(c) mm, h = 43+ mm; II: w = 62(c) mm; III: w = 71 mm; IV: w = 73e mm; V: w = 77e mm; VI: w = 76e mm; VII: w = 78e mm. The latter value must be close to the maximum molar width. The occlusal surface is plane. The molar is almost straight longitudinally so that it must be an upper one, and, judging from the tapering in posterior direction, an M^3. Seen from behind with the occlusal surface turned upward, the right side of the ridges is more worn than the left side. The more worn side in upper molars is the lingual side in regularly worn molars, so that it must be of the right side. The LF is 4.5. The double-layered enamel is scalloped with stepwise wear and has an ET of 3.2-4.1 mm. There are 2-4 folds per cm with an amplitude of 0.5-2.5 mm.

The last *S. florensis* M^3 from Flores to be dealt with here, is an isolated M^3 remnant of the left side (GRDC F/OB-3800). It was found in a pocket of rounded, polymict gravel downslope of Ola Bula, in what possibly represents a terrace fill of younger age than Member B of the Ola Bula Formation. The molar may have been in primary context or could have been reworked. The molar remnant has -8x ridges remaining, of which again only the posterior halfridge is unworn. The length as far as preserved is 226+ mm, the maximum width is 85.5 mm, clearly indicating a stegodont of large size. The measurements of the successive ridges is as follows: posterior halfridge: w = 57 mm, h = 40e mm; I: w = 68 mm, h = 48.5+ mm; II: w = 78 mm, h = 46+ mm; III: w = 84 mm; IV: w = 85.5 mm; V: w = 85 mm; VI: w = 82.5 mm. Ridges VII and VIII are completely worn and damaged lingually so that no widths could be measured. The LF is quite low compared to the other *S. florensis* M^3s, namely 3.9. The scalloped enamel is double layered and has an ET varying between 4.4 and 5.0 mm. It is wrinkled with 3 to 4 folds per cm and an amplitude between 1.5 and 2.5 mm. Ridge I has 7 comparatively large digitations. The occlusal surface is convex antero-posteriorly and also transversely in little worn ridges. In the more worn anterior ridges the transverse profile of the occlusal surface becomes concave. The buccal half of the ridges is worn less than the lingual half. The ridges that are half worn show enamel loops with weak median expansions. Cement is developed between the ridges but leaves the flanks free.

Molar fragments of uncertain rank: An almost complete upper molar fragment of the right side is represented by specimen F/OB-3801, collected in situ in the surroundings of Ola Bula. The molar carries $-^1/_2 7x$ ridges, three of which are worn. Of the anterior preserved ridge only a posterior fragment of the enamel remains. The second and third ridges increase rapidly in width, so that judging from the outline in occlusal view, the fragmentary anterior ridge almost certainly represents ridge 1 of the molar. This is also suggested by the presence of a median cleft in the wear pattern of this and the second ridge. In the other *S. florensis* molars examined, a median cleft is only developed in the first, and sometimes in the second ridge. Thus, this molar would have originally carried 8 full ridges. The length as far as preserved is 132+ mm. The estimated length of the undamaged molar would have been between 145e mm and 150e mm. The posterior ridge and halfridge are heavily damaged and the molar crownbase is broken at several places. Roots are completely lacking. The measurements of the ridges can be given as follows: 1: w = ?; 2: w = 55 mm; 3: w = 59 mm; 4: w = 61.5 mm, h = 40.5e mm; 5: w = 61.5 mm, h = 47e mm; 6: w = 62 mm, h = 47 mm; 7: w = 61e mm, h = 43 mm; ridge 8 and posterior halfridge: no measurements. The LF of this upper molar is 6.4. The enamel is double layered with stepwise wear and has an ET of 3.1 mm. Cement was originally covering the digitations and ridge flanks, but is largely broken away. The number of digitations on the ridges varies between 8 and 9. The present molar carries one ridge more than the complete M^1 described by Hooijer (1972a: pl. 3, fig. 4), and further it is slightly larger but with a similar LF. The upper molars determined as M^1s of *S. trigonocephalus* by Hooijer (1955b) possess either x7x or x8x ridges. According to the subspecies division proposed in this thesis (see chapter 2) the M^1 of the subspecies from Trinil and Kedung Brubus, *S. t. trigonocephalus*, has x7x ridges whereas the younger subspecies from Ngandong, *S. t. ngandongensis*, has x8x ridges in the M^1. In the M^2s of *S. t. trigonocephalus* the number of ridges varies between x8x and x9x. The M^2 of *S. florensis* has not been recorded yet. Specimen F/OB-3801 probably represents a somewhat large M^1, but a small M^2 cannot be excluded. Its measurements have not been included in the summary measurements of *S. florensis* (Table 37).

There are various isolated molar ridges in the GRDC and NNM collections from the Soa Basin, including one excavated in situ at Mata Menge (MM-4140). Their widths all exceed 63 mm and their h/w indices are larger than 74. Therefore, they can all be safely attributed to molars (not milkmolars) of *S. florensis*.

Tusks — In 1960 Hartono collected two tusks in the Ola Bula area. One tusk remained at the office of the *Raja* of Nage Keo in Boawae, the other (OB6) was brought to Bandung and described by Hartono (1961: 37-38). The whereabouts of these tusks are not known. The tusk was assembled from broken fragments that reportedly fitted together. From the accompanying drawing given by Hartono (1961) it follows that the distal tip was preserved, but from the description it is not clear whether the tusk included the proximal pulpa cavity or not. The following measurements were given: total length measured along the outer curvature of the tusk: 190 cm; straight length between the distal and proximal terminations: 122.5 cm. Proximal circumference: 34.5 cm. From the drawing and from the large difference between the straight length and the curved length it would appear that the tusk described by Hartono was strongly bent, if the assemblage had been carried out properly. *Stegodon* tusks are usually only weakly curved, especially proximally, and this tusk would seem an anomaly, the more because other, albeit smaller, *Stegodon* tusk fragments from Flores and Java do not show such strong bending. From the circumference given by Hartono it follows that the most proximally preserved diameter of the tusk would have been 11 cm.

Hooijer (1972a: 14-17) mentioned two tusks of c. 2.80 m long, excavated by Verhoeven at Boa Leza. They belonged to the same individual of which he described the complete dentition in 1972.

During the NNM/GRDC test excavation at Mata Menge in 1992 an almost complete tusk was unearthed from the sandstone at the base of Unit 1 (MM-3901). Unfortunately, the proximal part including the pulpa cavity was heavily damaged by plantroots and further broken during transport to Bandung. An other tusk, found broken in two large portions and a number of smaller fragments, was excavated at Mata Menge in 1994 from the uppermost siltstone level of Unit 1. The two portions laid close together (Fig. 68). The proximal portion was partially located at the boundary between Units 1 and 2 (Fig. 69), and must have been fragmented and partially eroded prior to deposition of Unit 2. The distal portion, entirely embedded in siltstone, was also heavily fragmented. Both portions, which were covered with a gypsum cap, were further damaged during an inspection of a local official and where not brought to Bandung.

A small piece of the tip of tusk MM-3901 was broken, but the proximal part including the pulpa cavity was found largely complete, the latter though heavily fractured. In the field the total preserved length of the tusk was measured as 160 cm along the outer curvature. Following transport damage, the remaining intact distal portion that could be examined in Bandung was 103 cm along the outer curvature and 94 cm measured straight. The tusk is moderately curved. The most proximal diameter of the portion studied in Bandung is 103 mm measured in the plane of the curvature (transverse diameter) and 99.5 mm perpendicular to the curvature (dorsoventral diameter). Halfway this tusk portion these diameters are 91.5 mm and 85 mm, respectively. An elongated wear surface is developed almost parallel to the plane of curvature on one side of the distal termination. This flat wear surface is 40 cm long to the broken tip of the tusk. Halfway of this wear surface the transverse tusk diameter measures 71 mm and the dorso-ventral diameter 64 mm. If the tusk is oriented with the wear surface downward, it curves to the left in distal direction. Therefore this tusk represents a sinistral one.

Of the other tusk not brought to Bandung several measurements were taken in the field. The proximal portion including pulpa cavity was c. 70 cm long. The distal portion, of which the more proximal part was found broken in many small pieces alineated along the original position of the tusk, had an estimated length of 70 cm. The original tusk must have been at least 140 cm long. The diameter of this tusk near the pulpa cavity measured 113 mm and 111 mm at the opposite end of the proximal portion. Its curvature is similar as compared to tusk MM-3901.

Some additional isolated tusk pieces were excavated at Mata Menge and are listed in Table 8. They do not provide additional information.

Mandible, description and comparison — Of the *S. florensis* holotype mandible from Ola Bula Hooijer (1957a) only described the molars. In Table 15 the size measurements that could be taken on this mandible are given. The measurements of the mandible excavated in 1994 at Dozo Dhalu (DD-4160; Pl. 18, figs. 1-2) are also given in this Table. The Dozo Dhalu mandible is complete anteriorly and has the worn remnants of both M_1s in front and the slightly worn M_2s with their posterior part still in the alveole. The sinistral horizontal ramus is broken medially, exposing the roots of the M_2. The posterior -2x ridges of the sinistral M_2 were found close to the mandible, but ridges III and IV could not be recovered and are missing. The sinistral coronoid process is intact, the dextral one largely so, but both the ascending ramii are damaged posteriorly and medially and lack the condyles. The exposed alveoles of both the M_3s in the making were found empty.

The holotype mandible is slightly smaller as compared to the smallest adult *S. t. trigonocephalus* mandible from Trinil, specimen CD-2896 (Table 15). Both mandibles belong to full-grown adult individuals: in the Flores mandible the anterior 6 ridges of the M_3 are worn versus 2 ridges of the M_3 in the Trinil mandible. Amongst the *S. t. trigonocephalus* fossils from Java, both dental and skeletal elements, the smallest specimens usually originate from the locality Trinil. This size difference can be seen in Fig. 55, where the L and W measurements of complete upper molars from Trinil and from other localities on Java are plotted. Other examples of this size difference are shown in Figs. 57, 58 & 74, in which the mandible measurements M5 (height of the horizontal ramus in front of the dental alveole), M6 (height of the horizontal ramus in front the ascending ramus) and M18 (maximum transverse width of the mandibular ramus) of mandibles in various dental wear stages from Trinil and from other localities on Java are plotted against dental wear age class. As can be seen in these figures, the *S. t. trigonocephalus* mandibles with the smallest sizes within each dental wear age class are from Trinil. The larger specimens from Trinil overlap in size with mandibles from other localities in Java. The adult mandibles from Trinil tend to split vaguely into two size-groups, presumably representing males and females. The four largest Trinil mandibles in Fig. 74 probably represent males. It must be noted that the largest Trinil specimen, Coll. Selenka no. 823, according to Pohlich (1911) originates from a younger layer than the so-called 'Hauptknochenschicht', from which the remaining Trinil specimens originate. Specimen CS-823 therefore should not be allocated under the Trinil specimens properly, but belonged to a younger population with possibly on average larger body-size. The 2 smallest adult Trinil mandibles, specimens CD-2433 and CD-2896 (Fig. 74), almost certainly belonged to female individuals. In the Figs. 57, 58 & 74 also the measurements of the *S. florensis* holotype mandible and the mandible from Dozo Dhalu (DD-4160) are plotted. The holotype mandible belonged to an old individual whereas specimen DD-4160 belonged to a young adult. As can be seen in these figures, the two mandibles have comparable M5 and M6 values, smaller than in the smallest *S. t. trigonocephalus* mandibles of comparable dental wear stage. The *S. florensis* holotype mandible has a thicker horizontal ramus (measurement M18, Fig. 74) than the Dozo Dhalu mandible. Its M18 value falls within the range of the values measured in the smallest adult *S. t. trigonocephalus* mandibles (specimens CD-2896 and CD-2433), that are thought to represent females.

It follows that apart from the differences in dental morphology already treated earlier, the *S. florensis* mandibles are smaller in size than *S. t. trigonocephalus* mandibles of comparable dental wear stage, with a slight overlap of some size parameters with the smallest (female) specimens from Java. The Dozo Dhalu mandible is relatively slenderly built, whereas the holotype mandible of *S. florensis* is more robust. Possibly, the latter mentioned belonged to a full-grown male and the Dozo Dhalu mandible to a subadult female of *S. florensis*. However, because both mandibles originate from different localities, an alternative explanation may be that the Dozo Dhalu mandible is slightly younger in age and represents an on average somewhat more size-reduced population of the same lineage.

In both mandibles the width of the molars and of the associated occlusal surface (measurement M25) is not excessively great compared to the width of the mandibular ramus (M18), as is the case in *S. sondaari*. The M25/M18 ratios observed in the two *S. florensis* mandibles (0.44 and 0.38, respectively) fall within, or are only slightly less than the range observed in adult *S. trigonocephalus* mandibles (M25/M18 ratios ranging between 0.40 and 0.53 versus 0.62e in the very small-sized *S. sondaari* holotype mandible; Tables 13 & 15).

Postcranial elements, description and comparison — Verhoeven collected various postcranial remains at the localities Ola Bula, Boa Leza and Mata Menge, all localities which have only yielded molars attributable to *S. florensis*. Hooijer (1957a, 1972a) gives size measurements of the following elements: atlas, epistropheus, vertebra thoracale, humerus, ulna, lunatum, magnum, unciforme, femur, tibia, patella, astragalus (juv.?), calcaneus (juv.), naviculare and metatarsal IV. Not all these bones are represented by complete specimens. For all the bones of which homologues of *S. trigonocephalus* are known, it followed that the Flores bones were smaller than the variation ranges of the Javanese stegodont, except for the height measurement of one thoracic vertebra (Hooijer 1957a, 1972a).

A tibia and various other postcranial elements from Mata Menge can be added here to the hypodigm of *S. florensis*, while more fossil material from Dozo Dhalu awaits preparation and examination in Bandung. The examined postcranials excavated at Mata Menge and Boa Leza are listed in Table 8.

Atlas: An atlas fragment from Mata Menge consists only of the right side of the arch (MM-4126). No measurements could be taken, but comparison with the *S. florensis* atlas from Ola Bula reveals that the present fragment has only slightly smaller proportions than the Ola Bula atlas.

Vertebrae: A vertebra thoracale (MM-3902) lacks the dorsal spine and the sinistral transverse process. The corpus has two costal articulation facets on both lateral sides, indicating that it is from the more cranial portion of the thoracic vertebrae sequence. The epiphysal disks are not yet fully fused in this specimen. An other thoracic vertebra (MM-4121) with a single costal facet on each side of the corpus, is of the caudal portion (vertebra thoracale XVI-XVIII). Measurements of both vertebrae are listed in Table 20 together with those of *S. sondaari*. The *S. florensis* vertebrae are clearly larger than those of *S. sondaari* and those of the pygmy elephantoids from Sulawesi (Table 18). Hooijer (1955b) gives some measurements of various thoracic vertebrae attributed to *S. trigonocephalus*. In two specimens from Trinil the transverse diameters of the fossa articularis on the corpus are 90 mm and 130 mm wide and the vertical diameters are 80 mm and 110+ mm, respectively. The smallest of these two vertebrae, which belonged to a full-grown individual, has a similar size as both Flores specimens.

Humerus: A complete, though poorly preserved *S. florensis* humerus was excavated at Mata Menge in 1994. The specimen awaits preparation and no measurements could be taken yet. A superficially eroded distal epiphysis of a sinistral humerus was surface collected on the Ola Bula plateau (GRDC F/OB-3806). This specimen has the same dimensions (Table 23) as the other humerus known from Ola Bula, of which Hooijer (1957a: 125) gave some measurements. Hooijer (1972a) also gave some measurements of a complete humerus from Mata Menge, which is slightly larger than the Ola Bula specimens (Table 23). Here a remark should be made concerning the morphology of the Ola Bula humerus, which is housed in the NNM collection (the present depository of the Mata Menge humerus is not known). The humeri of *S. sompoensis* and *"Elephas" celebensis* from Sulawesi can be distinguished based on a distinctive character mentioned by Ariëns (1995), as was mentioned earlier in this thesis. In *Stegodon* the deltoid crest is heavier built than in *Mammuthus* and *"E." celebensis*, and its lateral border is convex over its entire length, while it is straight in *Mammuthus* and *"E." celebensis*. Examination of the Ola Bula humerus revealed that its deltoid crest has the convex shape conform *Stegodon*.

Ulna: A sinistral ulna diaphysis (MM-4119) has a minimum transverse diameter (measurement U3) of 69 mm and a minimum antero-posterior diameter (measurement U4) of 64 mm. Measurement U3 ranges between 70 and 105 mm in *S. trigonocephalus* ulnae (Hooijer, 1955b: tables 31, 32). Specimen MM-4119 has larger proportions than a full-grown proximal ulna fragment from the Verhoeven collection, which was mentioned earlier by Hooijer (1957a: 125). The minimum diaphysis diameters could not be measured in this specimen because the shaft is broken more proximally. However, the diameters at the broken end are 62 mm (transverse) and 48 (antero-posterior), which is already smaller than the minimum diameter values in the Mata Menge ulna fragment.

Carpalia: A dextral lunatum (MM-4147) from Mata Menge is damaged on the posterior side. Its maximum transverse diameter over the articulation surfaces for radius and ulna and measured parallel to the anterior border is 102 mm. The antero-posterior diameter of the radius surface cannot be taken but was at least 74+ mm. The height measured anteriorly at the medial side 44 mm. Hooijer (1972a: table 10) gives some measurements of two lunata, one from Mata Menge and one from Boa Leza. The anterior heights at the medial side are given as 36 mm and 50 mm, respectively, so that the present specimen appears of intermediate size.

A dextral trapezoideum (MM-4127) is complete apart from some superficial damage of the distal articulation facet. The antero-posterior diameter of the proximal articulation facet (measured parallel to the medial surface with facets for articulation with the magnum = measurement Td1 of Mol et al., 1999) is 59 mm and the transverse diameter of the proximal articulation facet (measured parallel to the anterior surface = measurement Td2 of Mol et al., 1999) is 44 mm. The maximum height anteriorly (measurement Td4 of Mol et al., 1999) is c. 36e mm. The present specimen is even smaller than a trapezoideum attributed to *Anancus arvernensis* by Mol et al. (1999), in which the measurements Td1, Td2 and Td4 were given as 84 mm, 46 mm and 52 mm, respectively.

Pelvis: A dextral pelvis from Mata Menge (MM-4146) has the acetabulum and large portions of the ilium, ischium and pubis preserved. The symphysis is broken as well as the anterior edge of the ala ossis ilium. The least transverse diameter of the ilium just above the acetabulum (measurement P4) is 123 mm. The dorso-ventral diameter of the acetabulum (P2) is 112 mm. The least transverse diameter of the ischium (P5) is 64 mm, the least antero-posterior diameter of the pubis (P6) is 57 mm. Hooijer (1955b) presented some data on various *S. trigonocephalus* pelvis fragments. Taking only those specimens from Trinil, which include the smallest pelvis remains from Java of that species, measurement P2 was found varying between 125 and 150 mm (average 133 mm, n = 7) and measurement P4 between 120 and 165 mm (average 143 mm, n = 8). Again, the *S. florensis* pelvis is found slightly smaller than the smallest Trinil specimens, or equaling the size of the smallest Trinil pelvis. In *S. florensis* the anterior expansion of the ilium is less abrupt and the ilium relatively narrow and elongated as compared to the ilium of *Elephas* or *Mammuthus* and conforms the shape encountered in *S. trigonocephalus* as mentioned by Ariëns (1995).

