A revision of the Pliocene and Quaternary Lutrinae from Europe

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Willemsen, G.F. A revision of the Pliocene and Quaternary Lutrinae from Europe. Scripta Geol., 101: 1-115, 24 figs., 5 pls, Leiden, October 1992.

In this paper, a revision of the Pliocene and Quaternary Lutrinae from Europe is presented. Such a revision, including fossil material, has not been published since the work of Pohle (1919). Three tribes within the Lutrinae are recognized: the Lutrini, the Aonyxini and the Enhydrini. The latter comprises both *Enhydra* and the *Enhydriodon* group.

The genus *Nesolutra*, consisting of three insular species, is not retained. Two are included in *Lutra* and for *N. ichnusae* a new genus, *Sardolutra*, is proposed. The genus *Isolalutra* is not retained either. Its only species, *I. cretensis*, is included in the genus *Lutrogale*. Some new material of this species is described.

A number of well-preserved fossils of *Cyrnaonyx antiqua* are described, such as the hitherto unknown skull and upper carnassial as well as postcranial material from Tornewton Cave. The systematic position of the species and genus is reviewed in detail. A new specimen of *Enhydra reevei* from Bramerton is described. The morphology of the M_1 supports the inclusion of the species in *Enhydra*.

The functional morphology and the ecology of the reviewed species is discussed and compared to extant lutrines. Adaptations in the postcranial skeleton indicate a very aquatic way of life for *Lutra simplicidens*, *L. trinacriae*, *L. euxena* and, to an even greater extent, *Sardolutra*. *Lutrogale cretensis* on the contrary shows a more terrestrial adaptation. *Cyrnaonyx* shows adaptations similar to *Lutra* and probably was a stream dweller, thus differing from its extant relative *Aonyx*.

From the dentition and the endocranial cast, conclusions on the feeding habits are drawn. The described *Lutra* and *Sardolutra* species were probably all specialized on motile prey, viz. fish. *Lutrogale*, *Algarolutra*, *Megalenhydris* and *Cyrnaonyx* show adaptations to a mixed diet, consisting of both fish and shellfish, though differences in the feeding habits between those forms are noted also. *Enhydra reevei* probably fed on shellfish exclusively.

In the last part, the phylogeny and palaeogeography of the Lutrinae are discussed. It is argued that the oldest Lutrinae, *Mionictis* spp., originated from the Melinae. The phylogeny of the Lutrini can be reconstructed relatively well. The ancestry of the island forms in the Mediterranean is discussed in some detail. For the Aonyxini, the fossil record is rather poor and a reconstruction of the phylogeny is virtually impossible. The origin of *Cyrnaonyx* is uncertain and the ancestry of *Megalenhydris* is unknown. The origin of the Enhydrini is somewhat obscure. The group reached a wide distribution and gave rise to the *Enhydra* line. The relationships between the species are discussed.

The problems involved in island species are considered. Remarks on the presence of otters in unbalanced island faunas are made. The peculiar taphonomy of otter fossils on islands is noted.

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Introduction

Lutrine fossils are known to be rare, compared to some other carnivores. During the last 25 years, however, relatively much new and in some cases very complete and important material has been found in Europe. This new material, part of which is described for the first time in this paper, made a revision of the European Pliocene and Quaternary lutrines necessary. The last revision of fossil and recent lutrines was by Pohle (1919). Later, only revisions restricted to extant lutrines have been published (e.g. Harris, 1968).

The scope of this study is to describe all lutrine material from the Pliocene and Pleistocene of Europe and to give a taxonomical revision of the studied material. The Holocene material, which all belongs to the extant *Lutra lutra*, is only partly described. Furthermore, an attempt is made to reconstruct the phylogenetical and biogeographical history of the Lutrinae on the basis of the material which is known now. The last reconstruction of the phylogeny of the whole subfamily was also given by Pohle (1919) and this reconstruction is no longer tenable in the light of the abundant material that has become available since then.

I made an effort to study as many specimens as possible, but in some cases it was not possible to see the actual specimens. In those cases I had to do with descriptions, photographs and casts, which were kindly provided by some colleagues.

MATERIAL AND METHODS

Material

For this study, material from many different collections was studied. The following abbreviations are used for the institutions and private collections:

BM - British Museum (Natural History), unless otherwise is stated the Department of Palaeontology, London.
CM - Cromer Museum, Cromer.
GIA - Geological Institute, Athens.
IPP - Instituut van Pre- en Protohistorie, Amsterdam.
IQW - Institut für Quartärpaläontologie, Weimar.
IvAU - Instituut van Aardwetenschappen, Utrecht.
Ke - Collection Mr N. Kerkhoff, Schiedam.
KMBF - Kreis-Museum, Bad Frankenhausen.
LPM - Laboratoire de Paléontologie, University of Languedoc, Montpellier.
MCN - Museo Civico di Archeologia e Speleologia, Nuoro.
MD - Museum Darmstadt.
MNB - Museum für Naturkunde, Humboldt University, Berlin (FRG).
MS - Museum Sabadell.
NCM - Norwich Castle Museum, Norwich.
NHM - Natural History Museum, Mainz.
PIV - Palaeontological Institute, Vienna.
RGM - Rijksmuseum van Geologie en Mineralogie, now forming part of the Nationaal Natuurhistorisch Museum, Leiden.
RMNH - Rijksmuseum van Natuurlijke Historie, now forming part of the Nationaal Natuurhistorisch Museum, Leiden.
SM - Sedgwick Museum, Cambridge.
SMF - Senckenberg Museum, Frankfurt am Main.
UCBL - Department of Earth Sciences, University Claude Bernard, Lyon.
UHGI - University of Helsinki Geological Institute.
UP - Geological Museum G.G. Gemmelaro of the University of Palermo.
UR - Department of Earth Sciences, University of Rome.
ZMA - Zoologisch Museum, Amsterdam.

Measurements

All measurements were taken with a Vernier callipers and are given in mm. The following abbreviations are used for the measurements:

General: L = length, W = width, H = height, T = thickness, D = diameter, lat = lateral, med = medial, dis = distal, prox = proximal, ant = anterior, post = posterior.

Skull measurements: skull measurements are shown in Figs. 1 and 2. The following measurements were taken (between brackets the number of the corresponding measurements in Pohle (1919): Lb = basal length (1), Lcb = condylobasal length, Ld = dorsal length, Ln = nose length (4), Lit = intertemporal length (6), Lfac = facial length (11), Lcra = cranial length (10), Lpal = palatal length (14), Wc = snout width (between outer sides of canine alveoles), Wio = interorbital width (2), Wppo = width between postorbital processes (3), Wit = intertemporal width (5), Wl = lower skull width (7),

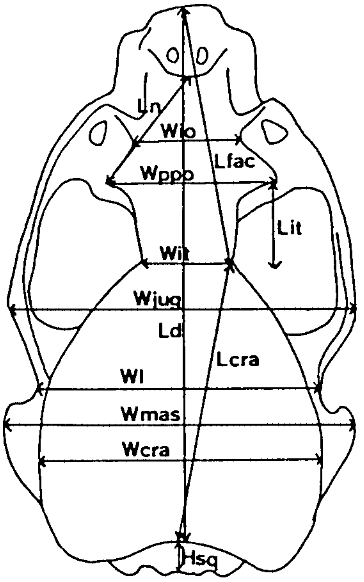


Fig. 1. Skull measurements used in this paper. Abbreviations are explained in the text.