Femur: In 1994 a dextral femur (MM-4120) was excavated from Unit 1 at Mata Menge, at close proximity from the above mentioned humerus. Though entirely embedded in the sediment, the poor preservation of both the epiphyses did not allow to recover the femur intact. Only the diaphysis is well preserved. The distal medial condyle is still connected to the shaft but superficially damaged. The poorly preserved caput does not fit to the broken proximal portion of the shaft. It could be noted in the field that the distal epiphysis was fused with the shaft and the present femur can be attributed to an adult individual. Its measurements, and those of some other *Stegodon* femurs from Flores and Java are given in Table 26. Specimen CD-4315 is a dextral femur which forms a pair with specimen CD-4314. The pair originates from Trinil and represents the smallest full-grown femurs that were attributed to *S. trigonocephalus* by Hooijer (1955b). The *S. florensis* femurs appear to be all smaller than those of *S. trigonocephalus*. The specimens from Ola Bula are somewhat smaller than those from Mata Menge, a tendency encountered in most postcranial and dental remains. The two Ola Bula fragmentary specimens, of which the larger fragment mentioned by Hooijer (1957a) was certainly mature, are even smaller or of equal size as compared to the two largest pygmy elephantoid femur remains from South Sulawesi (compare with femur measurements in Table 25). Furthermore, it can be noted that the excavated femur from Mata Menge (MM-4120) has well developed tuberosities for attachment of the biceps femoris on the disto-lateral edge of the diaphysis. The diaphysis bends markedly to the medial side at the level of these tuberosities, which is characteristic for *Stegodon* femurs as opposed to femurs of *Mammuthus*, which have a straighter femoral shaft (Ariëns, 1995).

Patella: A dextral patella (MM-4142) has a total length of 97 mm, a width of 76 mm and an antero-posterior diameter of 60 mm. In two patellae from Ola Bula mentioned by Hooijer (1972a: 23-24) the length is 75 mm and 120 mm and the widths 60e mm and 95 mm, respectively. Age differences rather than specific differences presumably account for the size variation.

Tibia: A dextral tibia (GRDC F/M-3807) was excavated at Mata Menge in 1991 from the sandstone interval of Unit 2. The medial portion of the distal epiphysis is broken as it was sticking out from the sediment, and the proximal epiphysis is much damaged. Both epiphyses are fully fused with the shaft. A rough estimate of the length, measured from the inter-condyloid eminence to the distal articulation surface, would be 450e mm. The proximal transverse diameter measures c. 145e mm but the proximal antero-posterior diameter cannot be taken. The minimum transverse diameter of the shaft is 71 mm and the minimum antero-posterior diameter of the shaft is 62 mm. The minimum circumference of the shaft is 216 mm. In eight adult *S. trigonocephalus* tibias from Trinil the length varies between 440 and 605 mm (Hooijer, 1955b). As pointed out by Hooijer (1955b), the tibias, like the other limb bones, are relatively more expanded in relation to their length as compared to *Elephas*. This is expressed by the greater ratio indices in *Stegodon* between the transverse and antero-posterior diameters on the one side and the length on the other. In specimen F/M-3807 the ratio between the minimum symphysal transverse diameter and the length amounts to 0.16, which is conform this ratio variation in *S. trigonocephalus* (ranging from 0.15 to 0.17). In two out of three *E. maximus* tibias mentioned by Hooijer (1955b) this ratio was found smaller than the smallest limit of the range of variation encountered in *Stegodon*, and equal to the lowest ratio of *Stegodon* in the other tibia (ratio varying between 0.12 and 0.15).

Discussion

The Stegodontidae have been rather conservative in their molar morphology relative to the more rapidly evolving molars of the Elephantidae genera *Elephas* and *Mammuthus*. The M_3s of the two terminal species within the latter genera, the extant *E. maximus* and the Late Pleistocene *M. primigenius*, have up to 29 and 25 lamellae, respectively (Maglio, 1973; Roth & Shoshani, 1988). The heights of the molar lamellae are almost 2 times their widths in *M. primigenius* and exceed even 2 times the width in *E. maximus*. The stegodonts with the most evolved dentitions, on the other hand, never reached more than half the amount of ridges in their M_3s as found in *E. maximus*, and their roof-shaped ridges became never higher than wide. Because the number of molar ridges increased more slowly in the stegodonts, it is sometimes difficult to distinguish species on molar morphology alone, let alone when the fossil material is fragmentary. Even if the molars are complete, specific distinction can be a tricky business. The Siwalik species *S. ganesa* and *S. insignis* may serve as an example. Both were first described by Falconer (1846). Though highly distinctive in skull morphology, Lydekker (1876) found it impossible to separate the two species on molar morphology and he concluded that *S. insignis* and *S. ganesa* were the females and males of a single collective species, respectively. This view was followed by Osborn (1943), who considered *S. ganesa* as a junior synonym of *S. insignis*. However, as pointed out by Saegusa (1987), *S. ganesa* and *S. insignis* with its aborted frontal region both share some unique derived characters with other stegodont species but not with one another, and therefore they should be really treated as two distinct species, despite their similarity in molar morphology.

The M^3s in the skull of *S. ganesa* in the BMNH (M-3008) cannot be differentiated from homologue molars of *S. trigonocephalus* either, apart from their superior size. Also in adult skull morphology, *S. ganesa* and *S. trigonocephalus* are very similar, only differing in absolute size and in the relatively narrower external nasal aperture in *S. trigonocephalus* (Seagusa, 1995). One could really ask whether the Javanese species should not be considered as a subspecies of *S. ganesa*, as was done originally by Dubois (1908).

On the other hand, the molars of the stegodont from Member B of the Ola Bula Formation on Flores, can be distinguished from *S. t. trigonocephalus* by their molar morphology. Apart from their smaller size, the Flores molars are relatively narrower and more hypsodont and, in the case of the M3s, possess one or two ridges more than equivalent molars of the Javanese stegodont. Hooijer (1957a, 1972a) found these differences not sufficient to allow for specific separation (from the Javanese stegodont), and he named it *Stegodon trigonocephalus florensis*.

In chapter 2 it was proposed to separate *S. trigonocephalus* from Java into 3 chronosubspecies, which are from old to young *S. trigonocephalus praecursor*, *S. t. trigonocephalus* and *S. t. ngandongensis*. This distinction is based on the notion that the number of ridges per molar was found higher in the fossils from the younger Ngandong locality as compared to those from the older Trinil and Kedung Brubus localities. A single M_3 predating the Trinil Fauna has only 11 ridges versus 13 in the Trinil specimens. Apart from these differences in ridge numbers, there are in fact no other criteria to discriminate between the molars, which is the reason why they were not treated as separate species.

However, the Flores stegodont does have additional distinctive characters in tooth morphology, apart from the higher number of ridges in the M3: 1) the larger hypsodonty, 2) its comparatively small overall size, and 3) the relatively narrow molars. Particularly the increased hypsodonty reveals an adaptation to a distinct type of food consumed as compared to the Javanese stegodont, and therefore suggests a different environment and way of life. Based on these considerations it is felt justified to abandon the view that the Flores stegodont would differ at most on a subspecies level from the Javanese stegodont. Consequently, the Flores stegodont is considered as a separate species: *Stegodon florensis* Hooijer, 1957.

The palaeogeography supports the view to consider the Java and Flores stegodonts as distinct species. The fauna that accompanies the Flores stegodont from Member B of the Ola Bula Formation, and the fauna that precedes it (from the locality Tangi Talo), are both very poor in species and clearly endemic, indicating isolated insular conditions. This indicates that the Flores faunas evolved under isolated conditions, favouring speciation. Most SE Asian mammals that became divided into various populations after the Holocene sea level rise, can be distinguished nowadays on the subspecies level, like e.g. *Elephas maximus sumatranus*, which is the smallest extant subspecies of the Indian elephant. Those that have been isolated from the mainland stock for longer periods tend to have evolved into distinct species, like various endemic mammals of Sulawesi and Flores, both fossil and extant (Figs. 44 & 70). Geological and faunistic evidence supports the view that Flores was separated from Java throughout the Pleistocene, and ample time would have been available to promote speciation.

Because skull material is still lacking it cannot be excluded that *S. florensis* is closely related to *S. trigonocephalus*, as was originally proposed by Hooijer (1957a). In that case it could have reached Flores by crossing the narrow straits between Bali and Lombok and between Sumbawa and Flores. Alternatively, the founder population of *S. florensis* may have arrived also from the North, via Sulawesi. On the latter island we now have proof for the existence of at least two stegodont species. One is *S. sompoensis*, inhabiting South Sulawesi at 2.5 Ma, and which, based on skull material, shows close relation with the *S. trigonocephalus* group. The other, *Stegodon* sp. B occurs in the Middle Pleistocene Tanrung Formation and has been also present on the island of Sangihe. Apart of having slightly larger molars and mandible proportions, *Ste-*

godon sp. B resembles *S. florensis* much in molar morphology. Skull material of *S. florensis* would be required to allow better resolution of its taxonomic relationships.

7. Palaeozoogeography

The Elephantoidea from the SE Asian islands

Since new material of pygmy stegodonts has become available from Flores and Sulawesi, and the stratigraphy of the vertebrate-bearing beds on these islands is better known now, it could be demonstrated in the preceding chapters that the pygmy stegodonts from Timor, Flores and Sulawesi are clearly different from one another. The observed differences in size and morphology between *S. sondaari* sp. nov., *S. sompoensis* and *S. timorensis*, are thought to reflect in the first place different ancestral mainland species and different times of island colonization, besides different degrees of dwarfing. The smallest of these dwarf stegodonts, *S. sondaari* from Flores, is slightly smaller than *S. timorensis* from Timor, whereas *S. sompoensis* from South Sulawesi is on average larger than the two just mentioned dwarfs. The earliest *S. sompoensis* remains are now dated as Late Pliocene, c. 2.5 Ma, while *S. sondaari* from Tangi Talo is dated late Early Pleistocene (c. 0.9 Ma). However, the latter seems to have been derived from a more primitive ancestor than *S. sompoensis*. *S. sondaari* was replaced on Flores by a larger, only slightly size-reduced stegodont, *S. florensis*, around the Early/Middle Pleistocene transition. For *S. timorensis* no datings are available as yet, but this species appears more advanced in plate formula than the other two dwarfs, and may have been derived from *S. florensis* somewhere during the Middle or Late Pleistocene. The same might be true for the poorly known *S. sumbaensis* Sartono from Sumba.

Apart from the true dwarf stegodonts, intermediate-sized stegodonts can be recognized on the same islands in younger strata. The already mentioned *S. florensis* has molar and mandible dimensions that are slightly smaller than those of *Stegodon* sp. B; the latter species is now recorded from Middle Pleistocene deposits on South Sulawesi and also from the small island of Sangihe. Both have larger molar and mandible dimensions than *S. sompoensis*. On Java even more varieties of stegodonts can be recognized. A huge mandible from Bukuran is attributed here to *S. elephantoides*. Its age can be estimated at 1.2-1.3 Ma. Three time-successive subspecies of *S. trigonocephalus* can be distinguished as well. The oldest, poorly known subspecies is *S. t. praecursor*, which predates the Trinil Faunal stage at 0.9 Ma. This subspecies is succeeded by *S. t. trigonocephalus*, which is best known from the localities Trinil and Kedung Brubus, and dates back from 0.9 Ma to 0.7 Ma. The fossils from Trinil are on average slightly smaller than those from Kedung Brubus, which may point to isolation of Java at the time of the Trinil Fauna. *S. t. ngandongensis* from the locality Ngandong appears to have a more advanced plate formula of the milk and intermediate molars, but it is insufficiently known. A late Middle or early Late Pleistocene age is estimated for the Ngandong Fauna.

Also on Java various dwarf stegodonts can be distinguished, though all are poorly represented in the fossil record. One is *S. hypsilophus*, from an unknown stratigraphic level in East Java. Two (yet unnamed) dwarf *Stegodon* species, one from Sambungmacam (Aziz & van den Bergh, 1995) and the other from the surroundings of Cirebon, West Java (this thesis), differ from *S. hypsilophus* in their lower hypsodonty and/or lower plate formula. The Cirebon dwarf *Stegodon* seems to be the most primitive one, and may have been derived from *S. elephantoides* during times of isolation. The occurrence of a pygmy *Stegodon* on the island of Sumba has been reported by Sartono (1979a), and also from the Philippine islands of Luzon and Mindanao dwarf *Stegodon* species have been recorded (von Koenigswald, 1956). The whole range of sizes encountered in Indonesian stegodonts is shown in Fig. 74, in which the values of size parameter (M18) taken on mandibles pertaining to various species are plotted against dental wear age classes.

Apart from dwarfed stegodonts, there are also a few dwarfed elephants known from island SE Asia. Best known is the Late Pliocene to Early Pleistocene dwarf elephantid *"Elephas" celebensis* from the Walanae Fauna on South Sulawesi, which co-occurs with *S. sompoensis*. An elephant of distinctly small size, but clearly more high-crowned, has been reported by von Koenigswald (1956) from Luzon. It has been named *Elephas beyeri* von Koenigswald, 1956, and probably evolved from *E. namadicus*. On Java the earliest known elephantid is represented by an isolated molar from Ci Panglosoran river in the Bumiayu area on west Central Java. This molar is attributed to *"E." indonesicus* (Kretzoi, 1950), a dwarfed form of presumably Late Pliocene or Early Pleistocene age (van den Bergh et al., 1992). *"E." indonesicus* seems to be closely related to *"E." celebensis*. Both are moderately hypsodont and share some primitive dental features. They were probably derived from the earliest mainland elephantids reaching SE Asia (van den Bergh et al., 1992).

A clearly high-crowned *Elephas* species originates from younger deposits in South Sulawesi (represented by a single unworn molar fragment, which presumably originates from the Middle Pleistocene Tanrung Formation). The molar fragment, though only consisting of 2 lamellae, indicates that probably a large-sized or in any case only slightly size-reduced *Elephas* species is concerned. Other, undoubtedly large-sized *Elephas* remains from South Sulawesi consist of 2 metacarpalia. These surface-collected metacarpalia probably originate from deposits unconformably overlying the Tanrung Formation, as suggested by their attached matrix.

The first advanced elephant with high-crowned molars that reached Java is *Elephas hysudrindicus*, present in the 0.8-0.7 Ma old Kedung Brubus Fauna. Perhaps also another specialized and high-crowned *Elephas* species reached Java during the Middle Pleistocene, but the lack of complete molars or skull material hampers identification at the species level of many molar fragments. Von Koenigswald (1934, pl. IV, fig.10; 1940, pl. III, fig. 13) figured a mandible with both M_3s from the 'unteren Konglomerat- und Tuffschichten östlich von Kampong Bapang bei Sangiran' (= Bapang Formation of GRDC-JICA joint study team, 1995). The mandible was attributed to *E.* ex aff. *namadicus*. The molars have at least 19 ridges, but are still partly concealed in the alveole. The molars are between 6.5 and 7 cm wide and at least 27 cm long as reported by the author. Hooijer (1955b) attributed this mandible, besides a large number of molars and molar fragments in the Dubois Collection, to *E. hysudrindicus*, noting that molars may show overlap with the extant *E. maximus*, but emphasizing that the skull of the Javanese fossil elephant is clearly distinctive from *Paleoloxodon namadicus* and *E. maximus*. However, there has been only one partial *E. hysudrindicus* skull from

Java described so far (from the locality Tinggang), which is figured in the same paper (Hooijer, 1955b, pl. XIV, figs. 1-2). It is possible that the widespread *Elephas namadicus* may be represented amongst the many molar fragments from Java. A molar fragment said to have been found northeast of Samarinda (East Kalimantan), was attributed to *P.* cf. *namadicus* by Hooijer (1952).

Elephas maximus may be present in the Punung Fauna, but the material on which this assumption is based is rather fragmentary. *E. maximus* is certainly present in a layer of Late Pleistocene age (c. 30 ka) at the recently discovered west Javanese locality Cipeundeuy. *E. maximus* is also recorded from the caves Lida Ajer, Djambu and Sibrambang in West Sumatra (Hooijer, 1955b). The material from Jambu cave has been dated at 60-70 ka, while the Lida Ajer material gave a date of 80 ka. (Skelton & de Vos, in prep.). Subfossil *E. maximus* remains have also been reported from Niah cave on Borneo (Medway, 1979) and from Bangka (Martin, 1884). A single M^3 of *Stegolophodon lydekkeri* Osborn, 1936, originates from Brunei, Borneo, from an unknown stratigraphic level and locality (Medway, 1972). Pleistocene or older fossils from Borneo are extremely rare. The lack of uplifted and eroded Pleistocene terrestrial deposits on nowadays stable Borneo may account for the scarcity of fossil sites on this island.

It follows that dwarf stegodonts clearly outnumbered dwarf elephants in the SE Asian region (7-9 versus 3 species). Obviously, in the SE Asian region stegodonts were more successful in colonizing islands than elephants. In contrast, many Mediterranean islands were exclusively colonized by elephantids during the Plio-Pleistocene. This must be ascribed to the fact that stegodonts never reached Europe and were only briefly present in Africa.

Ways of dispersal

Originally, the fossil mammalian faunas of Java were interpreted as descendents of an ancient Indian stock (Martin, 1884; Dubois, 1908). The dispersal to Java was attributed primarily to the former existence of land-bridges. The islands west of Sumatra as well as the Nicobar and Andaman Islands were seen as a continuous (nowadays mostly submarine) ridge, which could have been exposed during the Plio-Pleistocene, thus serving as a migration route from Burma to Sumatra and Java (Molengraaf, 1922; Rensch, 1936). However, none of these ‘ridge’ islands have produced fossils of an ancient continental fauna to date.

Von Koenigswald (1935a,b) distinguished 7 biostratigraphic units on Java. According to him the dispersal of mammalian faunas to Java took place in 3 steps: 1) During the Pliocene the exposed Sunda Shelf (Fig. 1) allowed migration to Java of the so-called Siva-Malayan Fauna. The land-connection was considered as of short duration and the mammal dispersal was thought to be not very extensive. 2) During the Pleistocene a more long-lasting connection via the Philippines and Borneo was suggested, which allowed dispersal of the so-called Sino-Malayan Fauna to Java. This hypothesis was based on the assumption that certain elements from the Javanese Pleistocene were of Chinese origin, on the presence of a Pleistocene fauna in Taiwan and on the Philippines and on the lack of fossil evidence from the Sunda shelf area. At that time fossil mammals from Sulawesi had not been discovered yet. 3) The modern fauna was thought to have entered Java during the latest Pleistocene, when Java, Borneo, Sumatra and the Malay Peninsula were united for a short episode.

De Terra (1943) and Colbert (1943) suggested that the Javanese Siva-Malayan and Sino-Malayan Faunal elements could have originated from a secondary ancestral stock, such as found in Burma, rather than from Indian and Chinese sources. They favoured migration to Java from SE Asia (Burma) via the exposed Sunda Shelf, though de Terra (1943) stated that the route via Taiwan and the Philippines to Sulawesi could have been an alternative, but not an exclusive Pleistocene route. On his map (de Terra, 1943) the route via the Philippines does not reach Java and also Colbert (1943) rejected the idea that a mammalian fauna could have reached Java via the Philippines.