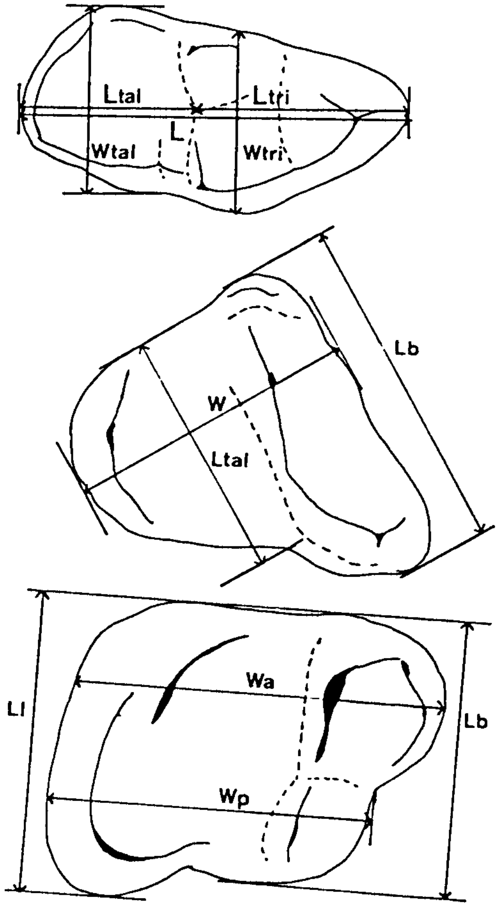


Fig. 2. Measurements of M_1, P^4 and M^1. Explanation in the text.

Wcra = upper skull width (cranial width) (8), Wmas = mastoid width (9), Wjug = jugal width (12), Wba = anterior basal width (15), Wbp = posterior basal width (16), Hsq = height squama occipitalis from foramen magnum (13).

Mandible measurements: L = length from anterior tip to condyle, H = height from angular process to coronoid process, Hra = height ramus between P_4 and M_1, Wra = width ramus between P_4 and M_1.

Dental measurements: Measurements which were taken on the alveoles are placed between brackets. See also Fig. 2. Lb = labial length, Ll = lingual length, Ltal = talon length, talonid length, Ltri = trigonid length, Wa = anterior width, Wp = posterior width.

Stratigraphy

In Figs. 3 and 4, the stratigraphical units used in this study, and their correlations are given. The Ruscinian-Villanyian boundary can be correlated with the Reuverian-Praetiglian boundary and it can be dated at c. 2.4 million years BP (Suc & Zagwijn, 1983; Reumer, 1985). This boundary can be correlated with the MN 16A-16B boundary (Reumer, 1984, 1985; see also Suc & Zagwijn, 1983). Many authors consider this border to be the lower boundary of the Pleistocene and this view is also expressed by the Dutch Geological Survey (see e.g. Zagwijn & van Staalduinen, 1975; van Staalduinen et al., 1979; Reumer, 1985). The boundary is then placed just above the onset of the Matuyama Reversed Polarity Zone. The horizon defined by the IGC in 1948, however, more or less coincides with the Olduvai Event and is thus much younger. When I use 'Pleistocene' or 'Lower Pleistocene' in this paper, I use it in the former sense, including the Praetiglian. The lower boundary in the marine stratigraphy would coincide with the lower Eburonian.

Acknowledgements

The author is grateful to all people who have contributed in some way to the completion of this paper.

The always stimulating and encouraging support of Dr P.Y. Sondaar (Utrecht) is highly appreciated. It was he who introduced me to mammal palaeontology and to the problem of island mammal faunas. He also made many improvements to the manuscript. For the support of Dr R.J. Schuiling I am grateful. I benefited very much from many fruitful and encouraging discussions with Dr J. de Vos (Leiden), who also read the manuscript critically at various stages. Dr M. Freudenthal made valuable comments on the manuscripts.

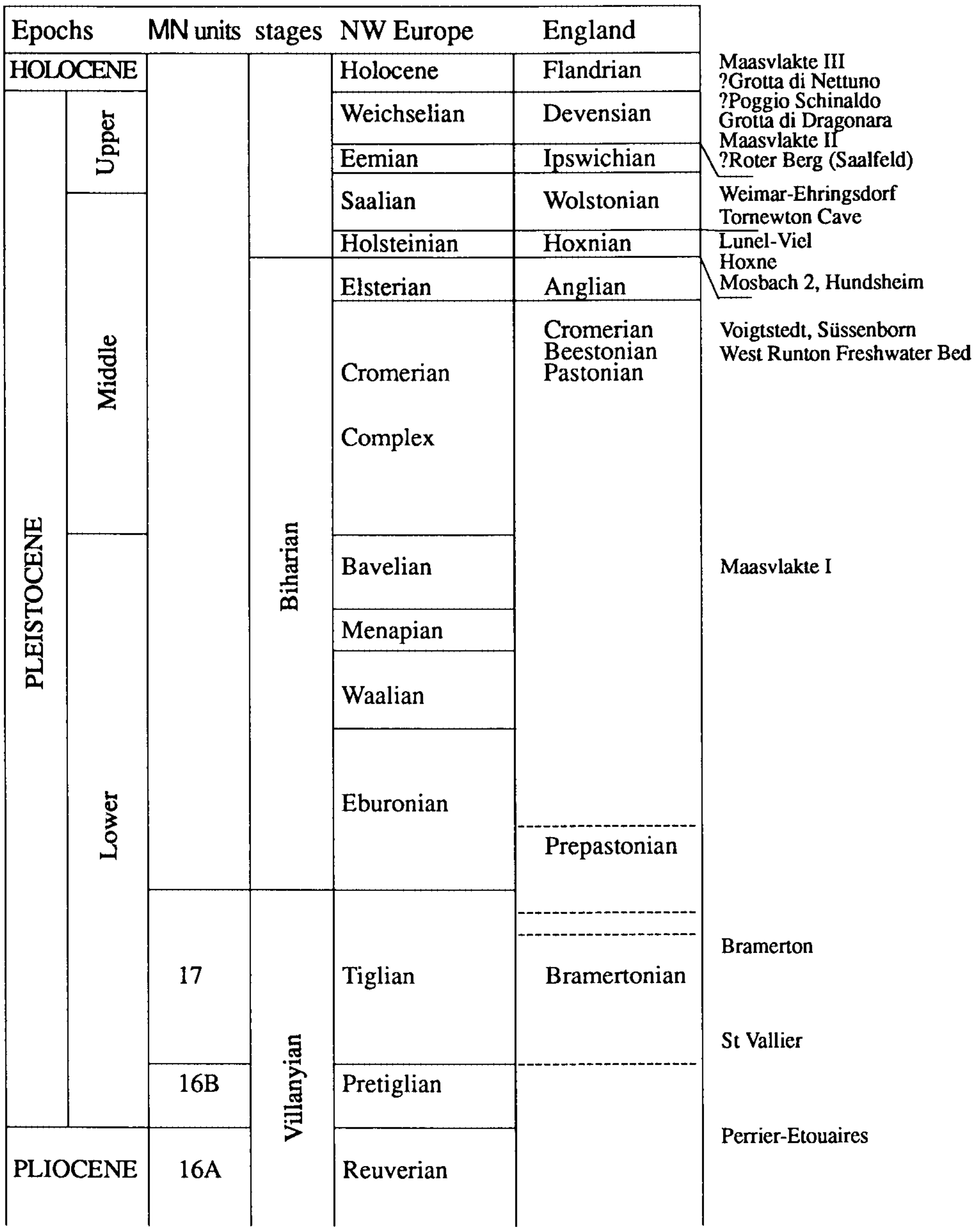
I want to thank Drs F. Angelelli (Roma), P.J.H. van Bree (Amsterdam), H. de Bruijn (Utrecht), E. Burgio (Palermo), P. Cambridge (Norwich), A. Currant (London), J.A. Davis (Brookfield) V. Eisenmann (Paris), W.-D. Heinrich (Berlin), L. Holthuis (Leiden), R.D. Kahlke (Weimar), T. van Kolfschoten (Utrecht), T. Kotsakis (Roma), J.J.M. Leinders (Heerlen), J. van der Made (Utrecht), A. Malatesta (Roma), D.F. Mayhew (Purmerend), A. van der Meulen (Utrecht), D. Mol ('s-Heerenberg), L. Radinsky (Chicago), A.J. Sutcliffe (London), M. Warren (Cromer), and L. Werdelin (Uppsala), for valuable remarks, discussions and help with obtaining various information.

I am grateful to all who allowed me to study material in their care and in some cases provided me with casts of important pieces, especially Drs L.E.M. de Boer (Rotterdam), P.J.H. van Bree, E. Burgio, P. Cambridge, A. Currant, H. Felten (Frankfurt), J.L. Franzen (Frankfurt), M. Freudenthal (Leiden), A.W. Gentry (London), C. Gurin (Lyon), W.-D. Heinrich, N. Kerkhoff (Rotterdam), B. Kurtn (Helsinki), A. Malatesta, M. Sangez (Nuoro), D. Smith (Norwich), C. Smeenk (Leiden), A.J. Stuart (Norwich), J. Sudre (Montpellier), A.J. Sutcliffe, N. Symeonides (Athens), J. de Vos (Leiden), M. Warren, and L. van Wijngaarden (Amsterdam).

Prof. Badoux (Utrecht) provided facilities for dissection. Mr J.P. Brinkerink (Utrecht) helped with many practical problems and prepared some of the material with

		MN unit	Stage		
PLEISTOCENE	U				
	M		'Biharian'		
	L				
		17	'Villanyian'		Bramerton St Vallier
		16B			
PLIOCENE		16A			Perrier-Etouaires
		15	'Ruscinian'		
		14			Montpellier
MIOCENE		13	Turolian		Monte Bamboli
		12			Concud, Los Mansuetos (Teruel)
		11			Pikermi, Baccinello VI
		10	Vallesian		
		9			Can Ponsich Eppelsheim
		8	Aragonian	'Astaracian'	
		7			
		6			
		5		'Orleanian'	
		4			
		3			
		2B	'Agenian'		
		2A			
		1			

Fig. 3. Stratigraphical units of the Neogene, used in this paper.



Epochs		MN units	stages	NW Europe	England	
HOLOCENE				Holocene	Flandrian	Maasvlakte III ?Grotta di Nettuno ?Poggio Schinaldo Grotta di Dragonara Maasvlakte II
PLEISTOCENE	Upper			Weichselian	Devensian	
				Eemian	Ipswichian	?Roter Berg (Saalfeld)
	Middle			Saalian	Wolstonian	Weimar-Ehringsdorf Tornewton Cave
				Holsteinian	Hoxnian	Lunel-Viel Hoxne
			Biharian	Elsterian	Anglian	Mosbach 2, Hundsheim
				Cromerian Complex	Cromerian Beestonian Pastonian	Voigtstedt, Süssenborn West Runton Freshwater Bed
	Lower			Bavelian		Maasvlakte I
				Menapian		
				Waalian		
				Eburonian	Prepastonian	
		17	Villanyian	Tiglian	Bramertonian	Bramerton St Vallier
		16B		Pretiglian		Perrier-Etouaires
PLIOCENE		16A		Reuverian		

Fig. 4. Stratigraphical units within the Quaternary, used in this paper.

great skill, for which I am grateful. I thank Messrs W.A. den Hartog and J. Luteyn, who made photographs and the plates and prepared part of the illustrations. I am grateful to Miss K.M. Stefels for her practical help at a number of occasions. The financial support of ZWO (now NWO) and of the University of Utrecht for field work is acknowledged.

This study would never have been completed without the continuous support and encouragement of my dear wife Gerdien.

Taxonomy

There is still much confusion about the supraspecific taxonomy of the Lutrinae. A division of the subfamily into two tribes has already been proposed by Gray (1865): the Enhydrina for the genus *Enhydra* and the Lutrina for all other lutrines known at that time. Pohle (1919) rejected this division, arguing that there is no reason to separate only *Enhydra* from all other genera.

A new attempt to erect a suprageneric taxonomy for the Lutrinae was made by Sokolov (1973). He divided the recent and fossil Lutrinae in four tribes. Davis (1978) proposed yet another subdivision. He only studied extant species. In the table on p. 9, the taxonomy as proposed by Sokolov (1973), Davis (1978) and in this paper are compared.

The taxonomy of Sokolov (1973) formalized the recognition of a lutroid and an aonychoid group, as well as the rather isolated position of *Enhydra* Fleming, 1822. This notion can be found with many earlier authors. Sokolov (op. cit.) placed *Potamotherium* Geoffroy, 1833 in a separate tribe. *Potamotherium* has long been regarded to be an otter (see e.g. Pohle, 1919; Thenius, 1949; Savage, 1957). In later years, several authors expressed doubts about this classification (e.g. Repenning et al., 1979). De Muizon (1982) convincingly showed the phocid affinities of *Potamotherium.* He included it in the Semantoridae, together with *Semantor macrurus* Orlov, 1933. The latter is a large, incompletely known aquatic carnivore from the Pliocene of Siberia (Orlov, 1933). Due to the incompleteness of the material, the systematic position of *Semantor* is unclear at this moment and a close relationship with *Potamotherium* is far from proven. Though there are clear affinities with the phocoid pinnipeds (Savage, 1957; Repenning et al., 1979; de Muizon, 1982), *Potamotherium* clearly shows many mustelid characters, as was pointed out by Tedford (1976). Therefore, in this paper, *Potamotherium* is tentatively placed in a separate subfamily, the Potamotheriinae, within the Mustelidae. It may be related to phocid origins, but no unequivocal conclusion about its phylogenetic position can be reached at the moment. It is clear though, that it is no lutrine.

Sokolov (1973) placed *Enhydriodon* Falconer, 1868 and related forms in a separate subtribe within the Aonyxini. Repenning (1976) pointed out the close relationship between *Enhydriodon* and *Enhydra.* More about this will be said in the chapter on phylogeny. Furthermore, there are a number of differences between the *Enhydriodon*-like forms on the one hand and the *Aonyx*-like forms on the other. In the P^4 of *Enhydriodon* and *Vishnuonyx* Pilgrim, 1932, hypocone and protocone are present as blunt, conical cusps. The same is true for paracone and metacone, which do not form a shearing blade. *Sivaonyx* Pilgrim, 1932 has the same type of morphology, if Pilgrim (1932, p. 89) is right in referring an isolated P^4 from Hasnot to this genus. This tooth differs slightly from both *Enhydriodon* species which are known from this area. No other upper dentition of *Sivaonyx* is known. In M_1 of *Enhydriodon* and *Sivaonyx*, the ento-

Suprageneric taxonomy of the Lutrinae.

Sokolov, 1973	Davis, 1978	this paper
tribus Potamotherini		subfamily Potamotheriinae
Potamotherium		*Potamotherium*
tribus Lutrini	tribus Lutrini	tribus Lutrini
Lutra	*Lutra*	*Lutra*
Pteronura		*Sardolutra*
Paralutra		*Lutrogale*
Nesolutra		*Pteronura*
Lutravus		*Satherium*
		Algarolutra
		Lutravus
	tribus Hydrictini	*Paralutra*
	Hydrictis	*Mionictis*
		Siamogale
tribus Aonyxini	tribus Aonychini	tribus Aonyxini
subtribus Aonyxina		
Aonyx	*Aonyx*	*Aonyx*
Amblonyx	(incl. *Amblonyx*)	*Amblonyx*
subtribus Enhydriodontina	*Lutrogale*	*Cyrnaonyx*
Vishnuonyx	*Pteronura*	*Limnonyx*
Sivaonyx	*Enhydra*	?*Megalenhydris*
Enhydriodon		
tribus Enhydrini		tribus Enhydrini
Enhydra		*Enhydra*
Sivalictis		*Enhydriodon*
		Sivaonyx
		Vishnuonyx

conid and the hypoconid are both present as large, blunt cuspids and more, smaller cuspids may be present at the talonid edge. A similar development of the M^1 is seen in *Aonyx capensis* Schinz, 1827. Because of the above-mentioned differences with other lutrines and because of the clear morphological resemblances and phylogenetic relationship with the sea-otter, I include *Enhydriodon*, *Sivaonyx* and *Vishnuonyx* in the Enhydrini. I do not include *Sivalictis*, since this probably is no lutrine at all. Pilgrim (1932) described the only species, *S. natans*, on the basis of a single M^1 from the Siwaliks. The author was not sure whether his new species is lutrine or not, but he noted similarities with *Potamotherium* (which he considered to be near the ancestral type of the otters). He further noted that the low cusps reminded of *Enhydra*. In fact, the tooth morphology is quite unlike any lutrine, as far as can be judged from Pilgrim's illustration (op. cit., pl. 1, fig. 1), and apart from the low cusps there are no resemblances with *Enhydra*. The strong cingulum on the outer side of the paraconid is not found in lutrines and the posterolingual expansion of the tooth, which is typical for lutrines, is not present.