The discovery of fossil vertebrates on Sulawesi and Flores and later on Timor and Sumba, proved that various large mammalian taxa, notably elephantoids, had been able to cross Wallace's line. Adhering to the hypothesis that dwarfing occurred repeatedly on different islands at different times, the dwarf stegodonts from Flores, Timor and Sulawesi were initially thought to be the result of parallel evolution (Hooijer, 1972a). This author believed that the Philippines might have played a role in the dispersal to Sulawesi. According to an alternative hypothesis, put forward subsequently by Audley-Charles & Hooijer (1973) and Hooijer (1975, 1982b), the dwarf stegodonts of the various islands would have formed part of a single interbreeding population. The various islands were supposed to have been connected by landbridges in the past, and the entire interconnected area was called 'Stegoland'. This idea was met with skepticism (Simpson, 1977; Sondaar, 1981; Musser, 1987; Aziz, 1990). It is shown in this thesis that the pygmy stegodonts on the various islands are clearly different from one another. But also other fossil faunal elements, such as the giant tortoises of Flores and Sulawesi, can be distinguished from each other at least on size (the tortoise material has not been studied in detail here, but perhaps also morphological differences will show up besides the observed size differences). Sondaar (1981) argued that different islands had different tortoise species, analogous to the various species inhabiting the Galapagos Islands. The postcranial *Geochelone* material recently excavated at Tangi Talo, Flores, is on average approximately two times smaller in linear dimensions than the *Geochelone* postcranials from South Sulawesi and Timor, suggesting isolation of the tortoise populations on these islands. If former land connections existed between the three islands, as has been suggested by various workers (Audley-Charles & Hooijer, 1973; Hooijer, 1982b; Azzaroli, 1996), it could be argued that other endemic fossil species, such as *Celebochoerus heekereni*, *"Elephas" celebensis* and *Varanus komodoensis*, should be common elements in the fossil faunas from the three islands, which is not the case, however (see also endnote 3).

Also the Recent mammalian faunas from Flores, Timor and Sulawesi have little in common besides some widely distributed flying mammalian species and terrestrial mammals that were certainly introduced by humans (Groves, 1976; Cranbrook, 1981; Musser, 1987). Based on an analysis of extant and fossil faunal elements, Groves (1976, 1985) concluded that the faunal elements from Sulawesi bear closest relationships with forms from the Middle Siwaliks. He thought it most likely that this fauna had entered Sulawesi via the Makassar Strait, some of the smaller elements even reaching Sangihe and Talaud. Mainly based on the Recent faunas, the author discarded faunal links between the Philippines and Sulawesi, but suggested instead a migration route to Sulawesi across the present Strait of Makassar, narrowed or closed by a land connection during the Pleistocene. Hooijer (1975), on the contrary, considered the Philippine islands Luzon and Mindanao as an important link in the dispersal route of ancient Asiatic faunal elements to Sulawesi.

Based on the total absence of species of freshwater fish in Sulawesi other than those likely to have been introduced by humans, Cranbrook (1981) concluded that there has been no direct, unbroken connection between Sulawesi and the principal landmass of the Sunda shelf. He considered the mammalian fossil evidence as too fragmented to draw firm conclusions concerning migration routes between Sulawesi, the Philippines, Java, and the islands of the Banda Arc. In his view the distribution of stegodonts and bats throughout the SE Asian Archipelago demonstrated the availability of dispersal routes only open to large herbivorous and flying mammals. He further noted that direct, ephemeral land connections might have existed between South Sulawesi and the Lesser Sunda Islands, as suggested by floral evidence. These conclusions were also reached by Musser (1987), who further noted that overseas migration of mammals to Sulawesi might have begun already during the Late Miocene or Early Pliocene.

With the exception of the phalangers, the origin of the native Sulawesi faunal elements was mainland Asia. Musser (1987) also speculated that the fossil fauna from South Sulawesi might have lived on a separate palaeo-island, and was unrelated to the extant Sulawesi fauna. Based on extensive fieldwork, Aziz (1990) was able to confirm this idea. He concluded that what he called the Walanae Fauna only contained extinct vertebrates, viz. *S. sompoensis*, *"E." celebensis*, *Geochelone atlas* and *Celebochoerus heekereni*, and that species that are still extant on Sulawesi, such as *Anoa depressicornis* and *Sus celebensis*, were not present in the Walanae Fauna. Aziz (1990) was also of the opinion that the ancestors of the various fossil vertebrates of Sulawesi could have reached Sulawesi only by means of overseas dispersal and that there had been no links with the Philippines. This opinion had also been expressed by Braches & Shutler (1984), who doubted that the Philippine route played a major role in the dispersal of the so-called Sino-Malayan Fauna to Java, and found it questionable that a landbridge ever existed between the Philippines and Taiwan or the Chinese mainland. They deemed it possible that elements of a land fauna, capable of crossing salt-water barriers and originating from Sundaland and/or China, became isolated on Luzon throughout the Pleistocene, allowing a typical endemic Philippine fauna to evolve. Heaney (1985) saw no evidence for the former existence of any substantial landbridges to the main body of the Philippines during the Middle or Late Pleistocene, but he postulated a Middle Pleistocene connection from the Palawan chain to Borneo at a time when Borneo was part of the Asian land mass.

Implications of the new chronological framework for the faunal succession of Java

The new biostratigraphic scheme for Java as proposed by de Vos et al. (1982) and Sondaar (1984) has been discussed already in chapter 2. Adhering to this new faunal succession, which is based on faunas originating from single localities, it follows that the faunal elements considered by von Koenigswald (1935a, b) to be typical of Chinese origin, such as *Pongo* and *Hylobates*, are not represented in the Early and Middle

Pleistocene faunas of Java. Von Koenigswald's (1935a,b) concept of the Early and Middle Pleistocene Djetis and Trinil Faunas was shown to be erroneously based on the mixing of the Late Pleistocene Punung fissure assemblage (which dóes contain purely Chinese elements) with older faunal assemblages (de Vos et al., 1982; Sondaar, 1984). In fact, older Javanese faunas are dominated by either species only recorded from the Siwaliks and SE Asia, or by species having a much wider distribution, including China (see also endnote 4). The typical Chinese elements had their first appearance on Java in the Late Pleistocene (Punung Fauna). The Punung Fauna is a tropical rainforest fauna which shows close resemblance to Late Pleistocene faunas recorded from Sumatra (Lida Ayer, Djambu and Sibrambang caves), Borneo (Niah), Vietnam (Lang Trang) and to the South Chinese fissure faunas of Kwangsi and Yunnan (de Vos, 1983; de Vos, 1996; Long, 1996; de Vos et al., in press). According to these authors dispersal towards Java initially took place by means of sweepstake dispersal (sensu Simpson, 1965) during the Early Pleistocene, via the Siva-Malayan route (Satir Fauna sensu Sondaar, 1984). During the late Early Pleistocene a limited land connection was thought to have come into existence between Java and the Asian continent, allowing more species to enter Java via the same Siva-Malayan route, this time constituting a filter route (Trinil H.K. Fauna sensu de Vos et al., 1982). This dispersal wave included *Homo erectus*. Towards the end of the Early Pleistocene and during the Middle Pleistocene periodically more extensive land connections came into existence, allowing fully balanced mainland faunas to enter Java via the Siva-Malayan route (corridor route). Van den Bergh et al. (1996) correlated the formation of this corridor route with the marked and long-lasting glacio-eustatic sea-level lowerings that started at c. 0.8 Ma. Faunal composition of the 0.8-0.7 Ma Kedung Brubus Fauna and the younger Ngandong Fauna suggests that palaeo-environments on Java were mainly marked by open woodlands (de Vos & Sondaar, 1982; Sondaar, 1984). Relatively dry conditions associated with this type of environment would be in accordance with fully emerged Sunda and Sahul Shelves (Bellwood, 1985).

A fauna of Chinese origin did not enter Java until the Late Pleistocene (de Vos, 1983; de Vos, 1996; Long, 1996; de Vos et al., in press). This dispersal probably took place during and shortly after the penultimate low sea-level stand of the Saale Glaciation, when the Sunda Shelf was fully emerged, allowing dispersal from southern China and Vietnam via the Sino-Malayan corridor route (van den Bergh et al., 1996) (see also endnote 5). The South Chinese fauna was supposedly driven south during the Saale Glaciation. At this stage *Homo sapiens* is thought to have first reached Java together with a tropical rainforest fauna (Punung Fauna sensu de Vos, 1983). During the Holocene break-up of the Sunda Shelf the faunas on the various greater Sunda Islands became impoverished in response to reduced land areas and changing climatic conditions.

Fossil faunas from Taiwan

Otsuka (1984) mentions the following taxa from the Pleistocene T'ouk'oushan Group in the Chochen district of Taiwan: stegodonts, *Mammuthus*, *Rhinoceros*, *Bubalus*, *Sus*, various cervids, *Macaca*, and *Panthera*. The author allocated these elements in the Chochen Fauna, which he considered to be of late Early Pleistocene to early Middle Pleistocene age. However, within the Chochen Fauna three time-successive zones were distinguished, from old to young: 1) the *Parastegodon akashiensis-Ste-*

godon sinensis Zone, 2) the *Elaphurus formosanus-Rhinoceros sinensis hayasakai* Zone, and 3) the *Mammuthus armeniacus taiwanicus* Zone. The oldest zone is characterized by the occurrence of 2 stegodonts, *Parastegodon akashiensis* and *S. sinensis*, and 3 to 5 cervids, including *Elaphurus formosanus*. Saegusa (1996) argued that *P. akashiensis* from Japan is synonymous with *S. aurorae*, a subhypsodont stegodont from Japan with diminutive size, which evolved from the Chinese *S. zdanskyi*. He further noted that subhypsodont *Stegodon* molars are known from Taiwan, which are very similar to those of *S. aurorae* from Japan, but that it is not clear whether their similarity is due to descendance from a common ancestor or due to convergence. As will be discussed in the next chapter, subhypsodonty is usually only encountered in dwarfed island stegodonts. Deer are also common elements in island faunas (Sondaar, 1977), and it appears likely that the fauna from the oldest mammal-bearing strata of the T'ouk'oushan Group represents an island fauna. Considering *S. sinensis*, Saegusa (1996) noted that this species is based on a fragment of a dP^3, and that several permanent molars which had been subsequently assigned to this species, can now be safely allocated to *S. orientalis*. The latter species is present in Southern China from the late Early Pleistocene until the Late Pleistocene, and invaded Japan around 0.5 Ma ago, replacing *S. aurorae* there (Kamiya, 1995; Saegusa, 1996). The Taiwanese specimens attributed to *S. sinensis* may as well turn out to be synonymous with *S. orientalis*. The latter species is in fact also recorded by other authors from different localities on Taiwan (Otsuka, 1984).

The next Zone distinguished by Otsuka (1984), the *E. formosanus-R. sinensis* Zone, is characterized by a wider range of taxa, including *Panthera* sp., *Sus* sp., *Bubalus* sp., *Rhinoceros sinensis*, and various cervids, whereas stegodonts are not recorded from this interval. *Macaca* sp. is only represented by fossils picked up from a river and has not been included in the zonation scheme of the author. The youngest, *M. armeniacus taiwanicus* Zone is similar to the foregoing zone, with the difference that it includes *Mammuthus* and that *Rhinoceros* is not recorded. In comparison to the Chinese mainland the younger Taiwanese fauna is somewhat impoverished, but the occurrence of *Panthera* gives it a continental character. Filter route dispersal has been the likely mode of dispersal towards Taiwan. It is tempting to speculate that the increased accessibility of Taiwan as recorded from the transition between the *P. akashiensis-Stegodon sinensis* Zone and the *E. formosanus-R. sinensis* Zone, could be correlated with the marked Pleistocene sea-level lowerings that started from about 0.8 Ma onwards (see chapter 2). The faunal succession of Taiwan shows much similarity with that observed in the Pleistocene of Japan, probably because both were derived from the same Chinese mainland faunas. In Japan pre-Middle Pleistocene faunas contain only stegodonts (*S. shinshuensis*, which later evolved into *S. aurorae*), cervids (including *Elaphurus*), and between c. 1 and 0.7 Ma, *Mammuthus shigensis*. From the Early/Middle Pleistocene transition onwards, an increasingly wide variety of mammalian species is recorded from Japan, including *Rhinoceros sinensis*, *S. orientalis*, *Panthera* sp., *Mammuthus armeniacus*, *Sus* sp., *Bubalus* sp. and several other mammalian species (Kamei, 1981; Kamei et al., 1988). Also here an island fauna seems to have been replaced by a more continental fauna around the Early/Middle Pleistocene transition, like in Java and Taiwan.

Fossil faunas from the Philippines and Sulawesi

The faunal succession from the Philippines is less well known, but seems to be more impoverished and endemic than the Taiwanese fauna. Von Koenigswald (1956) described various mammalian remains from the Philippines. From Luzon he mentioned some bovine and cervid teeth, a fragmentary jaw of a rhinoceros (considered an endemic species, *Rhinoceros philippinensis* von Koenigswald, 1956), remains of a giant tortoise, and various molar and tusk fragments of *Stegodon*. Amongst the *Stegodon* material is a sinistral mandibular ramus from Fort McKinley. The mandible contains an M_3 fragment with -7- ridges preserved plus a posterior rootmass showing that at least 2 more ridges were present posteriorly, judging from the plate accompanying the description (von Koenigswald, 1956: pl.IV). The molar is only 5 cm wide, indicating a dwarfed form, which was named *S. luzonensis* von Koenigswald, 1956. Two small molar fragments both consisting of two ridges were attributed to *S.* cf. *trigonocephalus*. However, the fact that the width of the preserved ridges does not exceed 64 mm, does not exclude the possibility that they belong to a pygmy stegodont. Von Koenigswald (1956) also identified a fragmentary lower molar as belonging to a pygmy elephant, which he named *Elephas beyeri*. The specimen was labeled as being from the Anda area of Cabarruyan Island. Its plate formula is -10x as far as preserved. Unworn ridges are twice as high as wide (67mm and 32 mm, respectively), suggesting that it is an highly advanced form, perhaps closely related to *E. namadicus*. The lamellar frequency is reportedly 5-6 in 5 cm, which would give a LF of 10-12 in 10 cm. According to Maglio (1973) the M_1 of *E. namadicus* has 9 to 11 lamellae, an average W of 46 mm, and a LF ranging from 6.5 to 8.1. Thus, the conclusion of von Koenigswald (1956) that the specimen represents a pygmy elephant seems valid.

A cast of a suid mandible originating from Cagayan Valley, Luzon, was kindly sent by Angel Bautista to John de Vos at the NNM. The specimen unfortunately lacks the canine and front teeth. Its molars resemble those of *Celebochoerus* as well as those of *Babyrousa*, both showing a simple molar structure. From Mindanao von Koenigswald (1956) mentioned the occurrence of a pygmy *Stegodon*. The fossil, a posterior fragment of a lower molar consisting of -4x ridges, was named *Stegodon mindanensis* by Naumann (1890). Judging from the plates originally presented by Naumann and reproduced by von Koenigswald (1956: pl. VI), the fragment most likely represents a dP_4, though von Koenigswald (1956) considered it to be a ‘permanent molar’. With a W of 37.3 mm this milkmolar would fall beyond the range of variation of the W of the dP_4 of *S. trigonocephalus* (W of dP_4 = 42.5-54 mm), and von Koenigswald was right by assigning it to a pygmy *Stegodon*. Interestingly, the unworn crown was said to be 33 mm high, which gives an h/w index of 88, comparable to that of molars of the pygmy stegodonts from Flores and Timor.

The Philippine fossil fauna appears clearly endemic and impoverished, lacking carnivores and containing various pygmy elephantoids, indicating island conditions. The ages of the Philippine faunal elements are still not ascertained.

Possible faunal links between the South Sulawesi and the Philippine fossil faunas could be *Celebochoerus*, a giant tortoise, *Stegodon*, and *Elephas*. Until more data become known of the Philippine fossil fauna(s), nothing can be stated positively concerning such relationships. What can be stated, however, is that the fossil faunal elements from Sulawesi which *possibly* bear close relationships with elements from the fossil faunas of the Philippines, are not recorded from the youngest faunal unit in South Sulawesi, namely the sub-Recent to Recent Fauna (Fig. 44). The present study revealed that there have been at least 2 *Stegodon* colonizations of South Sulawesi, widely separated in time. The Late Pliocene *S. sompoensis* present in the Walanae Fauna can be tied to the *S. ganesa/trigonocephalus* group (sensu Saegusa, 1996), and not to Chinese, Japanese or Taiwanese stegodonts, making a descendance from a Philippine invader highly unlikely. *Stegodon* sp. B occurs in Middle Pleistocene deposits on South Sulawesi and has also been found in Pleistocene deposits on Sangihe. Scanty *Stegodon* sp. remains have also been found in Central Sulawesi (van den Bergh et al., 1994). Due to a lack of skull material, phylogenetic relationships are difficult to assess. The advanced molar ridge formula of *Stegodon* sp. B suggest that it may have close links with *S. florensis* from Flores or with *S. trigonocephalus ngandongensis* from Java. Possible links with Philippine stegodonts remain questionable.

Recent faunas from Sulawesi and the Philippines

Some links may exist between the fossil mammalian faunas from Sulawesi and the Philippines, although the evidence is not convincing. The modern faunas of Sulawesi and Luzon/Mindanao, however, show marked differences, indicating that no faunal exchange took place in the more recent past. The Recent mammalian fauna of the island of Sangihe located in between Sulawesi and Mindanao includes, besides some more widespread mammals, *Phalanger celebensis*, *Callosciurus leucomus*, and *Tarsius spectrum*, all endemic species which also occur on Sulawesi (Groves, 1976). In contrast, Sangihe has no non-flying mammals in common with the Philippines, suggesting that its modern fauna originated entirely from Sulawesi. Combining a sea-level lowering of 200 m and the present-day bathymetry, it follows that still a distance of 175 km of sea would have to be crossed to reach Sangihe from the southernmost tip of Mindanao. From northern Sulawesi also a total distance of 170 km would have to be crossed, but 5 small islands in between could have been used as stepping stones, so that the largest overseas distance would be no more than c. 35 km.

Some terrestrial mammalian genera with two or more species endemic to Sulawesi appear to have undergone a radiation during a supposedly longstanding isolation. These genera include *Anoa*, *Macaca*, *Crocidura*, and various rodent genera (Fooden, 1969; Groves, 1976; Musser, 1987). Both radiative adaptations and multiple colonization events have been inferred. The modern mammalian fauna of Sulawesi has little in common with the Philippines, except for some widespread mammals and flying mammals. The extant Philippine dwarf buffalo, *Bubalus mindorensis*, is a derivative of the extant Indo-Burmese waterbuffalo, *B. arnee*, whereas the two species of Sulawesi dwarf buffalo, *Anoa depressicornis* and *A. quarlesi* are thought to have their closest progenitors in the genus *Hemibos* (Groves, 1969, 1976). *Hemibos* has been recorded from Late Pliocene Siwalik deposits older than 2.5 Ma (Hussain et al., 1992). The four to seven species of stumptail macaques living in Sulawesi nowadays are thought to have been derived from a single invader and are not closely related to the two extant subspecies of *Macaca fascicularis* living in the Philippines (Fooden, 1991). The Sulawesi macaques belong to the relatively primitive but widely dispersed *silenus-sylvanus* group. This group is thought to have spread out early, followed by extensive local extinction leading to wide gaps in the distributionary pattern of this group. The Philippine macaques, on the contrary, belong to the *fascicularis* group. One of the

Philippine subspecies, *M. f. philippinensis*, is restricted to the northern Philippine islands around the periphery of the species range, and is thought to have been isolated in the Philippines since the end of the penultimate glacial maximum (c. 160 ka). The other subspecies, *M. f. fascicularis*, occurs on the south central islands of the Philipines and also inhabits Borneo and other areas in SE Asia. It probably dispersed from Borneo to the Philippines during the last glacial maximum (Fooden, 1991).

A similar pattern can be observed amongst the suids from the area. *Sus celebensis*, a member of the *verrucosus* group and endemic to Sulawesi, is thought to have close affinity to the ancestral group of the *Sus* lineage, according to Groves (1981) who compared the various extant species and subspecies of the genus *Sus* in detail. *S. celebensis* presumably reached Central Sulawesi (not South Sulawesi as it is not recorded from the Walanae Fauna) as early as the Late Pliocene or Early Pleistocene. As a possible ancestor Groves (1981) mentioned the poorly known *S. stremmi* von Koenigswald from the Kali Glagah Formation in the Bumiayu area. Hardjasasmita (1987) studied the skulls and dentition of fossil and recent *Sus* from Indonesia. He considered the ancestor of *S. celebensis* to be either *S. macrognathus* Dubois (present in the Kedung Brubus Fauna and in the Ngandong Fauna) or *S. verrucosus* Müller & Schlegel, the extant Javanese warty pig, which descended from *S. macrognathus*. The Philippine suids, on the other hand, are considered by Groves (1981) as subspecies of *Sus barbatus*, and do definitely not represent *S. celebensis*, as had been suggested by various authors earlier. *S. barbatus* has a more widespread distribution than *S. verrucosus*, occurring in peninsular Malaysia, Sumatra, Borneo and the Philippines, but not Java. The same author further mentioned that the subspecies occurring on Palawan Island, *S. b. ahoenobarbus* Huet, is quite intermediate between the Bornean *S. b. barbatus* Müller and the subspecies distributed around the periphery of the species range, *S. b. philippensis* Nehring from the islands Luzon, Mindanao and Mindoro. This pattern again suggests that *S. barbatus* entered the Philippines relatively recently from Borneo via the Palawan ridge.

Mammalian dispersals to Sulawesi

Both the fossil and extant faunas of Sulawesi exhibit a high degree of endemism. Here I follow Cranbrook (1981) and Musser (1987) in their conclusion that there have been no uninterrupted sub-aerial connections between Sulawesi, the Philippines and Sundaland during the entire Neogene and Quaternary. The present data plead also in favour of the hypothesis proposed by Musser (1987), which implies that the southwestern Sulawesi peninsula once constituted a separate palaeo-island, separated from the northern part where the ancestors of the Recent Fauna are thought to have evolved into the modern fauna. Otherwise, it would be hard to explain why not even a single fossil, attributable to a species closely related to one of the extant Sulawesi mammals, was encountered amongst the thousands of fossils that have been excavated from layers pertaining to the Walanae Formation. Furthermore, the new fossil findings from Sulawesi and Flores described in this thesis, in combination with more accurate age assessment of the fossil faunas, allow rejection of the 'Stegoland' hypothesis. At least two waves of dispersal towards South Sulawesi can be recognized.

First wave — As has been pointed out earlier, some Walanae Fauna elements (*Celebochoerus*, *Geochelone* and perhaps *"Elephas" celebensis*) appear to have close affinity with Siwalik relatives (Groves, 1976; Cranbrook, 1981; Musser, 1987; van den Bergh et al., 1992). *S. sompoensis* can now be added to this list and it seems unlikely that the ancestors of the Walanae Fauna elements reached Sulawesi via the China-Taiwan-Philippine route. More likely, they reached South Sulawesi from the Sunda Shelf during the Pliocene (then constituting a separate palaeo-island), perhaps via one or more stepping stone islands (later on transformed into a shallow marine carbonate platform, the Recent Doang Doang Platform south of the South Makassar Basin). *"Elephas" indonesicus*, *Geochelone atlas* and the pygmy *Stegodon* from Sambungmacan, all from the older, Late Pliocene to Early Pleistocene fossil-bearing strata on Java, could represent descendants from the same ancestral stocks that continued their way towards South Sulawesi. *Anoa* and *Sus* may also have reached Sulawesi relatively early, but our evidence suggests that these taxa crossed the Makassar Strait towards what is now Central Sulawesi. These taxa do not seem to have reached the South Sulawesi palaeo-island until that part was connected with the rest of Sulawesi in the course of the Pleistocene. *Babyrousa* may be the only large mammalian taxon of which the progenitors reached Central Sulawesi at a very early date already, i.e. during the Paleogene. Thenius (1970) could see no common ancestor with the other Suidae more recent than Oligocene forms. It is possible that during the mid-Oligocene, when the last sub-aerial connection with the Sunda Shelf may have existed (see chapter 3), the ancestral population reached Sulawesi over land. From the above it may follow that multiple colonization events were probably responsible for the mammalian population of Sulawesi, rather than a single dispersal wave as suggested in the heading of this part. However, when considering the Walanae Fauna from the palaeo-island of South Sulawesi alone, the present data suggest a longstanding faunal equilibrium from c. 2.5 Ma until the end of the Early Pleistocene, without new arrivals.

Second wave — The second wave of immigrants to South Sulawesi, represented by two elephantoids, *Stegodon* sp. B and an advanced *Elephas* species as recorded from the Middle Pleistocene Tanrung Formation and/or younger deposits, may have come from either the Philippines or from Sundaland, in any case by means of sweepstake dispersal. The close affinities of these two elephantoids cannot yet be ascertained because the fossil material is scanty. It further seems that except for *Celebochoerus* the Walanae Fauna had become largely extinct during the Middle Pleistocene. The faunal turnover recorded in Sulawesi presumably occurred after 0.8 Ma. From that time onwards new dispersals towards Sulawesi may have been facilitated by periodically lower sea levels than those during the previous period. As shown earlier, also Java (see chapter 2), Japan and probably Taiwan experienced major faunal immigration events from the Asian mainland since the beginning of the Middle Pleistocene. The fact that dispersal to Sulawesi was of limited extent compared to the other areas mentioned, may be simply because it remained at relatively large distance from the mainland, this notwithstanding the strong sea-level lowerings (sweepstake dispersal). The other islands obviously became connected to some extent with the continent during the Middle Pleistocene (filter or corridor route).

During the Middle Pleistocene *Sus celebensis* and *Anoa depressicornis* may have reached South Sulawesi for the first time as well, presumably in response to the establishment of the first land connection with Central Sulawesi. However, it should be noted that no remains of these taxa have yet been found in situ in the Tanrung Formation. The surface collected specimens attributed to these species may originate from younger deposits overlying the Tanrung Formation, and thus *S. celebensis* and *A. depressicornis* may have reached South Sulawesi not until the Late Pleistocene.

Stegodont colonization of the lesser Sunda Islands

For the Early Pleistocene stegodont of Flores, *S. sondaari* sp. nov., close links with any of the Sulawesi stegodonts cannot be ascertained at present. As pointed out in chapter 6, *S. sondaari* has some primitive molar traits and, therefore, this species cannot have evolved from the more advanced *S. sompoensis* or *Stegodon* sp. B. Consequently, it is thought that the ancestral form of *S. sondaari* reached Flores from the Sunda Shelf (by crossing some water barrier) perhaps already during the Early or Late Pliocene.

On the other hand, *Stegodon florensis* may have reached Flores via Sulawesi, which contradicts the commonly held belief that all stegodonts on the Lesser Sundas entered these islands from the west (e.g. Hooijer, 1975). *Stegodon* sp. B may represent the ancestral group of *S. florensis*. Both are not yet fully dwarfed, they have relatively narrow molars and overlapping hypsodonty indices. However, skull material would be required to substantiate possible relationships between the Middle Pleistocene stegodonts on Sulawesi and Flores. Alternatively, *S. florensis* may have descended from a Javanese ancestor (*S. trigonocephalus*). If dispersal from Sulawesi to Flores has taken place, it must have been by means of overseas dispersal, because the two islands have no other faunal elements, both extinct and extant in common (apart from those extant species likely to have been carried around by humans). When entering the Lesser Sunda islands from the north by overseas dispersal, stegodonts would not have to cross the straits between Bali and Lombok and between Sumbawa and Flores, where very strong surface currents presumably constituted major barriers for sea-crossing stegodonts. Strong currents have obviously also prevented large herbivores from reaching the Balearic islands (Spain) during the entire Plio-Pleistocene time-span (Sondaar et al., 1995), whereas other Mediterranean islands were colonized time and again by elephants, cervids and hippos and a few small mammals (Sondaar, 1977).

The earliest seafarers

The present study shows that the island of Flores was occupied by humans already during the early Middle Pleistocene, as follows from palaeomagnetically dated Palaeolithic artefacts from Mata Menge (Sondaar et al., 1995; van den Bergh et al., 1996; Morwood et al., 1997; this thesis). This suggests that *Homo erectus* was the maker of these artefacts. The layer with artefacts also contains the remains of *Stegodon florensis*.

For the earliest seafarers three possible migration routes out of SE Asia into Wallacea and further towards greater Australia have been proposed (Birdsell, 1977; Sondaar, 1989; Irwin, 1992). Birdsell (1977) suggested that there were two possible routes, based on the assumption that routes with the shortest possible crossings would be the most favoured ones and further assuming that such voyages would have been easier during episodes of lowered sea-level. One route is from Java via the Lesser Sunda Islands to Timor and from there on to northern Australia. The other is from Sulawesi towards Halmahera and from there to West Irian. However, the assumption that probably the shortest overseas distances were crossed is rather unlikely, as it does not take into account prevailing surface water currents and wind directions, which may have been much more important factors for 'passive' or merely 'floating' seafarers. Besides, as noted by Irwin (1992) a boat that is seaworthy enough to cross 10 miles can also cross 100 or more miles, provided that it does not become waterlogged and that the weather remains stable for some time.

Sondaar (1989) added another route, which runs from China over Taiwan (as shown above likely periodically connected with the Chinese mainland since the beginning of the Middle Pleistocene) to the Philippines, Sulawesi and the Lesser Sundas, and from there to Australia. He called this the giant rat route, because from all these islands fossil and/or extant species of giant rats are known. Giant rats are still on the menu of modern humans living on those islands (Verhoeven, 1974; Musser, 1981) and could have served as an important protein source for Palaeolithic humans that had become stranded on one of the islands along this route. Sondaar further thought it likely that Pleistocene human dispersal along this route would have been interrupted by long periods of residence on the intermediate islands before crossing to the next island, so that local evolutionary and behavioral patterns could have developed.

So far, there is no convincing evidence that Sulawesi and the Philippines were inhabited by *Homo erectus* already during the Middle Pleistocene. Palaeolithic industries are known, though, from South Sulawesi, Luzon and Mindanao (Shutler & Mathisen, 1979; Glover, 1981; Bautista, 1991; Keates & Bartstra, 1994). Better age assessments of the early human occupation of in particular Sulawesi are needed. The present study could not provide any proof to show that the group 1 artefact assemblage of Bartstra et al. (1991) and Keates & Bartstra (1994) from the Beru area, South Sulawesi, are time-equivalent to those on Flores. However, it could be concluded that the conglomerates associated with the stone tools may be much older than the Late Pleistocene age which is assumed by Bartstra et al. (1991) and Keates and Bartstra (1994) (see also chapter 3). The recent indications for a very early human occupation of northern Australia, as evidenced by artefact-containing sediments dated by thermoluminescence to be at least 116 ± 12 ka old (Fullagar et al. 1997), are also very tempting indeed. Further evidence could be sought in the similar faunal turn-over patterns observed on Flores and South Sulawesi. The elephantoids from the younger Middle Pleistocene faunas on both islands show only a faint tendency to become smaller, not as small as the elephantoids from the older faunas that they replace. The absence of dwarfing in *Stegodon florensis* has been ascribed to the presence of a predator in the associated fauna: Palaeolithic hunters (Sondaar, 1989).

Possibly stegodonts could reach Flores from Sulawesi, which would have required a maximum sea-crossing distance of perhaps 100 km during times of lowered sea level (from the Bonerate Island group to the north coast of Flores, see Fig. 29). Could accidental or even deliberate human voyagers have accomplished the same during the Middle Pleistocene? In any case, the latter question is merely raised to suggest an alternative for the assumption that the earliest peopling of Flores took place from Java, which would have required only two crossings of less than 25 km. This, however, under the conditions of presumably very strong surface currents similar to those in the present-day situation.

8. Palaeobiological considerations

Body-weight of fossil elephantoids

The large number of endemic elephantoids with different body-sizes encountered on the various SE Asian islands certainly reflects the complex palaeogeographic and climatic changes that affected the region during the Plio-Pleistocene. The size-differences discussed before are mainly based on molar and mandible material. However, as dwarf forms tend to have relatively large molars (Gould, 1975), the tooth size differences cannot be directly translated to differences in body mass. For various reasons it would be of interest to know the body-weights of the insular dwarf elephantoids. If reliable body-weight estimates could be obtained, it would be possible to calculate population densities and population sizes, using estimated sizes of island areas, by applying the existing general relationships between various life history parameters (Damuth, 1981; Eisenberg 1981; Roth, 1990). The combination of such life history parameters would allow to gain insight into the probability of extinction versus sustainability of insular populations under certain circumstances and the selection pressures that acted upon these island populations. These insights may prove to be of importance for the conservation of endangered modern elephant populations (Wasserzug et al., 1979; Roth, 1992).

Body-weight estimates based on tooth size are very unreliable, even more so in the group of mammals with the highest variability in tooth size and morphology of all: elephantoids (Roth, 1992). If we want to make an estimate of the body-weight of the Flores and Sulawesi pygmy stegodonts, we should rely on the empirically obtained correlations between various limb-bone parameters and body-size. Even then a high degree of uncertainty should be taken into account, because some proboscideans have a sturdier built skeleton than others (Haynes, 1991). Like *Mammuthus* and *Mastodon*, also *Stegodon* limb-bones are sturdier than those of the extant *Elephas* and *Loxodonta* (Hooijer, 1955b). Therefore, extrapolation from least-square regression lines of body proportions in modern mammals, including elephants, may not be fully representative for the comparatively sturdy bones of stegodonts. Roth (1990) has presented a case study of body mass estimates of insular dwarf elephants, using various methods. One of these methods concerns body mass estimates based on minimum humerus and femur circumferences, using allometric equations obtained from regression of data on humeral and femoral circumferences of 33 species of quadrupedal mammals from *Microtus* to *Loxodonta* (Anderson et al., 1985). Another method tested by her was based on the regression of data from a similar sample of 36 quadrupedal species from various orders in a similar range of body-weights, this time, however, representing humerus and femur lengths (Alexander et al., 1979). The three elephant species for which these methods were tested were the dwarfed *Mammuthus falconeri* from Sicily (males and females) and *M. exilis* from the Californian Channel Islands, and the presumed ancestor of the latter, the large-sized *M. colombi*. Roth (1990) followed Maglio (1973) in considering the dwarf elephants from Sicily as being derived from *Elephas namadicus*, whereas in the present study it is considered to have originated from the *Mammuthus* lineage.

From this comparative study it followed that the mass-predictions for proboscideans smaller than two metric tons appeared to be best approximated by allometric equations based on bone lengths, while for larger animals body mass is best assessed through the use of allometric equations based on bone circumferences. For animals smaller than two metric tons (like *Mammuthus falconeri* and *M. exilis*) the mass estimates based on bone circumferences resulted in higher values than those based on the lengths of the same bone, resulting in body-weight estimates between 83% and 170% heavier.

Based on the raw data published by Alexander et al. (1979) and Anderson (1985), Roth (1990) recalculated the regression equations based on long bone circumference and long bone length, using log (mass) as the dependent variable. For the femur and humerus this resulted in the following 4 equations:
1) $\text{Mass (kg)} = 3.790 \times 10^{-4} \times F_C\ (\text{mm})^{2.827}$ $(5.5\ \text{mm} < F_C < 413\ \text{mm})$
2) $\text{Mass (kg)} = 9.448 \times 10^{-4} \times H_C\ (\text{mm})^{2.611}$ $(4.9\ \text{mm} < H_C < 459\ \text{mm})$
3) $\text{Mass (kg)} = 1.774 \times 10^{-5} \times F_L\ (\text{mm})^{2.654}$ $(6.0\ \text{mm} < F_L < 980\ \text{mm})$
4) $\text{Mass (kg)} = 2.767 \times 10^{-5} \times H_L\ (\text{mm})^{2.675}$ $(5.7\ \text{mm} < H_L < 830\ \text{mm})$

In these equations F_C and H_C represent femur and humerus circumference, and F_L and H_L represent femur and humerus length, respectively. For *Stegodon sondaari* sp. nov. from Flores we have only a fragmentary femur at our disposal with broken epiphyses. The total length could only be estimated indirectly with the help of the log-ratio diagram presented in Fig. 73, assuming that the femur of *S. sondaari* was not disproportionally short compared to other large-sized stegodonts. The mid-shaft bone circumference could be measured directly (Table 26). As argued in the section on the description of the femur fragment (see chapter 6), the specimen probably belonged to a full-grown individual with fused epiphyses. The length estimate and the direct circumference measurement can both be used for the bodyweight estimate. Using equation 1, the minimum circumference of 151.5 mm (Table 26) predicts a body mass of 553 kg. Filling in the estimated length of the *S. sondaari* femur (460 ± 50 mm; see chapter 6) in equation 3, gives a body mass prediction of 207 +65/-54 kg. This is less than half the estimate based on femur circumference.

The higher estimate based on circumference is in line with the results of the comparative analysis of Roth (1990). Stegodonts have relatively thick femora as compared to *Elephas maximus* (Hooijer, 1955b), but are of similar sturdiness as compared to *Mammuthus* (Ariëns, 1995). Mastodont and *Mammuthus* limb-bones may be c. 20% larger in mid-shaft diameter compared to homologue elements of equal or greater length in *Loxodonta africana* (Haynes, 1991). *Elephas* and *Loxodonta* appear to be more derived in their relatively smaller limb-bone circumferences, and have relatively 'weak' limb-bones. Probably limb strength correlates more with gait than with body mass in large terrestrial quadrupeds (Bakker, 1986). These considerations may explain the larger values found by Roth (1990) for the *M. falconeri* and *M. exilis* body mass estimates based on long bone mid-shaft circumference as compared to those based on length of the same bones. These dwarfed insular species presumably inherited the more sturdy limb-bones of their mammoth ancestors. Analogous, the relatively thick femurs of *S. sondaari* are expected to result in higher body-weight estimates when based on bone circumference than on bone length. This assumption could be further substantiated by comparing body-weight predictions for some other stegodonts, both dwarfed and full-sized species, calculated from total lengths and from mid-shaft diameters of full-grown long bones, respectively (Table 40). Both for *S. t. trigonocephalus* (femur) and for *S. sompoensis* (humerus) body-weight estimates based on mid-shaft diameter turned out to be 170-260% higher than those based on length.

Assuming that body-weight estimates based on long bone length measurements are more reliable in the case of stegodonts than those based on minimum circumference, we may conclude that the adult *S. sondaari* individual that provided the femur (male or female?) had a body-weight of at most 500 kg and at least 200 kg, but probably closer to the lower estimate. *S. sompoensis* had an estimated body-weight of between c. 350 kg (based on the length of a single full-grown humerus) and 950 kg (minimum circumference-based estimate of the same humerus). Three femurs of *S. t. trigonocephalus* with fused epiphyses gave lenght-based body-weight estimates of between 1017 and 1713 kg (Table 40). The smaller value was obtained from the smallest specimen on which the total length could be measured, specimen CD-4315 from Trinil, which represented also the second smallest specimen amongst a sample of 20 full-grown femur specimens (both complete and partial; Hooijer, 1955b). It therefore certainly must have belonged to a female individual. The largest of the three femurs of which the length could be measured, specimen CD-2889, was the second largest specimen of the same *S. t. trigonocephalus* femur sample, and presumably represented a male individual. In the case of body-weight estimates based on minimum femur circumference, much heavier weights for the same 3 *S. t. trigonocephalus* were obtained, between 3673 and 6287 kg. The latter estimates are again thought to be too high.

Hooijer (1972a: 23) gives 63 cm as the length of a full-grown dextral humerus of *S. florensis* from Mata Menge. This measurement gives a weight estimate of 852 kg, which is below the range obtained for femur length-based weight estimates of *S. t. trigonocephalus* and in accordance with data on molar and mandible sizes, showing the Flores stegodont to be smaller than the Javanese stegodont. The present whereabouts of this humerus is not known, so that no additional measurements could be made. The minimum circumference of another full-grown but fragmentary humerus from Ola Bula, which is in the NNM collection and which was mentioned by Hooijer (1957a: 125), could be estimated as lying between 273e and 280e mm. These values result in presumably too high circumference-based weight estimates of between 2169 kg and 2317 kg.