The classification of Davis (1978) is quite unconventional. Apparently, he was unaware of the work of Sokolov (op. cit.), since he did not use Sokolov's Aonyxini (which clearly has priority over his Aonychini) and since he explicitly stated that his tribes are new taxa, which is not true. Davis only studied extant species. He stated that 'Because of a high degree of both convergence and adaptive radiation within the group, a study limited to cranial morphology does not yield the true relationships between species.' (Davis, 1978, p. 15). Indeed, one should be careful and be aware of the possible occurrence of convergence and adaptive radiation. Therefore, one should try to use different kinds of characters in taxonomical work and to avoid using a single set of functionally related morphological characters as the sole basis for taxonomical conclusions. When one is aware of the limitations, cranial characters can give important indications for taxonomical relationships (see van Zyll de Jong, 1972).

The weak point in Davis' work is, that he totally excluded the type of characters normally used in lutrine taxonomy and based his taxonomy on five characters only: the form of the baculum, the form of the external genitalia, the anxiety call, the contact call and the affectional call. Davis' choice of characters is arbitrary. Ewer (1973) pointed out that the form of the baculum does not always simply reflect taxonomical relations. In otherwise closely related species, its morphology sometimes differs very much.

Davis (1978) further lumped all New World *Lutra* species together, basing himself on their almost identical vocalisation and on the occurrence of a successful mating of a male *L. canadensis* Schreber, 1776 with a female *L. longicaudis* Olfers, 1818 in captivity. Successful mating in captivity, however, is no valid reason to suppose conspecifity of two forms. Davis (op. cit.) neglected significant skull characters, on the basis of which van Zyll de Jong (1972) proved beyond doubt that *L. canadensis*, *L. longicaudis* and *L. provocax* Thomas, 1908 are valid species.

Davis (op. cit.) considered *Lutra maculicollis* Lichtenstein, 1835 to constitute a separate genus, *Hydrictis* Pocock, 1921, and even a separate tribe, the Hydrictini. Even by Davis' limited set of characters, the reason for a separate status of this species is not clear. Davis mentioned the morphology of the baculum, the fact that the contact call is sometimes disyllabic and a slight difference in the affectional call as only differences with *Lutra*. Taking the enormous resemblance in overall morphology, skeletal morphology and ecology into account, there is no reason to exclude this species from the genus *Lutra*. Davis (1978) did include *Aonyx congica* Lönnberg, 1910 (including *A. microdon* Pohle, 1919 and *A. philippsi* Hinton, 1921) in *A. capensis*. He argued that the species do not overlap geographically and that the tooth size shows a cline from the periphery of the geographical range of *Aonyx* to the central part. In his figure, he mapped the length of M_1. Indeed, on the basis of M_1 length, it is difficult to distinguish the species. If one plots M_1 or P^4 length and width, however, both species are clearly separated (Figs. 5, 6). The tooth morphology also differs. The teeth of *A. capensis* are relatively broader, more robust and have more blunt cusps. M^1 is relatively larger and M_1 has a relatively broader talonid. The species are clearly distinct.

In the classification, proposed in this paper, *Siamogale thailandica* Ginsburg, Ingavat & Tassy, 1983 is included in the Lutrini. The species is known by its M_1 from the Miocene of Thailand. According to Ginsburg et al. (1983) it shows resemblances to *Mionictis*, but the tooth has a very elongated talonid. *Mionictis* has been variously referred to the Mustelinae, the Lutrinae and the Melinae respectively. Ginsburg (1968)

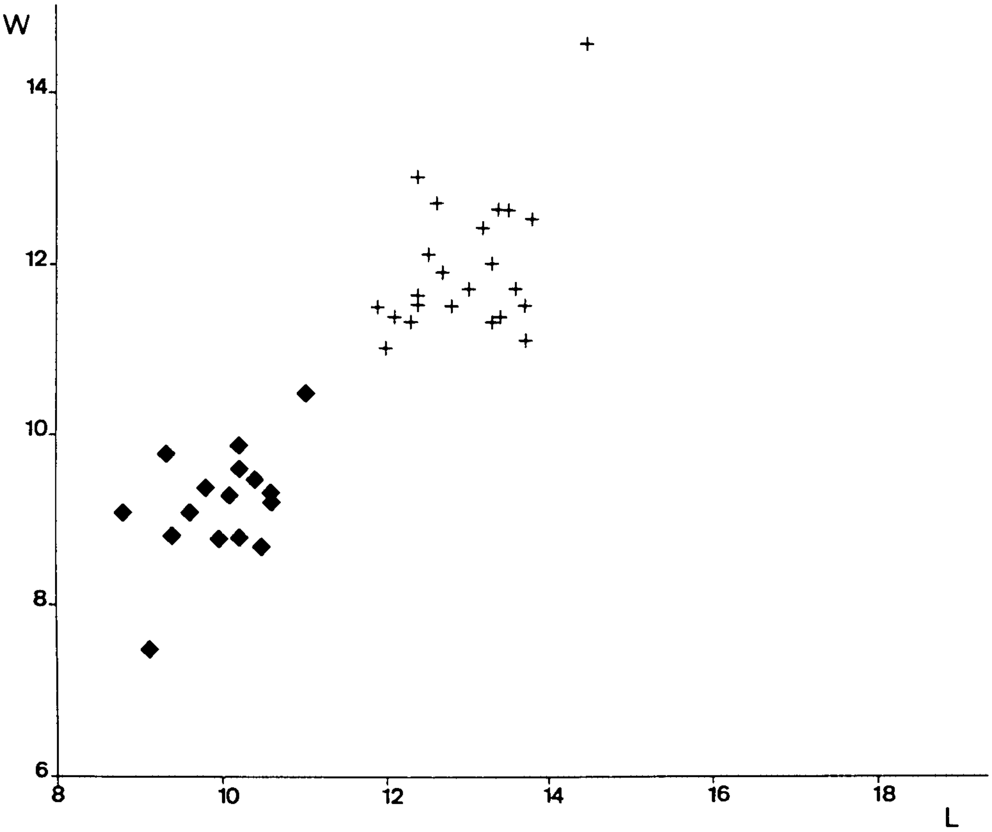


Fig. 5. P^4 length and width of *Aonyx capensis* (+) and *Aonyx congica* (triangle). Own measurements and measurements taken from Pohle (1919).

considered it to be a specialized, aquatic meline. Heizmann (1973) considered it to be lutrine, without giving his arguments. Ginsburg et al. (1983) referred *Mionictis* to the Lutrinae, arguing that it has too many characters in common with the Lutrinae and especially with *Paralutra* to separate it from this group taxonomically.

The classification of *Megalenhydris* Willemsen & Malatesta, 1987 as Aonyxini is tentative, as explained in the section on that genus.

Sokolov (1973) gave no formal diagnoses of his tribes. The diagnoses of Davis (1978) are only based on his five characters and of little use here. Therefore new diagnoses are given for the three tribes recognized in this paper.

Tribus Lutrini Gray, 1865

Type genus — *Lutra* Brisson, 1762.