S. trigonocephalus may have had on average a slightly lower body-weight as the Asian elephant, *E. maximus*, which has an average weight of 2720 kg (Shoshani & Eisenberg, 1982). The smallest of the Indonesian stegodonts, *S. sondaari* was comparable in body-weight to the extant dwarf hippopotamus, *Choeropsis liberiensis* (average weight = 272 kg, Eisenberg, 1981). Most other *Stegodon* species from Indonesia had a body-weight in between these two values, except perhaps for *S. elephantoides*, which must have been bigger than *S. trigonocephalus*.

Hypsodonty of insular stegodonts

In almost all insular stegodonts from Asia an increase in hypsodonty evolved. Subhypsodont teeth were reported for the size-reduced but not yet completely dwarfed *Stegodon aurorae* (Taruno 1991; Saegusa 1991; Kamya 1995; own measurements) and *S. florensis* (Hooijer, 1957a; this thesis), and for the dwarfed *S. timorensis*

(Hooijer, 1969a), *S. sondaari* (this thesis), *S. sompoensis* (van den Bergh et al., 1994), *S. mindanensis* (von Koenigswald, 1956) and *S. hypsilophus* (Hooijer, 1954d). *S. aurorae* from Japan, which evolved from the huge Chinese species *S. zdanski*, and which is not closely related to *S. trigonocephalus* (as shown by different skull morphologies, see Saegusa, 1987, 1996), developed subhypsodont molars and an increased number of molar ridges, independent from the Indonesian island stegodonts. Because *S. aurorae* lived on Japan from 2.5 until 1 Ma (Kamyia, 1995; Saegusa, 1996), this increase in hypsodonty took place relatively early, at a time when Java was not yet inhabited by stegodonts. This example represents a clear case of parallelism.

Sondaar (1984) suggested that in island stegodonts increase in hypsodonty occurred several times independently and was coupled with the process of dwarfing. In various cases, development of more hypsodont molars may have been a response to the absence of competition by Elephantidae on these islands (except for Sulawesi, where *S. sompoensis* occurred together with *"Elephas" celebensis*). Some island stegodonts may have been forced into an increased consumption of high-fiber foods such as grasses, because the climate on these islands was dryer and foliage sparser than in the tropical and subtropical mainland biotopes of their direct ancestors.

The tendency of island stegodonts to have generally more high-crowned molars than their continental counterparts has led to some confusion in classification. This is because the molar ridges of the dwarfed species resemble the lamellae of elephantine molars. For example, *Stegodon hypsilophus*, a pygmy stegodont from the Middle Pleistocene of Java, first described by Hooijer (1954d), was considered by Maglio (1973) a synonym of *Elephas celebensis* from Sulawesi. The presence of double-layered enamel identifies '*hypsilophus*' as a true, albeit hypsodont *Stegodon* (see also Sondaar, 1984; van den Bergh et al., 1992; Saegusa, 1996).

For the still poorly known *Stegodon* sp. B from South Sulawesi and Sangihe, hypsodonty indices of unworn molar ridges seem to occupy an intermediate position between the values observed for *S. trigonocephalus* on the lower side and those of *S. florensis* on the higher side. *Stegodon* sp. B appears to have been size-reduced compared to its direct ancestor, which must have been very large-sized, even larger than *S. trigonocephalus*. This follows from the fact that there is hardly any increase in maximum width between successive permanent molars, suggesting that mandible growth stopped at an early ontogenetic stage in this species, similar as in fully dwarfed stegodonts. Still, the dP^4 and M^1 of *Stegodon* sp. B are slightly larger than in *S. t. trigonocephalus* (the latter species shows an average increase in width between successive molars, up to the last molar, suggesting that growth continued until relatively old age, like in modern elephants). On the other hand, mandibles of *Stegodon* sp. B are smaller or have overlapping dimensions with the smallest mandibles of equivalent dental wear age classes in *S. t. trigonocephalus*. This suggests that *Stegodon* sp. B had relatively large teeth for its mandible size when compared to *S. t. trigonocephalus*, which is a characteristic of dwarfed species. Therefore, it may be concluded that the direct ancestor of *Stegodon* sp. B must have been of huge size. *Stegodon* sp. B has a slightly larger mandible and molar size than *S. florensis*, the latter having higher hypsodonty indices. It can be further noted that the smallest representatives under the island stegodonts, *S. sondaari* and *S. timorensis*, also have the highest hypsodonty indices. These observations suggest that the size-reduction was inversely related to the degree of hypsodonty, speaking in favour of the hypothesis of Sondaar (1984) that increase in hypsodonty was coupled with dwarfing. However, in the case of *S. sompoensis* from Sulawesi the scarce data suggest that dwarfing occurred first and that subsequently the degree of hypsodonty increased trough time (van den Bergh et al., 1994). This suggests that an increased hypsodonty is not an inherent effect of dwarfing, but evolved in response to selective forces after the size reduction had taken place.

Though increase in hypsodonty is a widespread trend in the Plio-Pleistocene Elephantidae, it seems to have been confined to insular, size-reduced forms in Stegodontidae. The question is why? In the section of chapter 6 dealing with *Stegodon sondaari* it was already speculated that the increase in hypsodonty might have been a compensation for the reduction in relative tooth durability by the loss of some ridges in the course of dwarfing. Fortelius (1985) sums up several theoretical factors that relate to hypsodonty. An important factor thought to be correlated with hypsodonty is the abrasiveness of food, either through the inclusion of phytoliths or by contamination with earth. The comminution of food that is itself unabrasive but which requires high occlusal stress may also cause increased wear leading to hypsodonty. Heavy wear may also be caused by the mastication of large quantities of low-grade food or increased energy demands.

Janis (1988) collected hypsodonty data for a large number of herbivores, and concluded that the amount of hypsodonty is not only correlated with the type of food consumed (browsers versus grazers), but also and in particular depends on whether the food is collected close to the ground or higher up on trees. For example, Janis distinguished between 'low' and 'high' browsers, and found that low browsers have more hypsodont teeth than high browsers. Food close to the ground is more contaminated with grit and dust, which plays an important role in the attrition of the teeth. It can be speculated that the more the size of island stegodonts was reduced, the more the animals were forced to collect their food closely to the ground instead of browsing on higher foliage. Increased contamination of their food with earth might therefore have been a selective force in the evolution of increased hypsodonty in the size-reduced stegodonts.

A proportional increase of high-fiber food in the diets may have contributed to the increase in hypsodonty in the insular stegodonts as well. Assuming that the low-crowned ancestral continental stegodonts were browsers, a shift towards a more mixed feeding habit could have been enhanced on islands by the absence of competition from elephants. Island elephantoids in search for food were not able to migrate over long distances, as modern elephants do. Exhaustion of food-resources is generally thought to be one of the leading factors resulting in dwarfing of large mammals on islands (Roth, 1990). On islands with extended dry seasons such as Flores, seasonal food shortages may have been even more severe, and the island stegodonts may have been forced to consume larger quantities of low-quality foods to fulfill their energy demands during periods of food shortages.

The loss of some molar lamellae, in combination with reduced availability of low-fiber foliage and an increased intake of dust and grit with food collected closer to the ground, were probably all factors contributing towards an increase in molar hypsodonty by selective pressures. The increase in hypsodonty in island stegodonts may be considered a real adaptation to island life.

Age mortality profiles

Because of the unique way of horizontal tooth replacement in stegodonts and elephants, it is possible to give a fairly accurate estimate of the composition of the thanatocoenosis or death-assemblage from a certain site, based on isolated dental remains. Besides, the individuals can easily be grouped into age classes based on the dental wear stages. If there is sedimentological or taphonomical evidence that a certain fossil elephantoid assemblage accumulated during a short time interval, it is theoretically possible to gain insight into the age structure of an ancient population. The age structure of the death assemblage from such a locality can tell us in some cases whether the mortality was selective or non-selective. In case of non-selective mortality, e.g. due to a catastrophic event that affected individuals of all ages to the same degree, the age structure of the death assemblage should correspond to the age structure of the living population (Haynes, 1987). Catastrophic death assemblages may provide clues concerning the conditions of the population, e.g. whether it was stable, declining or thriving under optimum conditions prior to the catastrophic event (Haynes, 1991). For the Indonesian elephantoids discussed in this thesis, molar material could usually not be collected in sufficiently large amounts from single fossil-rich layers to allow the reconstruction of age mortality profiles representing short intervals of time. There are some exceptions, however. For instance, there is a fairly high number of elements of *Stegodon sondaari* from a single layer at Tangi Talo, Flores. Also the *S. t. trigonocephalus* assemblage from the locality Trinil, Central Java, which was excavated by Dubois more than a century ago, mostly originates from a single layer, the so-called ‘Hauptknochenschicht’ (de Vos & Sondaar, 1982). Finally, when the *“E.” celebensis* assemblages collected by van Heekeren and our own team at the locality Sompe (FVL-25a), Sulawesi, are combined, a fairly large sample can be obtained from the main fossiliferous sandstone layer at Sompe, though the van Heekeren sample from Sompe may have been contaminated with some fossils from other localities.

At other localities in Indonesia elephantoid remains are relatively rare, and age profiles can only be reconstructed by combining the fossil assemblages from various localities, which however, are usually widely separated in time. The resulting ‘long term’ mortality profiles may still provide information concerning the average mortality conditions, as will be shown for *S. florensis* further on below.

Definition of age groups

In a sample of elephantoid molar remains from a single locality, it is relatively easy to attribute the molar remains to a minimum number of individuals by direct comparison and fitting. In the case of *Stegodon sondaari* sp. nov., most molars were found isolated. Still, certain elements could be assigned to a single individual with certainty, for example in the case of molars of the same rank that were in identical wear stages and wear patterns but of opposite sides, like the left and right upper dP^4s specimens TT-4033 and TT4034. Also the holotype mandible with dentition (TT-3837) could be associated with the upper dentition found as isolated elements (specimens TT-4037, sin.M^1; TT-4035, dex. M^1; TT-4030, sin.M^2; TT-4031, dex.M^2) based on dental wear progress and fitting of the occlusal surfaces. In other cases, two or more elements of different rank and representing upper and lower elements, could not be fitted. Such elements were counted as to have come from a single individual if they represent approximately the same dental wear age class. For example, the worn sinistral dP_4 (TT-3835) and the unworn sinistral M^1 (TT-4036) are assigned to one individual, though they might actually represent two individuals. Isolated elements that could not be associated with any of the other dental remains were counted as representing separate individuals, like for example the fully worn M^3 remnant TT-3856. In this way the 24 identifiable molar elements in the collection could be ascribed to a minimum number of individuals of 12. This amount excludes the pair of dP_3s described by Hooijer earlier (1964c), because it is not certain if they originate from the same layer at Tangi Talo. All *S. sondaari* sp. nov. dental elements from Tangi Talo are listed in Table 41 with their collection numbers, identifications and wear stages. Each element has been assigned to one of the 12 individuals distinguished, and the numbers in the second column of Table 41 refer to one of these 12 individuals. The estimate of 12 individuals is the most conservative one and probably more individuals are represented in the death assemblage.

The next step was to erect an age profile of the death assemblage. Various methods have been developed for age estimation of modern elephants based on dental wear stages. Laws (1966) used a method based on the examination of the dental wear 'figures' in 385 *Loxodonta africana* mandibles. He defined 30 successive wear stages, each characterized by a different combination of one or two molars in a half-mandible and their wear conditions. To each of these stages an average age was assigned.

Another method was developed by Sikes (1966, 1967), who studied more than 400 *L. africana* mandibles. She noticed that in the dental progress each molar moved regularly forward, lamella after lamella, each single lamella eventually passing over the fixed point of the mental foramen. Adding the number of plates of each successive molar, a total of 57 lamellae for the 6 successive molars was obtained for *L. africana*. By identifying which molar passes over the dental foramen in a certain mandible, one can simply calculate how many plates have passed over this fixed point so that one out of 57 'lamellar age classes' will be obtained, assuming that the number of lamellae per molar is constant. The disadvantages of these methods are that they can not be applied to upper dentitions, and that the method of Sikes (1967) can not be applied to other species with different amounts of lamellae per molar. Besides, the number of lamellae is usually variable, even within a single population (Haynes, 1991).

The classification method of Beden (1979) is of more practical use for our purpose of assigning dental wear age classes (DWAC) to stegodont dentitions. His method is based on that proposed by Laws (1966), each DWAC being characterized by a specific wear condition of the molars in use. One of the aims of Beden (1979) was to provide a DWAC system which could be used for fossil elephant dentitions as well, and which could also be applied to upper dentitions. Molar material of fossil elephants is usually scarce and one has to use all available material, including upper dentitions, to establish age profiles. Therefore, Beden (1979) based his classification on the study of both lower (132 mandibles) and upper (65 skulls) dentitions of *L. africana*, and studied the correlation between the wear patterns of lower and upper dentitions. Besides, he added 13 DWAC to the 30 classes originally distinguished by Laws (1966).

For single progressing molars 11 successive stages were defined, designated with the combination of a letter (A-D) and a number (Table 41). The letters correspond with the state of the entire molar (A = unworn, B = increasing number of ridges in function, C = all ridges in function, and D = progressive destruction of ridges). The numbers refine this division. For example, stage B (increasing number of ridges in function) can be subdivided into B1 (cementum worn), B2 (a few ridges worn), B3 (half of the ridges worn), and B4 (most of the ridges worn).

It should be noted that these dental progress stages were defined in such a way that there exists a relation between the stages of two successive molars. For example, a molar in stage A (unworn) is always preceded by a molar in stage C (all ridges in function) and a molar in stage B2 (B = increasing number of ridges in function, 2 = a few ridges touched by wear) is always preceded by another molar in stage D (progressive destruction of ridges), etc.

The 43 DWAC which were distinguished are based on the recognition of the progressive stages in the molar or molars in use in a single half-jaw, in combination with the identification of the serial position of the molar or molars in use. The 43 DWAC were grouped in such a way that one can see immediately which molar or which molars are in function in a particular DWAC group. The following DWAC groups were distinguished: dP2/dP3, dP3/dP4, dP4/M1, M1, M1/M2, M2, M2/M3 and M3. Each of these groups was further subdivided into as much classes as necessary, each one represented by a letter (A, B, C, D or E: not to be confused with the lettercodes used for the progress stages of single molars). Each combination of group + lettercode characterizes the observed wear patterns according to the scheme erected by Beden (1979), which is shown here in Fig. 75A.

The 30 age classes distinguished by Laws (1966) correspond with 28 out of the 43 DWAC distinguished by Beden (1979). Two of the DWAC of Beden correspond with double age classes of Laws. The extra DWAC defined by Beden (1979) have their lettercode followed by a (‘), for example dP4-A’ or dP4/M1-B’. The 43 DWAC were defined in such a way that they characterize the wear stages of both lower and upper dentitions, though upper and lower molars of the same rank do not necesarily show identical wear patterns (Fig. 75B). For example, according to the definition DWAC M2-A has all the lamellae of the M_2 in function (wear stage C), whereas of the upper M^2 the posterior lamellae are still unworn (wear stage B4). This slight difference in molar progress between upper and lower molars has also been noted by others. For example, Haynes (1991) noted that in elephantoids the upper dentition ‘looks’ slightly younger than the lower one of the same individual, because the upper molars erupt and start to be worn slightly later than their lower homologues. Due to natural variation or pathogenic processes (Roth, 1989) the wear stages of upper and lower molars may deviate from the correlation shown in Fig. 75B, which are based on observations in only 65 associated upper and lower dentitions. Deviations from the defined correlation between upper and lower dentitions may also arise when the method is applied to other species than *L. africana*. Only when large amounts of associated upper and lower dentitions of fossil species would be available one could redefine the DWAC correlation chart of Beden (1979) for other species than *L. africana*, but this is at present not possible for the fossil elephantoids that form the subject of study in this thesis. Fortunately, the number of lamellae in successive molars of *L. africana* does not deviate too much from those encountered in homologue elements in *Stegodon*. The 6 lower molars of *L. africana* bear on average successively 5, 7, 10, 10, 12 and 13 lamellae

(Sikes, 1966), whereas in *S. t. trigonocephalus* the successive number of ridges are 3, 6, 8, 8-9, 10 and 13. Some clues concerning the validity of the method of Beden (1979) when applied to stegodonts, can be found in the lower and upper dentition of a single *S. florensis* individual, which was described by Hooijer (1972a). In this dentition the first 2 ridges of the M_3s were worn but none of the M^3s. According to the correlation scheme of Beden (1979) both the upper and lower dentitions correspond with DWAC M2-C. In the associated upper and lower dentition of *S. sondaari* sp. nov. (holotype) the lower one corresponds with DWAC M1/M2-C, whereas the upper one is one stage more advanced: DWAC M1/M2-D. In these 2 examples the DWAC of the lower and upper dentition are either the same or they differ 1 class, suggesting that the correlation scheme of Beden (1979) can be applied safely to stegodonts.

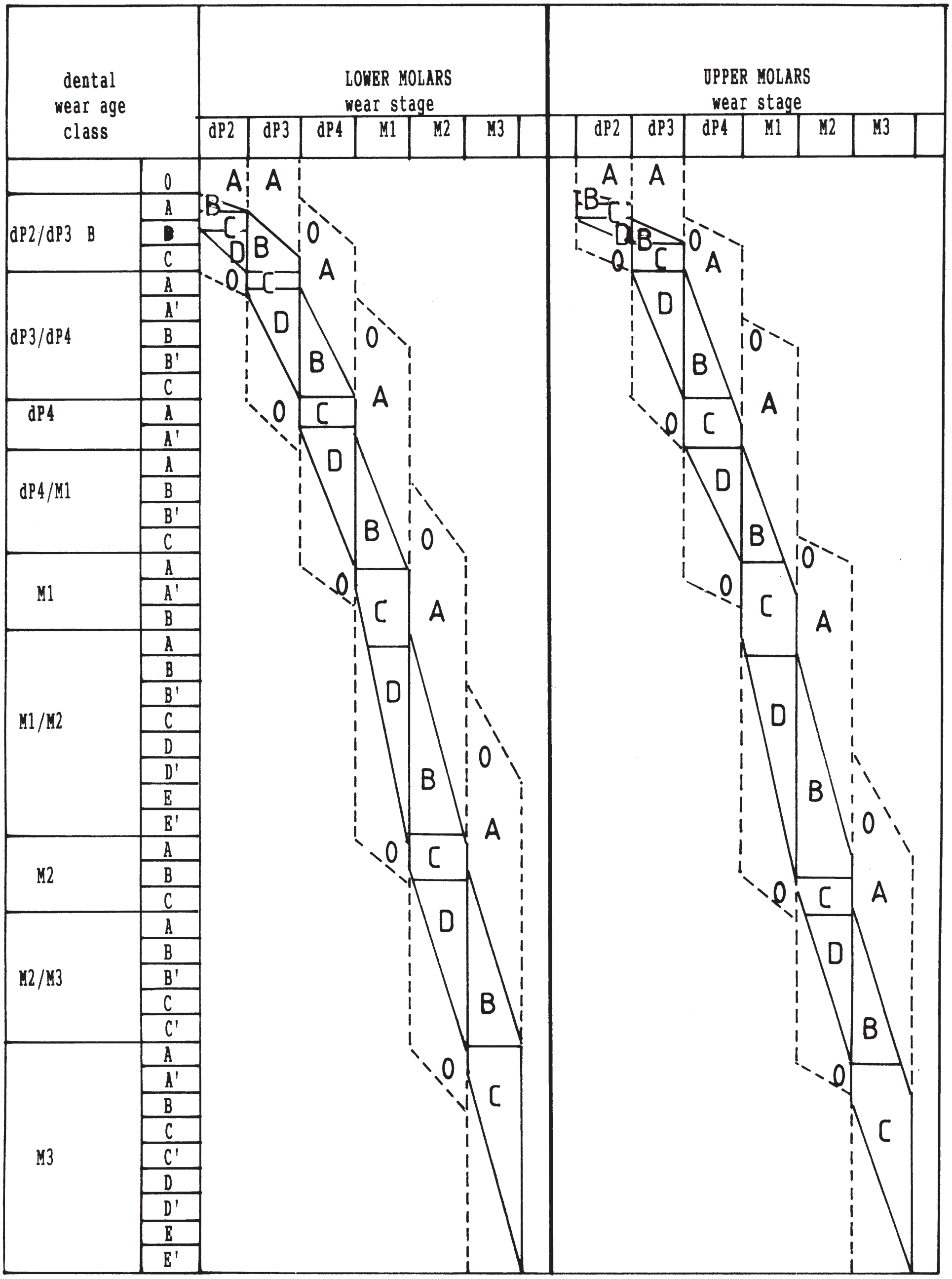
For the purpose of reconstructing age mortality profiles of fossil stegodont molar assemblages, it should be tried to obtain age groups which represent approximately equal amounts of lifespan, as was also done in the age profile studies of *Loxodonta africana* by Haynes (1991). The 43 DWAC distinguished by Beden (1979) cover the entire lifespan of *L. africana*. As growth is faster and the dental wear stages succeed each other more rapidly during early life as compared to the later adult stages, we can not simply subdivide the 43 DWAC of Beden (1979) into 6 groups of 7 successive dental wear stages. In that case the juvenile age classes would represent less ‘lifetime’ than the adult age classes. The following method was used in order to obtain age groups representing approximately equal amounts of lifetime. The 43 DWAC of *L. africana* were plotted against real (estimated) ages given by Sikes (1971) and Craig (in: Haynes, 1991) (see Fig. 76). DWAC that could not be attached to a real age were extrapolated by connecting the various data points in the graph. Haynes (1991) based his dental wear age class determinations on the identification criteria of Laws (1966), but used the real ages of Craig (in: Haynes, 1991), which were also used here to assign real AEY ages to the 43 DWAC of Beden (1979). The presumed average total lifespan of *L. africana* is generally considered by most researchers to be 60-65 years, though some have given higher estimates of up to one hundred years (e.g. Sikes, 1971). Taking 60 years as a fair estimate for the total lifespan of *L. africana*, the last DWAC (M3-E′) should correspond with an average age of 60 years. The lifespan of 60 years was divided into 5 age groups of 12 years each, and vertical lines were drawn in Fig. 76 from the points on the diagram corresponding with real ages of 12, 24, 36, 48 and 60 years. The points where these vertical lines intersect the x-axis denominate the DWAC boundaries between these 5 successive age groups. The dental wear age class boundaries for each of these age groups are given in Table 42.