Diagnosis — Lutrine with elongated body, claws on all fingers, long face. Skull rather

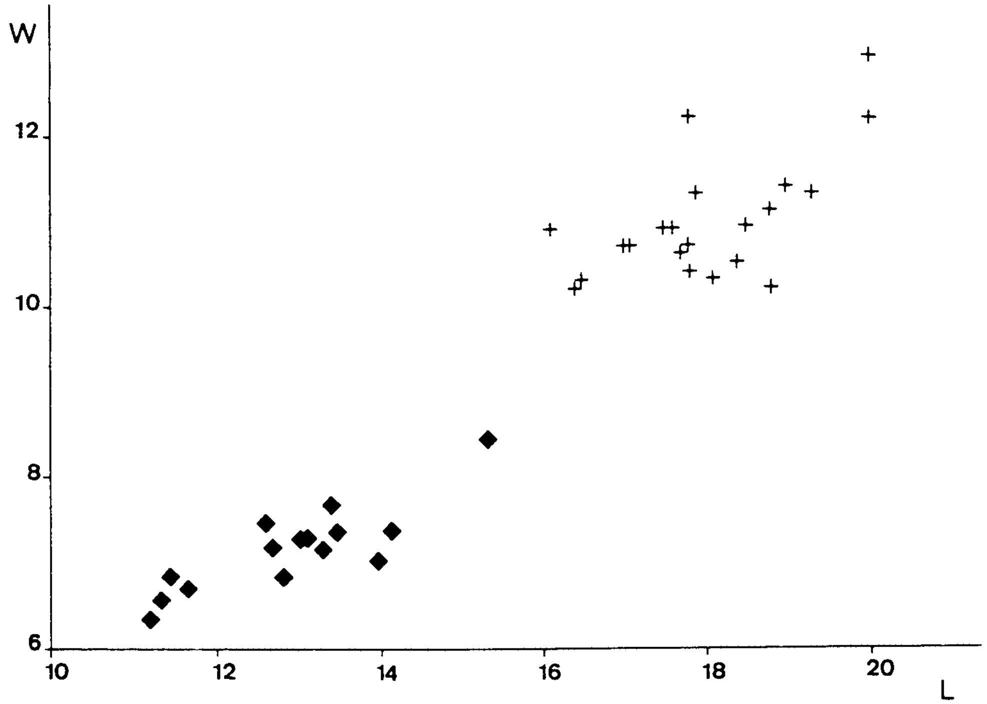


Fig. 6. M_1 length and width of *Aonyx capensis* (+) and *Aonyx congica* (triangle). Own measurements and measurements taken from Pohle (1919).

elongated, postorbital constriction narrow. Dentition with sharp cusps, sometimes rather robust but never as much as in the Aonyxini. P^4 with sharp shearing blade, protocone elongated, forming the anterolingual cingulum of the talon, no hypocone.Talonid of M_1 narrower to somewhat wider than trigonid, outer cingulum not very well developed; hypocone never cusp-like, present as an elongated ridge, forming the outer edge of the talonid; no entoconid.

Remarks — Species in this tribe have a dentition suited for fish-feeding or a dual-purpose dentition, suited for both fish- feeding and crushing shellfish. Only *Lutra provocax* is an exclusive shellfish-feeder and has a dentition, resembling the Aonyxini. This species is, however, clearly a case of convergence with the Aonyxini in this respect.

Genus *Lutra* Brisson, 1762

Selected synonyms — *Mustela* Linnaeus, 1758 (partim); *Lutris* Dumeril, 1806; *Lutrix* Rafinesque, 1815; *Lataxina* Gray, 1843; *Lataxia* Gervais, 1855; *Barangia* Gray, 1865; *Hydrogale* Gray, 1865; *Latax* Gray, 1865; *Lontra* Gray, 1865; *Nutria* Gray, 1865; *Lutronectes* Gray, 1867; *Hydrictis* Pocock, 1921; *Nesolutra* Bate, 1935.

Type species — *Mustela lutra* L., 1758.

Original diagnosis — Brisson (1762, p. 277-279).

Emended diagnosis — Lutrine with wide, flat head; fingers and toes extensively webbed and with well-developed claws. Tail tapering evenly, somewhat flattened. Skull long and depressed, facial part rather long, intertemporal region not swollen. Dental formula 3/3 1/1 4/3 1/2. Teeth with sharp cutting edges, never blunt and not very robust. P^4 with a sharp cutting blade at the labial side, formed by paracone and metacone, talon not covering the entire lingual side of the trigon. M_1 with sharp cuspids, the hypoconid forming a sharp edge, external cingulum of the talonid not strongly developed.

Stratigraphic occurrence — (?Vallesian) Ruscinian to Recent.

Geographic distribution — Eurasia, Africa, New World (since Middle Pleistocene).

Systematic remarks — Originally, all otters were included in the genus *Lutra*. Nowadays, the genus is considered to be more restricted, but too often the genus has been used as a waste-basket for fossil otters which were difficult to place. Especially in the older literature, many species have been described which do not belong in this genus. There is still no consensus about the genus. Many authors include *Lutrogale* Gray, 1865 in *Lutra* (e.g. Pohle, 1919; Harris, 1968; Corbett & Hill, 1986), others prefer not to do so (e.g. Pocock, 1921, 1941; van Zyll de Jong, 1972; Davis, 1978; van Bree, 1968a, b; Willemsen, 1980, 1986). Van Zyll de Jong (1972) treated the extant New World species as a separate genus, *Lontra* Gray, 1865; Davis (1968) maintained the genus *Hydrictis* Pocock, 1921 for *L. maculicollis*. I consider these two genera to be junior synonyms of *Lutra*, as most authors do.

In this paper, *Nesolutra* is also considered a junior synonym of *Lutra*. This genus was established for *N. euxena* from the Pleistocene of Malta. The remains of this species, however, are rather incomplete and most bones are of a juvenile individual, which makes the value of many characters difficult to evaluate. In 1977, Malatesta described a complete skeleton of a new species, which he attributed also to this genus (*Nesolutra ichnusae*) and a third species, *N. trinacriae*, was described by Burgio & Fiore (1988). All three species have many characters in common with *Lutra simplicidens*. In fact, only *N. ichnusae* shows characters justifying generic separation, but as is shown in the section on this species, *N. ichnusae* should be considered a separate genus, apart from the other two species and thus the genus *Sardolutra* is proposed for that species. The two remaining *Nesolutra* species differ in a number of characters from *Lutra lutra*, as was noted by several authors (Bate, 1935; Malatesta, 1977; Burgio & Fiore, 1988). They resemble, however, *L. simplicidens* in those characters, especially the structure of the limb bones and the lower dentition. Unfortunately, skull characters cannot be compared, since the skull of the latter is unknown. When we take the intrageneric variation within the genus *Lutra* into consideration, the skull nor the postcranial skeleton provide sufficient reason to consider the two species as belonging to a separate genus. The resemblances between *Nesolutra euxena* and *Lutra simplicidens* were already noted by Thenius (1949), who described the first material of the latter species as *Nesolutra* sp. Later, he included his material in *N. euxena* and transferred the species to the genus *Lutra* (see Thenius, 1965). In 1965, Thenius described *Lutra simplicidens* and put *N. euxena* back in its original genus. He stated that both species show differences in the postcranial bones, which is true, but the differences are small. Thenius correctly concluded that his new species was not identical with the Maltese *N. euxena*, but why he did not retain the latter in the genus *Lutra* is not clear.

In this paper, *Lutra sinerizi* de Villalta Comella, 1952 is not included in the genus *Lutra*. Viret (1954) showed that the specimen described by de Villalta Comella (1952) in fact is an *Enhydrictis*. Especially the structure of the M_1, showing a narrow talonid and a much reduced and posteriorly situated metaconid, is characteristic for that genus. Pennacchioni & Cassola (1986) did mix up *Lutra sinerizi* de Villalta Comella, 1952 with *Limnonyx sinerizi* Crusafont Pairò, 1950, mentioning *Limnonyx sinerizi* de Villalta Comella, 1952. They pointed out that Crusafont (1950) did establish the genus on a mandible from Can Ponsich, which indeed is true. Then, they wrote: 'La specie, rimasta inizialmente nomen nudum (Crusafont & Villalta, 1951), fu poi descritta da Villalta Comella (1952) su un reperto di Villaroya (Spagna).' (op. cit., p. 128). This is not true. De Villalta Comella (1952) did not describe *Limnonyx sinerizi*, as Pennacchioni & Cassola (1986) suggested, but *Lutra sinerizi*. Crusafont & de Villalta (1951) mentioned both *Lutra sinerizi*, referring to de Villalta Comella's 1952 paper, which was in press at that moment, and *Limnonyx sinerizi*, referring to Crusafont (1950), then also in press. It is clear that *Lutra sinerizi* de Villalta Comella, 1952 and *Limnonyx sinerizi* Crusafont Pairò, 1950 are two different species. Crusafont (1950) described a new genus and species, de Villalta Comella (1952) described a species in another lutrine genus having the same species name, which is rather confusing in this case but formally correct. Viret (1954) referred to *Lutra sinerizi* from Villaroya and not to *Limnonyx* when including it in *Enhydrictis*.