Ages of fossil elephants based on comparison with tooth wear criteria in modern African elephants are usually expressed as African Elephant Years (AEY). It should be kept in mind that the real ages of dwarf stegodonts expressed in AEY might, but not necessarily will, deviate considerably from the AEY ages. Because of their small body size, their lifespan was possibly much shorter than that of African elephants. If so, their age based on dental wear stage and expressed in AEY would be higher than the real ages at death. Though the 5 DWAC defined age groups are approximately representing equal amounts of lifespan for the African elephant, this has not to be necessarily true if the same age groups are applied to a dwarf such as *S. sondaari* sp. nov. Dental wear and succession might have proceeded at different relative rates during

Lower molars								
			progress stage					
Laws 1966	**dental wear age class**		**dP2**	**dP3**	**dP4**	**M1**	**M2**	**M3**
I		0	(A)	(A)				
II	dP2/dP3	A	(B/C)	(A/B1)	- (0)			
		B	D	(B2/B3)	(0)			
III		C	D	B4^{C}	(A)			
IV	dP3/dP4	A	0	C	(A/B1)			
		A'		D2	(B2)	- (0)		
V		B		D3	(B3)	(0)		
		B'		D4	B4	(A)		
VI		C		D4	B4	(A)		
	dP4	A		0	C	(A)		
VII		A'		0	C	(A/B1)		
VIII	dP4/M1	A			D1	(B2)		
IX		B			D2	(B3)	- (0)	
		B'			D3	B4	- (0)	
X		C			D4	B4	(0)	
XI	M1	A			D4/0	^{B4}C	(0/A)	
		A'			0	C	(A)	
XII		B				C^{D1}	(A)	
	M1/M2	A				C	(A/B1)	
XIII		B				C^{D2}	(B2)	
		B'				D2^{D3}	(B2)	- (0)
XIV		C				D3	(B3)	- (0)
XV		D				D3^{D4}	(B4)	- (0)
		D'				D3^{D4}	(B4)	(0)
XVI		E				D4	B4	(0/A)
		E'				?	B4/C	(A)
XVII	M2	A				0	^{B4}C	(A)
XVIII		B				0 -	C^{D1}	(A/B1)
XIX		C					C^{D2}	(B2)
XX	M2/M3	A					D2	(B2)
XXI		B					D3	(B3)
		B'					D3^{D4}	(B3)
XXII		C					^{D3}D4	B3^{B4}
		C'					D4	B4/C
XXIII	M3	A					0	B4^{D1}
		A'					0	B4^{D1}
XXIV		B					0	B4^{D1}
XXV / XXVI		C						C^{D1}
		C'						C/D2
XXVII / XXIX		D						D2^{D3}
		D'						D3/0
XXX		E						D4/0
		E'						D4/0

Fig. 75. Division of 43 dental wear age classes for elephantoid dentitions.

A: Scheme used for determining elephantoid dental wear age classes (DWAC) based on the lower molar progress stages defined in Table 41 (after Beden, 1979). The scheme was originally established for *Loxodonta africana* but can be used for other elephantoids as well. Each DWAC is defined by the serial position of the molar or molars which are in function in a single half-jaw, combined with the state of the molar or molars according to the progress stages from Table 41. For further explanation, see chapter 8.



B: Dental wear age class correlation chart for lower and upper molars (after Beden, 1979).

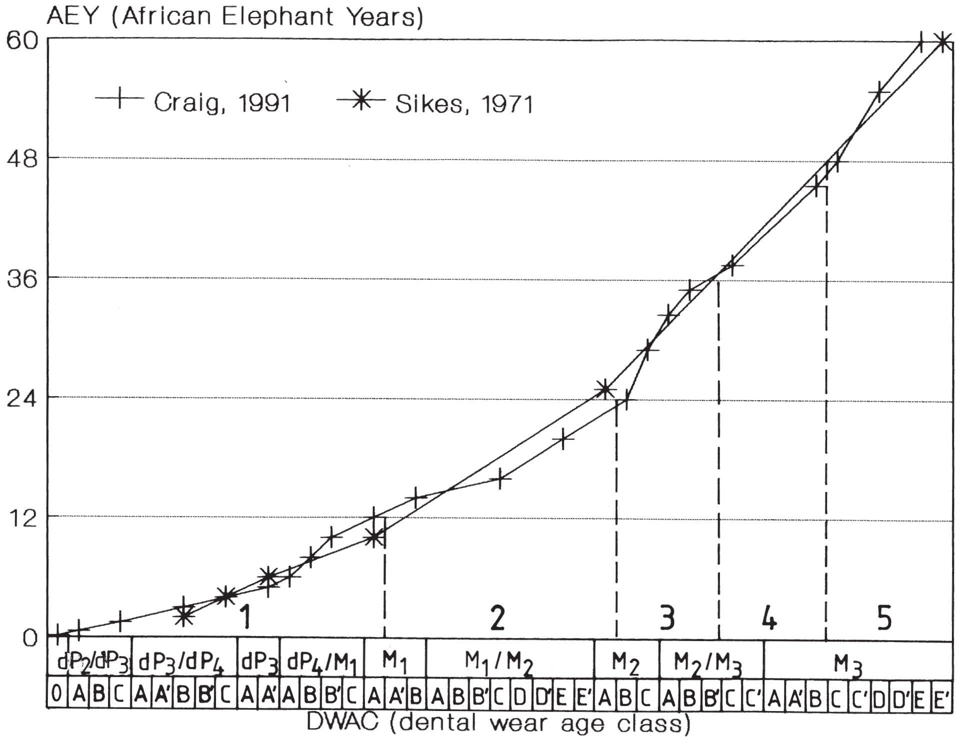


Fig. 76. Diagram showing the relation between dental wear age classes and real ages for *Loxodonta africana*, used to define five elephantoid age groups. Real ages are from Sikes (1971) and Craig (in Haynes, 1991). The dental wear age classes of Sikes (1971), were translated to the dental wear age class system of Beden (1979) using his correlation chart. Intermediate dental wear stages for which no real age data were available, were extrapolated. The total lifespan of *L. africana*, ca. 60 years, was divided into 5 age groups, all representing approximately equal amounts of lifespan of 12 African Elephant Years. The dental wear age classes that define the boundaries of the 5 age groups were then derived from the horizontal axis and are listed in Table 42.

parts of the lifehistory in the dwarf *Stegodon* as compared to *L. africana*. However, to date there is no more adequate way of defining age groups that represent approximately equal amounts of lifespan for fossil elephantoid species of highly deviating body-weights. An improvement to the accuracy of correlating dental wear stages to real ages in fossil species could be made in ideal cases when dentitions are found associated with tusks. When sectioned and studied under the microscope the tusks could provide real ages at death, by counting the annual growth increments (Fisher, 1996).

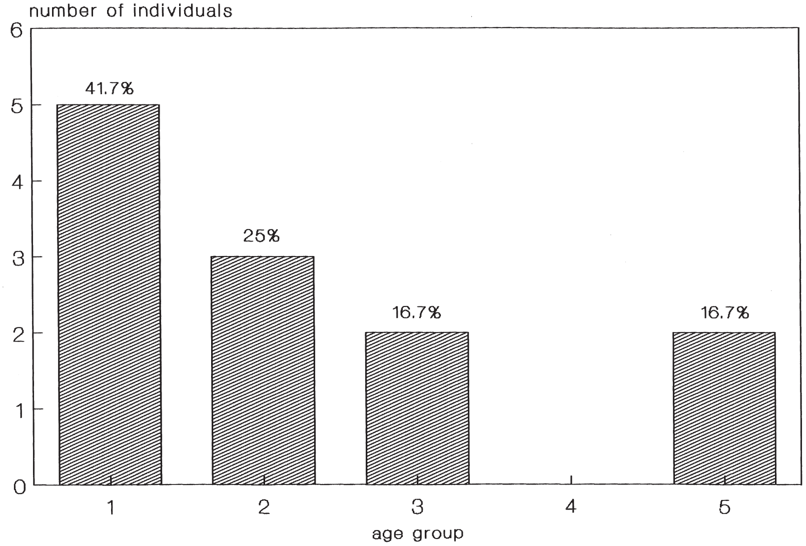
It was chosen to define 5 age groups in order to allow comparison with the age profiles of Haynes (1987, 1991), who argued that 12-year age classes separate important intervals in the life history of the modern elephants. Animals younger than 13 years old are not sexually mature and are growing fast. Animals in the next age group (13-24 years old) continue to grow but have reached sexual maturity. During the interval from 25 to 36 years old, males continue to grow but the growth in females levels off. During this age interval some females establish themselves as group leaders or matriarchs and some males establish themselves as dominant bulls. In the age group from 37 to 48 years old, male statural growth levels off and males are most active in a competitive and reproductive way. Females continue to have offspring, but are passing beyond prime condition by the end of this age interval. During the last interval, 49 to 60 years old, both sexes pass into old age and sometimes senescence. Arthritic and degenerative bone conditions are common and females become relatively more vulnerable to drought stresses than younger females (Haynes, 1991).

Age profiles of fossil elephantoids from Indonesia

The twelve *S. sondaari* sp. nov. individuals from Table 7 are assigned a dental wear stage using the method described above. Each individual that could be recognized was classified into one of the 5 age groups of Table 42. The resulting age profile of the Tangi Talo sample is shown in Fig. 77A. Age profiles of other species from selected localities are given in Fig. 77B (*S. florensis* from 4 localities in the Soa Basin, Flores), 77C (*"E." celebensis* from Sompe = FVL-25, South Sulawesi), and 77D (*S. t. trigonocephalus* from Trinil, Central Java). Only the *S. t. trigonocephalus* sample from Trinil forms part of a more balanced continental type faunal assemblage including mammalian carnivores, whereas the 3 others originate from impoverished island faunal assemblages with large predators represented only by reptiles, either crocodiles or Komodo dragons. The *S. t. trigonocephalus* sample is also the largest one studied (MNI = 32). The bulk of the Trinil dental assemblage is supposed to originate from the so-called 'Hauptknochenschicht' at Trinil, and includes both material present in the CD/NNM and from the Selenka expedition as published by Janensch (1911). Fossils which, according to the registers of the CD were originating from Trinil, but which show an aberrant type of fossilization and/or matrix than considered characteristic for the Trinil fossils (de Vos & Sondaar, 1982) were disregarded. From the material described by Janensch (1911) we included only those specimens that were said to originate from Trinil. Specimens reportedly coming from other places, like for example 'surroundings of Trinil', and the large skull and associated mandible (specimens CS-304 and CS-823, respectively), which originate from a level 5 m above the 'Hauptknochenschicht' (Oppenoorth, 1911), were disregarded as well.

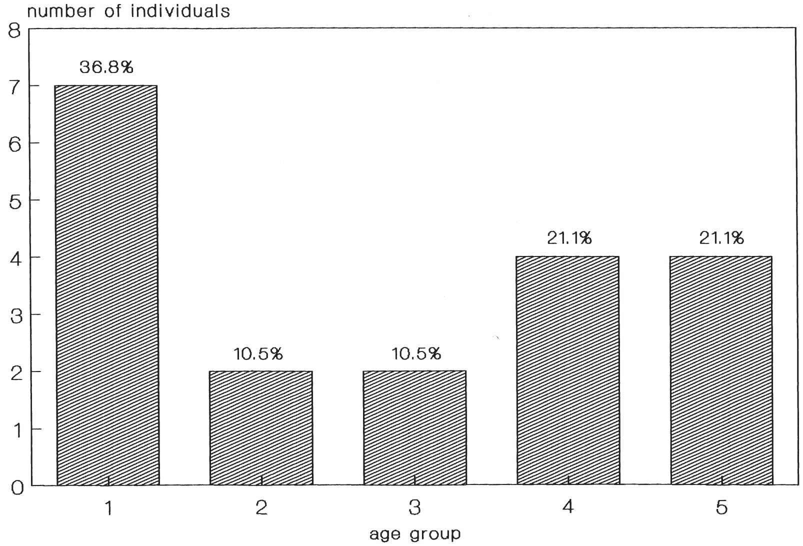
The *"E." celebensis* assemblage (MNI = 23) constitutes material from Sompe in the CVH, which was described by Hooijer (1949, 1953a,c, 1954e, 1972b), plus the material we collected at that locality. The CVH sample may be contaminated with some material from other levels than the main fossiliferous sandstone layer at Sompe. Many fossils in the CVH bear the inscription 'S.', which stands for Sompe.

The *S. florensis* sample (MNI = 19) is a composite sample in the sense that the material originates from 4 different localities from Member B of the Ola Bula Formation. This assemblage includes material collected by us as well as material in the CV and described by Hooijer (1957, 1967, 1972a). I had the impression that old individuals were over-represented in the *S. florensis* material, but unfortunately, so far none of the localities has yielded sufficient suitable material for the reconstruction of a meaningful age profile (MNI is 7 in the most proliferous locality, Ola Bula). Therefore it was decided to lump the material from the 4 localities Mata Menge, Ola Bula, Boa



A *Stegodon sondaari* nov.sp.
Tangi Talo, Flores

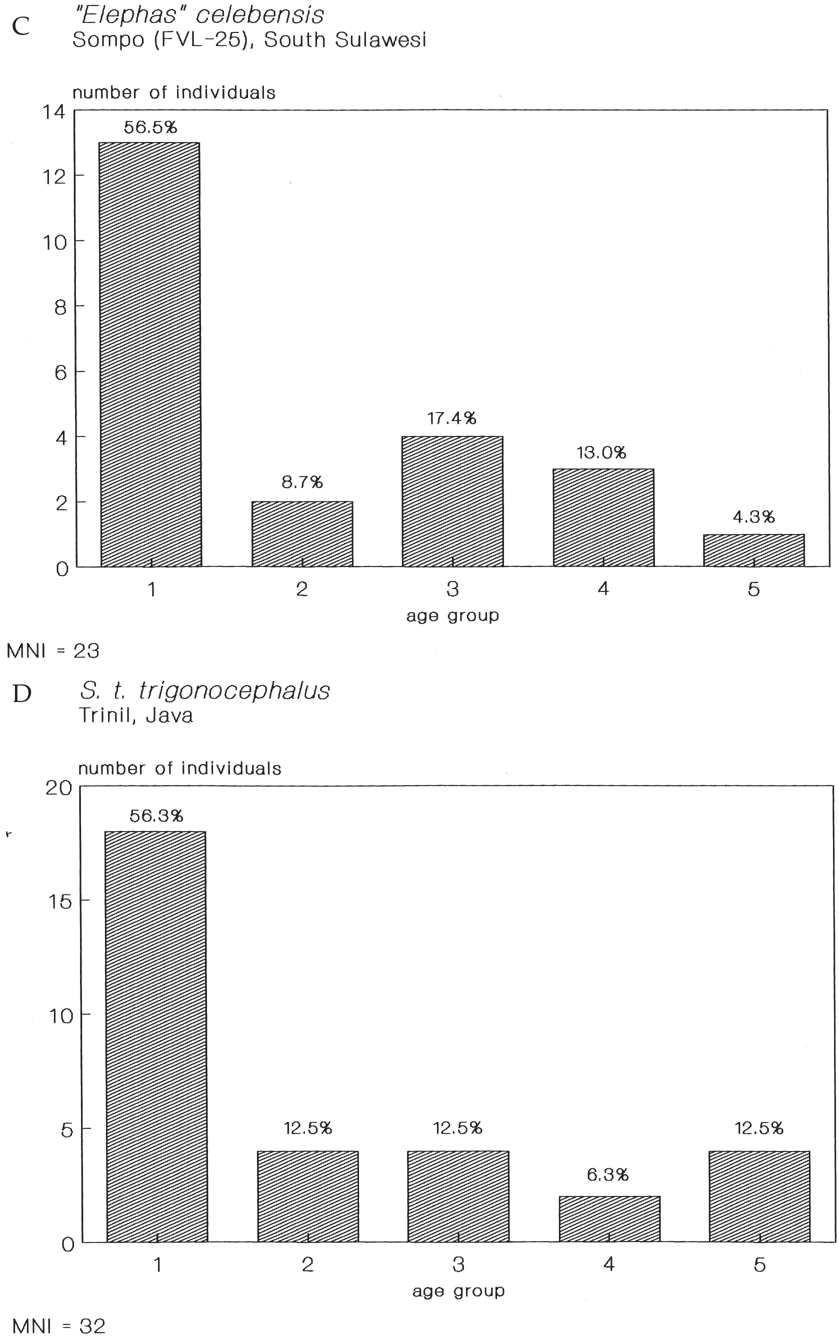
MNI = 12



B *Stegodon florensis*
various localities, Soa Basin, Flores

MNI = 19

Fig. 77. Age profiles of fossil elephantoid assemblages from various localities in Indonesia. The boundaries of the 5 age groups are defined by the dental wear age classes of Beden (1979) (see also Table 42 and Fig. 75). A: Age profile of the *Stegodon sondaari* sp. nov. dental assemblage from the loc. Tangi Talo.



B: Age profile of *S. florensis* based on the combination of fossil material from the localities Boa Leza, Mata Menge, Ola Bula, and Dozo Dhalu, all pertaining to Member B of the Ola Bula Formation, Soa Basin, west Central Flores. C: Age profile of *"Elephas" celebensis* from the locality Sompe, base of the Beru Member, Walanae Formation, South Sulawesi. D: Age profile of *S. t. trigonocephalus* from Trinil, Central Java.