Lutra lutra (L., 1758)

Selected synonyms — *Mustela lutra* L., 1758; *Lutra vulgaris* Erxleben, 1777; *Lutra nudipes* Melchior, 1834; *Lutronectes whiteleyi* Gray, 1867; *Lutra roensis* Ogilby, 1834.

Holotype — Unknown.

Type locality — Sweden.

Stratigraphic occurrence — Holocene.

Geographic distribution — Eurasia.

Measurements — See Tables 1, 3, 12, 13, 15, 17.

Original diagnosis — Linnaeus (1758).

Emended diagnosis — *Lutra* with naked, W-shaped rhinarium. Moderate size (90-125 cm). Skull depressed with a rather long facial part. P^4 talon covers approximately 2/3 of the inner side of the trigon, leaving the metacone almost free, parastyle not completely free. M_1 with talonid slightly broader than trigonid; the paraconid is the largest cuspid, the metaconid much smaller than the other two trigonid cuspids; talonid concave, outer edge formed by hypoconid and hypoconulid, inner edge smooth.

Material — Fossil material is known from many Holocene localities in Europe. In this paper, some material from The Netherlands will be dealt with: a left mandible from Ellewoutsdijk (RGM 146 662), a right mandible from Kapel-Avezaath (RGM 147 002) and several specimens from the Maasvlakte near Rotterdam: 4 (parts of) mandibles (Ke RM 238, RM 2974, RM 3246, RM 4109), a left innominate fragment (Ke RM 233), an atlas (Ke RM 230), 2 left humeri (Ke RM 228, RM 229), a right ulna (Ke RM 231) and a right tibia (Ke RM 235).

Description — A left mandible (RGM 146 662) sucking-dredged from the Westerschelde near Ellewoutsdijk: all premolars and molars are present. The dental morphology is in all respects typical of extant *L. lutra*. The talonid and the trigonid of M_1 are equally wide. The same can be said about a right mandible with dentition, of which only the incisors and M_2 are lacking. This mandible (RGM 147 002) was dredged from the river Linge at Kapel-Avezaath. Though both specimens have a rather narrow talonid (usually the talonid is slightly broader than the trigonid) it is not as narrow as in *L. simplicidens*. The morphology of M_1 is not at all like in the latter species. M_1 does not have the large metaconid of *L. simplicidens* and the inner cingulum extends backward to the basis of the metaconid.

From the Maasvlakte, three left mandibles (RM 238, RM 2974 and RM 3246) and a right one (RM 4109) are preserved in the Kerkhoff collection. Four more mandibles or mandibular fragments with more or less complete dentition from the Hombroek collection have been described by Erdbrink (1988). RM 2974 is rather small (Table 1). Of the teeth, only the carnassial, which is not very worn, is preserved. In the carnassial, a hypoconulid is present. There are three mental foramina. In RM 238, a heavily damaged M_1 and a part of P_4 are present. The specimen is rather small and has three mental foramina. RM 3246 is also a rather small specimen with three mental foramina. No teeth are preserved. RM 4109 is larger than the other three specimens. It is a right mandibular ramus with P_3, P_4 and M_1. The anterior tip is missing. In the M_1, the talonid is wider than the trigonid. A small hypoconulid is present. Around the trigonid, the cingulum can be distinguished labially along the basis of the protoconid and the paraconid and medially at the paraconid.

A proximal part of a left humerus (RM 228) and a complete left humerus (RM 229) both show a smaller deltoid tuberosity than a recent specimen which was used for comparison (RMNH 12915). RM 229 is very small, though it belonged to an adult animal (Table 12). Also small are a right ulna (RM 231), a right tibia (RM 235), which has a smaller astragalar facet than RMNH 12915, and an incomplete left innominate

(RM 233) (Tables 13, 15 and 17). The innominate shows some differences with the Recent specimen: the attachment area for the m. gluteus maximus is somewhat less developed, the area for the m. iliopsoas is larger and the iliopsoas tubercle is less pronounced. An incomplete atlas (RM 230) is also known.
None of the differences, observed in the postcranial material, is such that the material could not be referred to *L. lutra*. The closest relative would be *L. simplicidens*. At least for the humeri it is clear that this possibility is out of the question, since *L. simplicidens* is characterised by a large deltoid tuberosity, which is not present in these specimens. Though all postcranial material from the Maasvlakte can be referred to *L. lutra* without a problem, it is striking that all specimens are rather small. They do, however, fall within the size-range of *L. lutra*.

Systematic remarks — One of the differences between *L. lutra* and *L. simplicidens* is the relative width of the talonid of M_1. In *L. simplicidens*, Wtal/Wtri is 0.96-0.97 (n = 4, see Table 2), in extant *L. lutra* it is 1.03-1.28 (mean 1.11, n = 8). In the Ellewoutsdijk specimen it is 1.00 and in the Kapel-Avezaath specimen it is 1.02 (Table 1). In the Maasvlakte specimen RM 2974 it is 1.05, which is within the range for extant *L. lutra*. The Ellewoutsdijk and Kapel-Avezaath specimens fall outside the range of both species. We must bear in mind, that the samples are very small. As pointed out above, the tooth morphology of both specimens resembles *L. lutra* rather than *L. simplicidens*. Their rather young age also makes a determination as *L. simplicidens* improbable. Four *L. lutra* specimens from Neolithic sites in The Netherlands (from Vlaardingen, IPP G20d/B7, I21c/B4 and F20b/B2 and from Leidschendam IPP L 387/8), have ratios of 1.00, 1.03, c. 1.12 and 1.05; a specimen from an archaeological site c. 200 BC at Weesp (IPP We 2/1) has 1.00. The samples are too small to allow a conclusion whether there is a difference in this ratio between subfossil and Recent populations. Degerbøl (1933) gave a review of the abundant Danish material. According to him there are no morphological differences between (sub)fossil and actual specimens.

Stratigraphic remarks — The specimens from Ellewoutsdijk and Kapel-Avezaath are difficult to date, as usual when dealing with dredged material. Neither of the two seems heavily fossilized and a Holocene age seems quite possible. The Kapel-Avezaath specimen (RGM 147 002) is registered in the museum catalogue as '2nd to 12th century', but it was not possible to find out what the basis for this statement was.
The Maasvlakte specimens described above are not heavily fossilized and can be referred to the Holocene assemblage (Kerkhoff, 1984; Vervoort-Kerkhoff & van Kolfschoten, 1988). Some specimens are black and not brown like the others, but they are rather light in weight and comparison with the other fossils from this site makes it quite clear that they cannot be referred to the oldest assemblage. The specimens described by Erdbrink (1988) also have to be referred to the Holocene assemblage. The Maasvlakte site is discussed in more detail in the section on *Cyrnaonyx antiqua*.
No Pleistocene material of this species is known from the Netherlands. Some material is dredged and cannot be dated (the two specimens described above and two other specimens described by Erdbrink, 1983). Most material is from archaeological sites and is of Neolithic age or younger (Clason, 1967, 1984).

Holocene material is also known from other European countries, often from archaeological sites. Material that can be dated as Pleistocene is not known. *L. lutra* is mentioned from Taubach (Eemian) sometimes (Pohlig, 1890; Soergel, 1926), but, as Hemmer (1977) pointed out, it is mentioned without any specific information and nothing is known about the supposed specimens. *L. lutra* was described by Kahlke (1958) from Weimar-Ehringsdorf (Saalian), but the specimen, a canine, turned out to be a badger (Daxner-Höck, 1975).