Leza and Dozo Dhalu, in order to reconstruct a time-averaged age profile, which could be used for comparison with the *S. sondaari* sp. nov. age profile.

The sites from which the 3 island elephantoid assemblages originated (Tangi Talo, Sompe and the Member B localities of the Ola Bula Formation), invariably have yielded other vertebrate taxa besides elephantoids. The faunal assemblages from these sites are characterized by very limited numbers of endemic species. However, based on the abundance of fossils from those localities and from other localities in the same stratigraphic units, these assemblages are thought to be representative for the large vertebrate island faunas (not the small vertebrates). In the two Flores assemblages stegodont remains predominate (Fig. 78). At Tangi Talo a large proportion of the identifiable fossils consists of *Geochelone* sp. (a species smaller than *Geochelone atlas*), and to a lesser degree, *Varanus komodoensis*. A single tooth of a small crocodile was found. No mammals other than *S. sondaari* sp. nov. are thought to be present in this fauna. In *S. sondaari* sp. nov., dental elements are much better represented than skeletal elements.

Mata Menge yielded only minor amounts of non-*Stegodon* remains (only *Hooijeromys nusatenggara*). At Mata Menge, skeletal elements of *S. florensis* are more abundant than dental remains (Fig. 78). Additional taxa from the same stratigraphic unit (Member B of the Ola Bula Formation) are *V. komodoensis* and a small crocodile (Fig. 70). The presence of Palaeolithic humans follows from the associated stone artefacts from this site.

In the Sompe faunal assemblage remains of the suid *Celebochoerus heekereni* predominate (Fig. 46A), comprising 76% of the total amount of identifiable fossils. The *"E." celebensis* sub-assemblage contains mostly surface collected specimens. Because isolated molars and molar fragments may have been more easily noticed than the smaller milkmolars, the sample could be biased in favour of the older age classes. There are also indications for fluvial transport prior to burial, which may have caused biases in the death assemblage. Other taxa present at Sompe are *Geochelone atlas*, a large *Crocodylus* sp., Trionychidae sp., and possibly *S. sompoensis* (see also chapter 3).

The Trinil faunal assemblage contains at least 15 taxa, including large mammalian carnivores (Table 1), but percentages have not been calculated. De Vos & Sondaar (1984) note that the Trinil assemblage is dominated by bovids. Cervid remains are also well represented and outnumber the *S. t. trigonocephalus* fossils. For the *S. t. trigonocephalus* sample we can feel confident that both male and female adults are present in the assemblage (Figs. 57, 58 & 74). The Trinil sample originates from a fluviatile volcanoclastic sandstone layer.

The 4 elephantoid age profiles from the sites shortly described above (Fig. 77A-D) have in common that the juvenile individuals constitute the largest age group, constituting between 56.5% (*"E." celebensis* and *S. t. trigonocephalus*) and 37% (*S. florensis*) of the total MNI. There are some differences, however. The age profiles of *S. t. trigonocephalus* and *"E." celebensis* are similar (Fig. 77C & D), with the combined age groups 4 and 5 constituting 17-19% of the MNI. The *S. sondaari* profile differs from the latter two by portraying the young adults as the second largest group (Fig. 77A), representing 25% of the total MNI. The *S. florensis* sample, on the other hand, is dominated by senior and very old individuals, together comprising 42% of the total MNI, which is more than the total percentage of the juvenile age group 1 (37%).

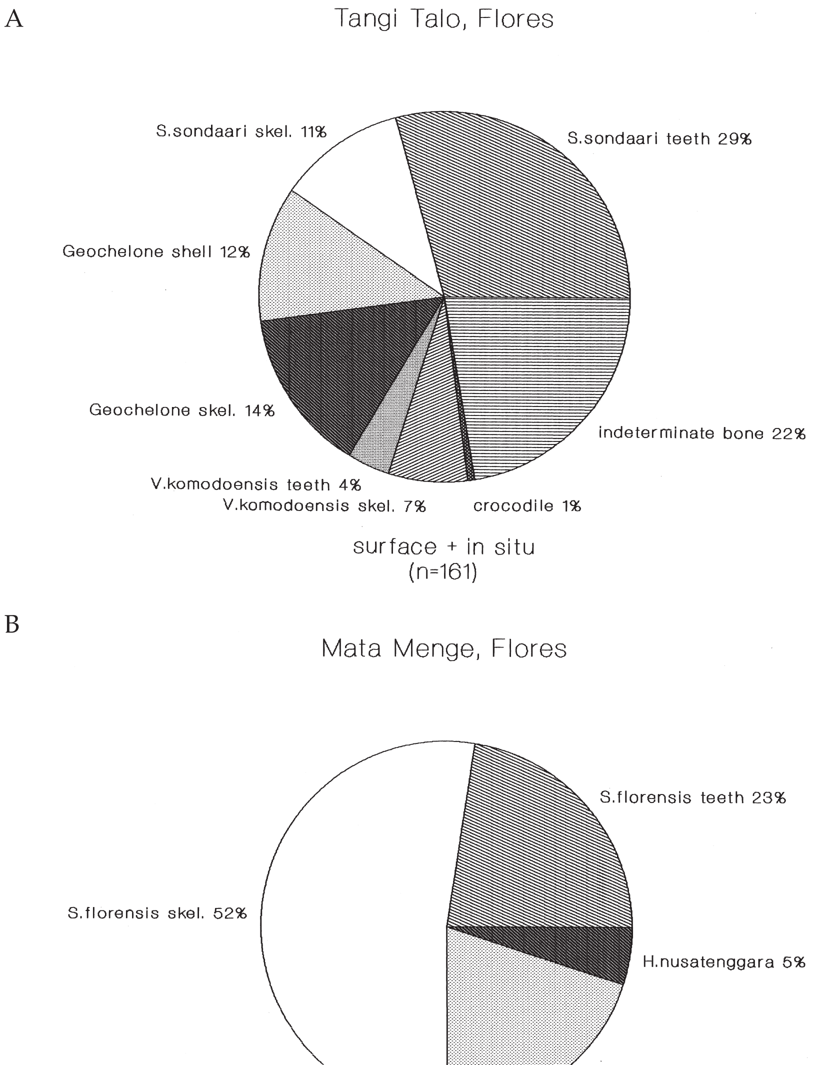


Fig. 78. Taxon representation graphs of two fossil localities on Flores. A: Tangi Talo, B: Mata Menge. Each taxon is expressed as a percentage of the total number of fossil specimens (n) of that taxon. In situ and surface collected fossils have been lumped together for Tangi Talo. For *Varanus komodoensis* and elephantoids, the teeth (molars + molar fragments + tusk fragments) and skeletal parts are represented separately. For *Geochelone* skeletal parts and shell fragments (plastron + carapace) are represented separately. At Mata Menge the only vertebrate taxon found apart from *Stegodon florensis*, is *Hooijeromys nusatenggara*, but at the localities Boa Leza and Dozo Dhalu small crocodile and *V. komodoensis* teeth have been found in association with *S. florensis* and *H. nusatenggara*.

Interpretation of the age profiles

Haynes (1987, 1991) performed extensive studies on the structure of death assemblages of both modern and fossil elephantoids and elaborated existing literature on this subject. He distinguished 4 types of age profiles, designated with the letters A-D.

Type A. This age profile is characterized by a predominance of juveniles (age class 0-12 AEY) and decreasing proportions of successively older age classes. The juvenile age class comprises 30-60% of the total MNI. Type A resembles the age profile of living populations. When encountered in a death assemblage it is attributed to nonselective mortality that affected stable populations. This age profile may result from abrupt, catastrophic events that affected individuals from all age classes to the same degree. Theoretically, it may also result from time-averaged but nonselective mortality acting over a longer period.

Type B. In this age profile the juveniles are greatly outnumbering the mature animals that could have borne them. The juvenile age group may constitute more than 80% of the total MNI. Hence, the causes of death must have selectively affected the juveniles. Type B has been documented by actualistic studies on elephant bone assemblages resulting from severe drought stress in Hwange National Park, Zimbabwe, between 1980 and 1984 (Haynes, 1991). This mortality profile may also be the result of predators preferentially killing juvenile individuals.

Type C. In this type, prime-age adults predominate while juveniles are conspicuously rare. This assemblage represents selective mortality over an extended period, like for instance time-averaged selective death of males only. An example of this type is the *Mammuthus columbi* site at Hot Springs (SD). The mammoth remains were found in sediments deposited in a spring-fed pool occupying a sinkhole. Most individuals were young adults, predominantly males, which are thought to have become trapped in the steep-walled pond. The accumulation is thought to be the result of behavioral factors. Young males that had left the maternal herd after reaching sexual maturity were subject to high mortality at the sinkhole trap. These animals would have displayed greater tendencies to explore and wander alone, but due to their lack of experience were preferentially trapped at the sinkhole (Agenbroad, 1990). A type C age profile might also result from non-selective mortality affecting a declining population with low numbers of juveniles.

Type D. This profile is patternless, usually representing sites with only a few individuals.

All four age profiles from Indonesia seem to reflect the type A of Haynes (1991), although the best fit with this type of profile is shown by *S. sondaari* sp. nov. (Fig. 77A). The *S. sondaari* sp. nov. age profile is the only one with age group 2 as the second largest. Its shape matches exactly those of living elephantoid populations. This could either mean that the cause of death was catastrophic and non-selective, affecting individuals of all ages in a short period, or that it was non-selective but acting over a long period of time. As has been mentioned in the sedimentological description of the Tangi Talo site, the bone accumulation is concentrated in a single horizon on top of a tuffaceous pumice layer. These observations, in combination with a type A age profile, strongly plead in favour of a catastrophic (volcanic) event, that caused the death of many *S. sondaari* nov sp. individuals, independent of their age.

Mass death of the dwarf stegodonts may have been due to food or water shortage after a volcanic event, which caused coverage of the vegetation in the area with volcanic ash. The animals may also have been killed instantaneously during the volcanic event by means of choking. The mortality profile of the dwarf stegodonts is similar to a mortality profile of cervids killed in the 1980 eruption of Mount St. Helens (Lyman, 1989). Interestingly, in this case there was evidence that partly buried cervid carcasses were visited and exploited by scavenging carnivores in the summer and autumn after the eruption. In the case of the Tangi Talo site at Flores, *S. sondaari* sp. nov. carcasses might have attracted Komodo monitors, which could explain the disarticulation and removal of skeletal parts from the original death assemblage. The fact that the matrix inside a *Geochelone* plastron-carapace at Tangi Talo contained several teeth of the Komodo monitor strongly suggests that this reptile indeed fed on carcasses at this site.

However, there remain some doubts concerning these interpretations. First, the Tangi Talo sample number is rather small (MNI = 12), while it has been argued that a minimum sample size of 30 individuals is necessary for reliable age profile analysis (Lyman, 1987). Conclusions regarding the causes of death based on the mortality profile of Tangi Talo should therefore be considered with care until more fossil material is available. Furthermore, the *S. sondaari* sp. nov. material is rather fragmented, and many bones have been removed or disintegrated prior to burial, as follows from the strong under-representation of skeletal relative to dental elements (Fig. 78A). Dental elements of juvenile animals could have been filtered preferentially out of the assemblage, thus creating a type A assemblage out of a type B assemblage. Bone removal by *Varanus komodoensis* is likely to have occurred at the site.

Auffenberg (1981) studied the ecology and behaviour of the extant Komodo monitors, or oras as they are also called by the local inhabitants. Oras are highly opportunistic scavenger-predators which feed on anything they can catch or kill, including marine turtles and their eggs. Their main food source consists of deer and pigs, but occasionally waterbuffaloes are attacked as well. With an average adult body-weight of 425 kg, waterbuffaloes are heavier than the adult pygmy stegodonts were, and pygmy stegodonts may safely be assumed to have been on the menu of the oras as well. When oras feed, practically nothing remains of their prey except for the gut contents; occasionally ora droppings even contain horn fragments of waterbuffaloes! It is further of importance to notice that oras do not bring their prey to specific places, but feed on the site were their prey perished. Oras are not able to move fast over long distances, which is why they prefer to ambush their prey. It could be argued that preferential ambushing at for example a drinking place could have resulted in the stegodont bone accumulation at Tangi Talo. However, oras cannot kill large prey animals instantaneously in most cases, but can only cause ugly wounds with their sharp teeth. Bacteria present in their saliva take care of the killing, but usually several days after the attack. With their excellent sense of smell oras relocate the dying prey animals, which is usually far away from the original site of ambush. It is thus unlikely that the dwarf stegodont bone concentration at Tangi Talo resulted from ora behaviour. However, ora activity might have selectively removed juvenile skull and mandible elements of *S. sondaari* from the original death assemblage, including their dentitions.

These considerations should serve as a warning to avoid ‘jumping to conclusions’. Nevertheless, a catastrophic death cause at Tangi Talo seems most plausible, because it agrees with the nature of the deposits. The sedimentology of the site shows that volcanism was actively occurring and may have been the direct cause of death. Alternatively, selective mortality of juveniles may have led to a type B death assemblage first. In this case death may still have been caused by a volcanic event, but acted selectively on juvenile individuals. Perhaps shortage of clean water after a volcanic eruption preferentially killed juveniles, analogous to observed mortality patterns of modern elephants during drought (Haynes, 1991). Selective post-mortem removal of juvenile skulls from the death assemblage by ora activity could subsequently have led to a type A age profile.

The composite *S. florensis* age profile (Fig. 77B) differs from that of *S. sondaari* by an higher proportion of old individuals, whereas young adults (age group 2) are comparatively rare. Still, the profile corresponds better with type A of Haynes (1991) than with any of the other types. The *S. florensis* molar material described by Hooijer (1967, 1972a) may be biased, because the easily recognizable tapering M3 fragments could have been preferentially treated by Hooijer (1967, 1972a). However, such a bias cannot explain satisfactorily why young and juvenile individuals are relatively rare, because milkmolars or unfused postcranials are also absent amongst the material collected during the recent GRDC-NNM excavations at Mata Menge. One could argue that small milkmolars could have escaped attention more easily during the excavations, but this is unlikely. During the excavations, Verhoeven (1974) had all larger lumps of sediment broken down into small pieces before they were discarded. In this way even the small *Hooijeromys nusatenggara* bones and jaws were discovered, and this excavation procedure was also followed during our own excavation. Juveniles do indeed appear to be relatively rare in the *S. florensis* sample (37%), but are not extremely rare when compared to the age structures of stable or declining elephant populations (Haynes, 1991). Out of 27 *S. florensis* individuals recognizable in total (including all dental material of unknown locality described by Hooijer, 1967, 1972a), only 3 had either the dP3 or dP4 in use, and 4 more the M1. These 7 individuals together make up age group 1 in Fig. 77B. This means that more than 50% of age group 1 (juveniles) are individuals that almost reached sexual maturity. Out of the 27 individuals 8 are represented by fossil molars from unknown localities, which were presumably surface collected, and which have not been included in the age profile of Fig. 77B. These 8 specimens all represent M3 fragments (as they were not figured by Hooijer it was not possible to determine their precise DWAC, but they represent individuals of either age group 4 or 5). By including these 8 specimens in the reconstruction of the age profile, the percentage of age groups 4 and 5 would increase further at the cost of the juveniles, only then becoming excessively large, together comprising 59% of the total MNI. This would suggest selective mortality of old individuals (a variation of type C age profile of Haynes, 1987). However, surface collected specimens may be biased towards larger teeth and therefore older individuals. If these 8 specimens are left out from the age profile, as done in Fig. 77B, the percentage of the combined age groups 4 and 5 amounts to 42%. Though still rather high amounts of senior individuals are present in this way, the profile better reflects type A. Similar age profiles were presented by Haynes (1987) for a simulated stable elephant population (Haynes, 1987: fig. 1a) and for a sample of *Mammuthus* bones (MNI = 61) from the Fairbanks and Goldstream Creeks area, Alaska (Haynes, 1987: fig. 2a). Both the Flores and the Alaskan sample are time-averaged, and therefore their composition cannot reflect single catastrophic events. As the age profile of the Alaskan sample was found to be very similar to that of the simulated stable elephant population, it was interpreted that it resulted from a time-averaging effect over a long period of bone accumulation due to numerous different causes of death. Temporary peculiarities in age profiles caused by occasional resource stress and elevated selective mortality rates were thought to be evened out over the long period, resulting in a 'normal' type A age profile (Haynes, 1987).

In case of the Flores sample, the very low representation of very young juveniles in age group 1 could mean that their dental remains were selectively lost from the death assemblages at the various localities, either prior to burial by biological agents such as the oras, or after burial due to poor fossilization. Possibly, juvenile stegodont skulls, including their dentitions, could have been swallowed by oras entirely, as happens with skulls of adult pigs and deer. It is hard to imagine, however, that skulls of adult stegodonts were within the swallowing capacity of these ferocious beasts.

Alternatively, the relatively high percentage of old adults in the *S. florensis* assemblage could be the result of selective mortality in these age groups due to hunting activities by humans, whose presence is evidenced by stone artefacts in the same layers. Sondaar (1987) believed that due to the human presence on Flores, the large *Stegodon* did not become fully dwarfed because one of the conditions for dwarfing of large mammals on islands would be that there were no predators present. Human hunters may have selected the older and weakened individuals, instead of the juveniles and prime adults. However, for the moment there are no indications, like for instance butchering marks on bones, that the stegodonts of Flores were actually killed by humans. Another explanation for the relatively high numbers of old individuals in the sample could be that living circumstances on Flores were quite optimal and that mortality among the juveniles and prime aged individuals was exceptionally low, at least at the sites in the Soa Basin. Adults of *S. florensis* may have effectively protected their young from ora attacks with their long tusks, so that very few juveniles fell prey to oras.

The age profiles of *S. t. trigonocephalus* from Trinil (Fig. 77C) and *"E." celebensis* from Sompe (Fig. 77D) also correspond to type A, but tend towards type B in their high percentages (56%) of juveniles. However, healthy modern elephant populations may be composed of up to about 60% of juveniles as well, as illustrated by a sample of culled elephants from Hwange National Park, Zimbabwe, as reported by Haynes (1987). In both the age profiles from Trinil and Sompe young adults (age group 2) tend to be somewhat underrepresented relative to prime age adults (age group 3). The profiles could be explained as being the result of both catastrophic death causes over a short time interval or as time-averaged (almost) non-selective mortality over a longer time interval. As young adults tend to be slightly underrepresented in these profiles, this age group may have been slightly less affected by the main causes of death, whatever these were. For the Sompe assemblage a time-averaged interpretation is the most likely one, as follows from other evidence. Size variability in the *Celebochoerus heekereni* assemblage from the same site is larger than from other sites where bones were not reworked by flowing water and which are thought to have accumulated during a relatively short period of time. CV's of size measurements of *C. heekereni* canines from Sompe (= FVL-25a: CV's varying between 12.9 and 21.9) are larger than those from samples certainly representing short time intervals, like FVL-5 and

FVL-24c (CV's varying between 12.1 and 14.8 and between 8.8 and 16.4, respectively). This suggests that the Sompe sample contains individuals widely separated in time and not from a single population representing a short time-interval (DIRSP, 1995). In addition the low percentages of skeletal elements at Sompe suggest that reworking by water-transport has been extensive (chapter 3).

For the Trinil assemblage a catastrophic event may be the more plausible explanation to account for the type A profile. Generally at Trinil the bones of all taxa are well preserved and show little damage due to weathering. This suggests that they were rapidly covered by sediments, which happen to be of volcano-clastic origin. Volcanic eruptions could very well have generated the large quantities of sediment necessary for rapid bone coverage. In a cumulative site, for example caused by preying animals, bone damage would be probably more severe (Haynes, 1988) than is the case at Trinil. If the Trinil age profile indeed approximates the age structure of the stegodont population prior to catastrophic death, then it could be concluded that the Trinil population was in a healthy, expanding state, judging from the high percentage of juveniles.