In the United Kingdom, *L. lutra* was described from East Runton by Newton (1891), as *L. vulgaris*, and mentioned by several later authors (e.g. Stuart, 1974). The East Runton specimen (BM 6089) must be referred to *L. simplicidens*, however, as I will show further on. Stuart (1974) mentioned *L. lutra* from Mundesley, but this is probably based on an error in Newton (1891), as I will point out in the section on *L. simplicidens*.

Only in a few cases there was no opportunity to check on claimed Pleistocene finds. Jánossy (1979) mentioned one *L. lutra* specimen from Pilisszánto 1, which he placed in a Pilisszánto substage, dated 31 000 to 18 000 BP. However, no information is available on the specimen or on the reliability of its determination. A second problem is the occurrence of *Lutra lutra* in Skjonghelleren Cave, Western Norway, mentioned in a faunal list in Larsen et al. (1987). The layer was dated c. 30 000 BP in the Ålesund Interstadial. Attempts to obtain more information did not yield results.

A problem is posed by the material from Hoxne, which at the moment cannot be determined specifically. This material will be discussed below as *Lutra* sp.

It can be concluded that *L. lutra* in Europe is only known with certainty from the Holocene. Claimed Pleistocene finds are either *L. simplicidens* or impossible to determine to species level because of incompleteness of the specimens, or, in two cases no information at all is available. Up to now, no indisputable proof of Pleistocene occurrence has come up.

Lutra simplicidens Thenius, 1965

Synonyms — *Lutra vulgaris*, in Newton (1887, 1891) (partim); *Lutra* sp., in Soergel (1926); *Nesolutra* sp., in Thenius (1948); *Lutra euxena* partim, in Thenius (1951, 1962); *Lutra* cf. *lutra*, in Kahlke (1962); *Lutra* sp., in Kahlke, 1962; *Lutra lutra* partim, in Stuart (1974); *Lutra* sp., in Stuart (1981, 1982).

Holotype — Left mandible with P_2, P_3 and M_1, stored in the Palaeontological Institute of the University of Vienna, coll. nr. Hdsh. VIII/36.

Type locality — Hundsheim, near Deutsch-Altenburg, Austria, bed VIII of the fissure filling.

Other localities — Voigtstedt, Süßenborn, Mosbach 2, East Runton, West Runton.

Stratigraphic occurrence — Middle Pleistocene (Cromerian s.l.) to Elsterian or Holsteinian.

Geographic range — Central and Western Europe.

Measurements — See Tables 2, 12-14, 16.

Original diagnosis — Thenius (1965, p. 552).

Emended diagnosis — *Lutra* with P_2 and P_3 broader than in *L. lutra*. M_1 with short and narrow talonid in comparison with *L. lutra*, no hypoconulid, hypoconid is a ridge forming the outer border of the rather flat talonid, inner cingulum only present at the anterior basis of the paraconid. Radius more curved than in *L. lutra*, with smaller caput and more robust distal part. Ulna more compressed laterally and with more curved olecranon than in *L. lutra*. Femur short and robust with strongly developed trochanters.

Material — Mosbach: Left humerus (NHM 1956/296), right mandible with M_1 (SMF PA/F 8718); Hundsheim: holotype mandible, right radius, right femur, left tibia and right calcaneus (PIV, see Thenius, 1948, 1951, 1965); Voigtstedt: right upper C (IQW Voi. 2097), D^3(IQW Voi. 2998), right radius (IQW Voi. 2306), left ulna (IQW Voi. 1216 and 2850), left metacarpal II (IQW Voi. 1953), right calcaneum (IQW Voi. 2341), right astragalus (IQW Voi. 2447), phalange II (IQW Voi. 2738)(for all IQW specimens see Thenius, 1965), right M_1 (KMBF I-711 K, Heinrich et al., 1986); Süßenborn: mandibular ramus (Soergel, 1926); East Runton: left mandible with M_1 (BM 6089); West Runton: right mandibular fragment with M_1 (CM CR4.984), humerus (BM 17895), caudal vertebra (BM 17893); Easton Bavents: humerus. Possibly also 3 specimens from Uppony (Hungary).

Description — The holotype mandible (PIV Hdsh. VIII/36) was described by Thenius (1965). According to him, P_2 and P_3 are broader than in *L. lutra* and M_1 has a less differentiated, flat and relatively shorter talonid, no hypoconulid is present, the metaconid is somewhat larger than in *L. lutra* and an external cingulum is present at the base of the paraconid and the talonid. In his diagnosis of the species, Thenius stated that the inner cingulum is only present at the anterior base of the protoconid. This must be an error, since the protoconid is situated at the outer part of the trigonid and not at the inner part. Probably, Thenius meant the paraconid: in his figure indeed the inner cingulum can be seen at the anterior part of the paraconid. Thenius (1965) seems to suggest that the small cuspid at the posterior base of the protoconid is not present. He stated (op. cit., p. 551): 'Eine Differenzierung des Außenrandes des Talonides ist nicht vorhanden. *Lutra lutra* unterscheidet sich durch den in Zwischenhügel (am basalen Hinterabhang des Protoconids), Hypoconid und Hypoconulid differenzierten äußeren Talonidrand...' (Thenius, 1965, p. 551). Not only is this cuspule present in all material which can be referred to this species, it can also be seen in Thenius (1965, pl. 2, fig. 4), where it appears like a backward protruding part of the base of the protoconid.

The M_1 from Voigtstedt (KMBF I-711 K) is referred to this species. It is illustrated in Heinrich & Fejfar (1988). From their drawings it is clear that in this case the cuspule posterior to the protoconid is present. It is, however, more integrated in the protoconid than in *L. lutra*. Heinrich and Fejfar did not describe the tooth in detail, but in their figures some characters can be seen. The tooth is two-rooted, the metaconid seems to be a little bit larger than in *L. lutra*, the trigonid is broader than the talonid and no hypoconulid is present.

From Mosbach 2, part of a right mandible with M_1 (SMF PA/F 8718) is known (Pl. 1). Part of the ramus is preserved, showing the alveoles of P_2, P_3, P_4 and M_2. The ramus is lower than the length of M_1. Two foramina mentalia can be seen, under the anterior roots of P_3 and P_4 respectively. M_1 has a trigonid which is broader than the talonid. The paraconid is the largest cuspid. The metaconid is somewhat larger than in *L. lutra*. The outer edge of the talonid is formed by the small cusp at the posterior basis of the protoconid, which is smaller than in *L. lutra*, and the hypoconid. The two are separated by a transversal groove, as is usual in *Lutra*. Posterior to the hypoconid the talonid edge is somewhat swollen and this probably represents the hypoconulid. It is not developed as a real separate cuspule as in *L. lutra*. The inner edge of the talonid is not differentiated. The talonid has an outer cingulum. The trigonid has a cingulum around the paraconid, at the lingual side extending only a little bit backward, not covering the entire lingual side of the paraconid. At the labial side it extends to the anterior base of the protoconid. Even though a hypoconulid-like structure can be recognized, it is clear that this specimen must be referred to *L. simplicidens*. All other characters of the species (large metaconid, narrow talonid, restricted inner cingulum) can be recognized and the hypoconulid is not developed as it usually is in *L. lutra*.

From East Runton (East Anglia, UK) a left mandible with M_1 (BM 6089; Savin coll. 532) is known (Pl. 1; Fig. 7). The Museum catalogue states that it was found in sandy loam in the 'Forest Bed, 25 yds from cliff opp. gangway'. The specimen was mentioned and figured by Newton (1887, 1891). Of the mandible, only part of the ramus is preserved. The alveoles of the premolars and of M_2 can be seen. The ramus is lower than the length of M_1. Of the M_1, the paraconid is damaged and the posterior part of the talonid is lacking. The hypoconid is also damaged. It can be seen clearly, however, that the trigonid is broader than the talonid. It can also be estimated, that the talonid was shorter than the trigonid. Probably, no hypoconulid was present. The extra cuspule between protoconid and hypoconid is present. The talonid is flat rather than concave. An inner cingulum is present only at the anterior part of the paraconid. On the basis of the narrow and flat talonid, the restricted inner cingulum and the absence of a hypoconulid the specimen has to be referred to this species.