Summarizing, it may be concluded that selective mortality was generally low for most elephantoid assemblages studied, except for that of *S. florensis*. The 'model' type A age structure of the *S. sondaari* assemblage and its sedimentological setting convincingly illustrate that a volcanic catastrophic event caused the sudden death en masse of the population. In contrast, the other three age profiles from Indonesia are less unambiguous in their interpretation. Future excavations at the rich *S. florensis* sites of Mata Menge and Dozo Dhalu may provide age profiles based on substantial numbers of individuals from single localities. Peculiarities of the age profile treated here, like the high proportion of senior and very old adults in the *S. florensis* sample, may turn out to be due to specific 'island' circumstances.

9. Conclusions

The new stratigraphic data from Sulawesi and Flores, the study of the fossil faunas from these islands, and the new age assessments and comparisons with faunal successions from surrounding areas, together provide a better understanding of the regional palaeozoogeography during the Plio-Pleistocene. The study provided new insights in the evolution of the Elephantoidea in the Indonesian region and the very early dispersal of hominids beyond 'Wallace's line' already in early Middle Pleistocene time.

Sulawesi

Stratigraphy

Terrestrial vertebrates occur in various stratigraphic units on South Sulawesi. Most proliferous is the upper, terrestrial part of the deltaic Walanae Formation, which accumulated in the Neogene Sengkang Basin. This upper part is designated as the Beru Member. The vertebrate fauna recovered from the Beru Member is called Walanae Fauna, which ranges in age from Late Pliocene (c. 2.5 Ma) to Early or even early Middle Pleistocene. In the West Sengkang Basin (WSB) downfolding and deposition along the depocentral axis continues until the present day, whereas the eastern margin of the WSB has been folded into a thrust-cored anticlinal structure, the Sengkang Anticline. Left-lateral displacements and uplift along this fault zone, which constitutes the boundary between the West and East Sengkang Basins, are inferred to have occurred during the Pleistocene.

Palaeolithic stone implements seem to be associated with conglomerates, which crop out at various altitudes in a fault-bounded structure, called the Lakibong Triangle (LT), located west of the Sengkang Anticline near the village of Beru. Because of the horizontal layering in the LT, these conglomerates have been interpreted as being related to a Late Pleistocene terrace system of the Walanae River by previous authors. Here these conglomerates are included in the uppermost (exposed) part of the Beru Member, based on new geological evidence.

Other occurrences of stone artefacts are associated with coarse alluvial fan deposits, which are locally preserved along the fault-bounded southern margin of the WSB. They were deposited after the Early-Middle Pleistocene deformation phase recorded throughout the area. This implies that the Cabenge artefacts may well be older than Late Pleistocene, but as they have not been found in situ so far, they may be relatively young as well.

Whereas deposition locally continues up to Recent time in the WSB, erosion has begun during the Middle Pleistocene in the East Sengkang Basin (ESB). This was followed by recurrent, short episodes of deposition and renewed erosion. In the ESB the lower part of the Walanae Formation is unconformably overlain by the vertebrate-bearing Tanrung Formation, with an estimated Middle Pleistocene age. The fauna from this unit is called Tanrung Fauna.

The oldest indisputable occurrence of fossil taxa that are still extant on Sulawesi is represented by the findings from the locally developed younger colluvial and alluvial deposits, and from cave deposits, all of Late Pleistocene and Holocene age.

Faunal succession

From c. 2.5 Ma until Recent three successive terrestrial faunas can be distinguished in South Sulawesi, all unbalanced, endemic and indicating island conditions. The fossil suid *Celebochoerus heekereni* is the most abundant representative of the Walanae Fauna. The other elements of the Walanae Fauna are *Geochelone atlas*, *"Elephas" celebensis*, *Stegodon sompoensis*, crocodiles and Trionychidae sp. The fauna can be recognized in primary context throughout the fluvio-estuarine Beru Member. The two proboscideans in the Walanae Fauna are dwarfed and approximately of equal size, with an estimated adult body-weight between 350 and 950 kg. A *Stegodon* of larger proportions may be present in the youngest exposed layers of the Beru Member, but is not recorded from in situ remains. The Walanae Fauna is of Siwalik affinity and it probably inhabited a separate palaeo-island corresponding with today's southwestern Sulawesi peninsula south of the Tempe depression. Its elements are thought to have entered South Sulawesi from the eastern margin of the Sunda Shelf by means of sweepstake dispersal.

At an ill-defined level during the late Early to Middle Pleistocene a faunal turnover occurred in South Sulawesi, but the exact timing of this event is difficult, due to a gap in the sedimentary record. The Middle Pleistocene Tanrung Fauna is documented by fossils originating from the Tanrung Formation. The faunal turnover is characterized by the disappearance of *Geochelone atlas* and two species of pygmy proboscideans, and the arrival of two new large-sized elephantoid immigrants, *Stegodon* sp. B and an advanced hypsodont *Elephas* species. Of the large mammals *Celebochoerus* seems to be the only element from the Walanae Fauna which extended its range into the Middle Pleistocene Tanrung Fauna. The new elephantoid immigrants entered South Sulawesi by means of sweepstake dispersal, presumably by crossing the Makassar Strait. *Stegodon* sp. B was size reduced compared to its direct ancestor, but is of clearly larger dimensions than *S. sompoensis*. It is also recorded from the island of Sangihe.

The (sub)Recent Fauna of large mammals on Sulawesi is different from the Walanae and Tanrung Faunas and lacks proboscideans. This Fauna must have evolved in isolation for a long period of time, but its elements do not occur in the now well-known Walanae Fauna. Neither are they recorded in the still insufficiently known Tanrung Fauna with certainty (surface-collected fossils of *Anoa* and *Sus* most likely originate from younger coastal terrace deposits unconformably overlying the Tanrung Formation unconformably). This strongly suggests that ancestors of modern faunal elements, such as *Babyrousa*, *Sus*, and *Anoa* were effectively separated from the Walanae and perhaps Tanrung Faunas, which inhabited South Sulawesi during the Late Pliocene/Early Pleistocene and the Middle Pleistocene, respectively. The ancestors of the Recent Fauna presumably lived on a separate island, which corresponded with today’s Central and North Sulawesi. Early human influence in the extinction of the Walanae and Tanrung Faunas remains highly speculative.

Flores

Stratigraphy

On Flores the stratigraphy of the vertebrate-bearing strata is relatively simple. The horizontally layered fossiliferous sequence has a thickness of about 80 m and rests unconformably on slightly tilted volcanic breccias in a small basin, the Soa Basin. The fossiliferous beds pertain to the Ola Bula Formation, which can be subdivided into three members, tentatively called Member A, B, and C. The oldest Member A consists of tuffaceous sediments. At one site, called Tangi Talo, Member A yielded a fossil assemblage, which has been designated as Fauna A. Member A is conformably overlain by fluvial deposits of Member B. Various localities in Member B have yielded fossil vertebrate remains (Fauna B) and Palaeolithic artefacts. Member B, in turn, is overlain by thin-bedded lacustrine limestones with tuffaceous intercalations (Member C). Palaeomagnetic dating indicates that Fauna A is of late Early and Fauna B of early Middle Pleistocene age (see endnote 6).

Faunal succession

Fauna A contains the dwarfed *Stegodon sondaari* sp. nov., a giant tortoise (*Geochelone* sp.), a large predatory reptile (*Varanus komodoensis*) and a small crocodile. Based on compositional differences with the Walanae and Tanrung Faunas from South Sulawesi it may be assumed that there were no direct land connections between South Sulawesi and Flores.

Fauna A is replaced by a fauna with a medium-sized elephantoid (*Stegodon floren-*

sis) and a giant rat (*Hooijeromys nusatenggara*), while *V. komodoensis* and a small crocodile continue into this younger fauna. Perhaps human influence may have been responsible for the extinction of *S. sondaari* and the giant tortoises of Fauna A, though a volcanic catastrophe may account for the observed faunal turnover as well. Like *Stegodon* sp. B from Sulawesi, *S. florensis* underwent some size reduction, but it is not fully dwarfed.

Java

The faunal evolution on Java has been far more complex than that on Flores and Sulawesi, because Java formed part of the Sunda Shelf since its emergence during the Late Pliocene and it was intermittently connected with the SE Asian mainland during the Pleistocene. Proboscideans have always been an important constituent of the successive faunas recognized. One of the first proboscideans to have reached Java, perhaps as early as Late Pliocene, is *Sinomastodon bumiajuensis*. This species occurs in the Satir Fauna, an island fauna with an age of 2.0-1.5 Ma. Also the dwarfed *"Elephas" indonesicus*, thought to be closely related with *"Elephas" celebensis*, may have formed part of this island fauna, although it has not been recorded from in situ remains as yet. Also *Geochelone atlas* was amongst the first invaders of Java. Dispersal to Java is thought to have been by means of sweepstake dispersal at this stage. The approximately 1.2 Ma old, but poorly known Ci Saat Fauna was originally defined by the first occurrence of *Stegodon*. Due to the relative scarcity of fossils of this age, the transition between the Satir and Ci Saat Faunas is poorly known. New is the first recording from Java of *Stegodon elephantoides*, originating from black clays deposited between 1.3 and 1.2 Ma ago. Remains of *Geochelone* were found in a layer several meters above the layer yielding *S. elephantoides*, which suggests that the transition between both faunas was gradual.

The succeeding faunas, the 0.9 Ma Trinil 'Haupt-Knochenschicht' Fauna and the 0.8-0.7 Ma old Kedung Brubus Fauna, are well known and document an increasing continentality of Java. The Trinil H.K. Fauna, is somewhat impoverished but contains carnivores; it contains *Stegodon trigonocephalus* as the only elephantoid. Local evolution is documented by the recognition of three successive chrono-subspecies of *S. trigonocephalus*, each one with an increasing number of molar ridges. The oldest, still poorly known subspecies is *S. t. praecursor*, which predates the Trinil Fauna. In the Trinil and Kedung Brubus Faunas *S. t. trigonocephalus* is present, while the most advanced subspecies, *S. t. ngandongensis* occurs in the late Middle or early Late Pleistocene Ngandong Fauna.

Apart from full-sized elephantoids, several dwarf stegodonts once inhabited Java. Dwarfing could develop during times of isolation of Java or parts of Java. The most primitive dwarf stegodont is documented by a single M_3 of unknown age from the Cirebon District. A more advanced Late Pliocene or Early Pleistocene dwarf *Stegodon* species is recorded from Sambungmacan, Central Java. Furthermore, there is a dwarf stegodont from Eastern Java (stratigraphic level unknown), named *S. hypsilophus*. It differs from the other two dwarf stegodonts by having unusual hypsodont molars for a stegodont. Increased hypsodonty is also encountered in other island stegodonts from the region, and seems to have been an adaptation to island environments.

On Java the disappearance of *Stegodon* and the first recording of *Elephas maximus* corresponds with environmental changes from open woodland to rainforest environments, as documented by the clear differences between the Ngandong Fauna and the Punung Fauna. These changes took place after the penultimate glaciation around 125 Ka. The first unambiguously identifiable molar remains of *E. maximus* originate from Cipeundeuy, West Java, from a layer dated at 30 Ka.

Dispersal routes

The geological evidence suggests that Sulawesi has not been connected with the Sunda Shelf at least since the Paleogene. Of the large mammals *Babyrousa* may be the only taxon of which the progenitors became isolated on an eastward drifting continental fragment which corresponds to Central Sulawesi. Apart from the phalangers, which must have come from the east, the ancestors of all other large mammals, fossil and extant, must have reached Sulawesi by crossing the sea between the Sunda Shelf and Sulawesi. Overseas dispersal from the Philippines is unlikely, at least during the later part of the Quaternary, but stratigraphic data and fossil remains from the Philippines have been insufficiently studied so far.

South Sulawesi was a separate palaeo-island until at least the Middle Pleistocene, because the Walanae Fauna does not contain any ancestors of the modern Sulawesi fauna and because the latter fauna must have been isolated for quite some time as well. Faunal stability on the South Sulawesi palaeo-island prevailed until the Middle Pleistocene, and only local evolution occurred (e.g., shortening of the metapodials in *Celebochoerus heekereni*). During the Middle Pleistocene new immigrants started to arrive and most elements from the Walanae Fauna apparently became extinct, resulting in a faunal turnover.

Flores emerged from the sea during the Miocene by volcanic activity. *Stegodon sondaari* sp. nov. from Flores bears some primitive molar characters, and is not related to the more advanced *S. sompoensis* from South Sulawesi. Therefore, former land connections between South Sulawesi and Flores are unlikely, and presumably the ancestors of *S. sondaari* reached Flores from the west, perhaps already in the Pliocene. Also on Flores a faunal turnover is recorded, which took place around the Early Pleistocene/Middle Pleistocene transition. *S. sondaari* became extinct and was replaced by *S. florensis*. *S. florensis* is more progressive in molar morphology than *S. t. trigonocephalus*, the latter inhabiting Java at that time. Based on molar similarities, there may be a link between *S. florensis* and *Stegodon* sp. B from Sulawesi. *S. florensis* may have arrived from South Sulawesi via Selayar and the Bonerate islands, in contrast to the widely held view that Flores was populated from Java via Bali, Lombok and Sumbawa. However, more fossil material is needed to test this hypothesis.

The terrestrial faunal elements that initially colonized Java since its emergence during the Late Pliocene, show close affinity either with exclusively Siwalik taxa or with more widespread taxa. An exception is *Sinomastodon bumiajuensis*, one of the earliest invaders of Java, which has a purely Chinese origin.

A fauna of Chinese affinity did not enter Java until the Late Pleistocene, as documented by the Punung Fauna. The faunal turnover at this stage marks a transition from more open towards tropical rainforest environments.

Sea-level fluctuations

On Java a maximum number of species is recorded in the Kedung Brubus Fauna (0.8-0.7 Ma B.P.). For the first time a full corridor must have connected Java with the Asian mainland at that time. The formation of this corridor route can be correlated with pronounced glacio-eustatic sea-level lowerings that started at c. 0.8 Ma ago. This episode of low sea-levels may also have triggered the faunal turnovers observed on Sulawesi and Flores, by enhancing the chance for new dispersals to these islands. Like Java, also the islands of Japan and Taiwan experienced major faunal immigrations during the Middle Pleistocene, whereas the older faunas on these islands indicate island conditions. Unlike Sulawesi and Flores, these islands clearly became connected with the Asian mainland, supposedly as a result of low sea-levels, though tectonics may have been involved as well in these cases.

Stegodont evolution on islands

Owing to their good swimming capacities and long endurance, elephantoids, particularly stegodonts, were able to cross sea-barriers and colonize SE Asian islands that never became connected with the continent. It may be concluded that Plio-Pleistocene stegodonts were the most successful island colonizers in the SE Asian region prior to humans. By diminishing their size and by developing hypsodont teeth (enabling them to consume different types of food), they were successful in adapting themselves to the island environment. These adaptive trends constitute an excellent example of parallel evolution. One may wonder why stegodonts never reached Australia. Perhaps 200 km of sea crossing was too much, even for stegodonts.

The earliest seafarers

A final conclusion, but certainly not the least important one, is based on puzzling evidence from Flores. At various localities (Mata Menge, Dozo Dhalu) *Stegodon florensis* remains are associated with stone artefacts. Because of the inferred early Middle Pleistocene age, which is based on palaeomagnetic data, these artefacts are thought to be the work of *Homo erectus*. The authenticity of the artefacts has been confirmed by archaeologists, and also alternative dating techniques (fission-track dating, ESR) confirm the old age of the layer from which the artefacts were excavated (Morwood et al., 1998). The associated fauna clearly points to island conditions. An unexpected conclusion looms up: hominids were able to cross sea-barriers half a million years earlier than is generally thought. If this conclusion will stand critical examination in the near future, it will alter the image of our direct ancestors.

10. Notes

1) Confusion has partly originated from the imprecise and inconsistent designation of sites and localities in the past. For example, the locality name Marale has also been used for the locality referred to here as FVL-18; on the topographic maps

published in 1932 and the more recent Indonesian versions published by the cartographic section of the Geological Directorate, Marale is indicated as a place 2.5 km S of the village of Calio. FVL-16 and FVL-17 occur within a distance of 500 m from Marale. It is not clear weather the name 'Marale' used by Hooijer (1972b) to refer to a vertebrate locality, represents the Beru II excavation of van Heekeren or one or more places more to the south, since no map was presented. Bartstra et al. (1994: p.13) mention an upper molar fragment ascribed to *Stegodon* cf. *trigonocephalus* from some 200 m E of Marale. In fact, this fragment, which bears the registration number C3-27-86 of the Prehistory Museum at Calio, has been collected in the year 1986 at what is referred to by the curator of that museum, Mr Anwar Akib, as Marale III. In 1991 I asked Mr Akib to show us the place referred to by him as Marale III, which appeared to correspond with our FVL-17 (Encl. B). Many data on the finding localities of fossils and artefacts in South Sulawesi appear to be rather vague indeed.

2) No micromammals have been found in the Beru Member of the Walanae Formation so far. Only limited amounts of sediments have been sieved, without results. However, it is very likely that at least some small mammals were present in the Walanae Fauna, seen in the light of the abundance of extant endemic species. Some groups, e.g. rats, seem to have undergone their own radiation on the former islands now constituting Sulawesi.

3) Vertebrae of a large *Varanus* sp., of similar dimensions as *V. komodoensis*, have been reported from the Pleistocene of Timor and Java (Hooijer, 1972c). The author noted some small morphological differences with the recent *V. komodoensis*, which he considered as of subspecific value at most. However, as skulls and teeth are lacking, this interpretation may not be valid, and some of the Javanese vertebrae mentioned by Hooijer had been previously assigned to a different species, *V. bolkayi* Fejérváry, 1935. Six isolated teeth, a dextral humerus diaphysis and various vertebrae recently excavated at the late Early Pleistocene locality Tangi Talo on Flores are conform the extant *V. komodoensis*, but will be described in another paper. Another endemic subfossil varanid from Flores was described by Brongersma (1958), *V. hooijeri*, with blunt conical teeth much different from those of *V. komodoensis*.

4) Recently it has become clear that a purely southern Chinese faunal element is also present in the oldest fauna recognized on Java, the Satir Fauna. Saegusa (1996) demonstrated that certain fossil remains from the Bumiayu area in west Central Java and from the Sangiran area, which were originally attributed to *Tetralophodon bumiajuensis* by van der Maarel (1932), should be assigned to *Sinomastodon* instead. *Sinomastodon* is known from Late Miocene to Early Pleistocene deposits from China and Japan (Tobien et al., 1986; Saegusa 1996), but has not yet been recorded from the Indian Subcontinent. *Sinomastodon* may have been driven south during one of the earlier cold episodes during the Late Pliocene.

5) Movius (1944) mentioned that Tabuhan, one of the two Punung fissures sampled by von Koenigswald, contained *Stegodon* according to the determinations of von Koenigswald. However, when Badoux (1959) studied the fossil collection from the Punung fissures he did not find any *Stegodon*. It is hard to imagine that von Koenigswald erroneously misinterpreted *Elephas* molar fragments (also present in

the assemblage) for those of *Stegodon*. Is it possible that *Stegodon* elements were lost from the assemblage prior to the study of Badoux? In the concept of von Koenigswald the Punung assemblage was of similar age as the Trinil fauna. According to the new biostratigraphic scheme of Java, Punung has been shown to be much younger and representing the first recognizable tropical rainforest fauna on that island, which originated from southern China during the Late Pleistocene. If originally present, the *Stegodon* remains referred to by Movius could perhaps belong to *S. orientalis*.

6) The early Middle Pleistocene age of the artefact-bearing stratum has recently been confirmed by fission-track ages on zirkons (Morwood et al., 1998).

11. Acknowledgements

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