Stuart (1974) mentioned a *L. lutra* from Mundesley. Stuart (1982) did, however, not mention an otter in the Mundesley fauna. In his 1974 paper he may have based himself on Newton (1891). In the caption to pl. 1, fig. 16, which clearly represents an otter jaw, Newton stated: '*Lutra vulgaris* Erxleben (...) Forest Bed, Mundesley' In the text, however, Newton did not mention an otter from Mundesley at all. He only mentioned a lower jaw which '... has been found by Mr A. Savin, of Cromer, in the Forest-Bed at East Runton...' (Newton, 1891, p. 12). Newton further stated that this specimen is shown on his pl. 1, fig. 10, which, however, represents, as the caption correctly says, a hyaena. The only otter shown on pl. 1 is fig. 16. As can clearly be seen from the drawing, this represents BM 6089. The museum catalogue gives indeed East

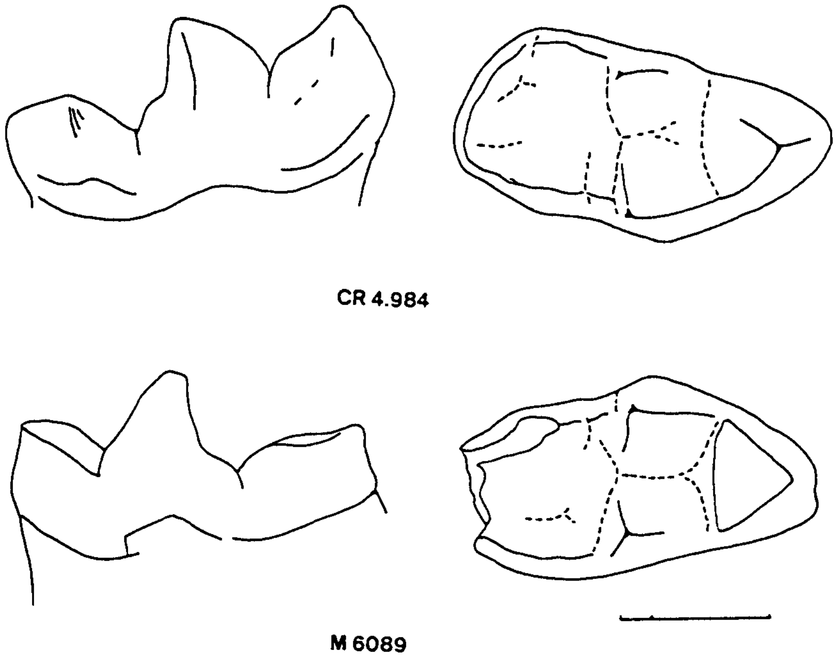


Fig. 7. *Lutra simplicidens* M_1, buccal (left) and occlusal (right) view. CM CR 4.984, West Runton, and BM 6089, East Runton; scale = 5 mm.

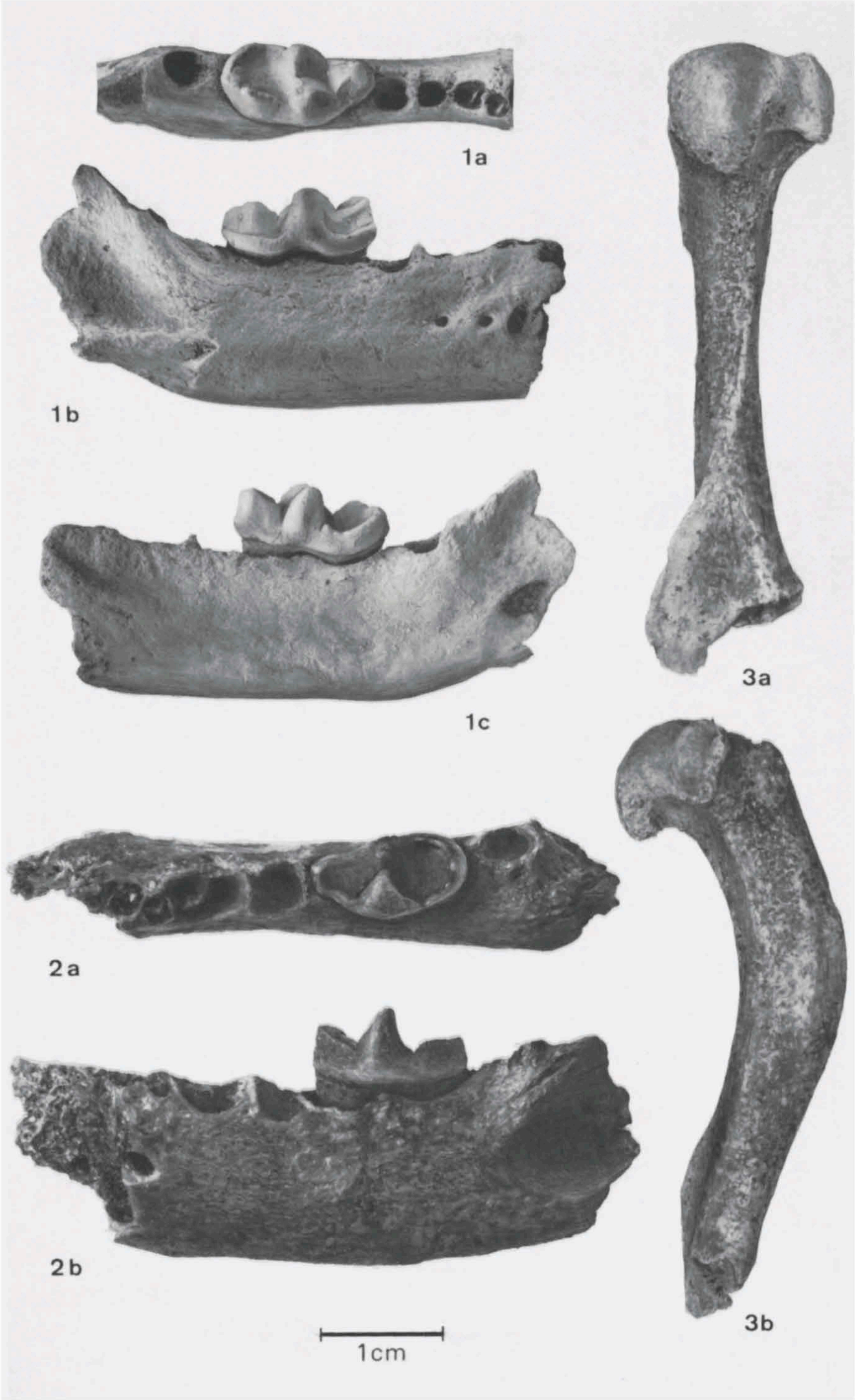
Runton and not Mundesley as the locality where this specimen has been found. It must be concluded, that no otter from Mundesley was known to Newton and that all later reports, going back on Newton, are incorrect.

From the West Runton Freshwater Bed (WRFB, East Anglia) there is a right mandibular fragment with M_1 and the alveole of M_2 (CM CR4.984; Pl. 1; Fig. 7). It was found 25 m west from Goss' Gap, West Runton, 10 cm above the basis of a red-brown shelly breccia within the WRFB (M. Warren, pers. comm.; see Stuart, 1975). The carnassial shows no wear facets. The trigonid is broader than the talonid. Posterior from the protoconid there is a small cuspule, separated from the hypoconid by a groove. There is no hypoconulid. The talonid is rather flat and its inner edge is smooth. The outer cingulum of the tooth is visible along the paraconid and the talonid, where it is less developed than in *L. lutra*. On the lingual side, the cingulum extends backwards along the paraconid, though it is not as well developed as in *L. lutra*.

Plate 1

Lutra simplicidens Thenius, 1965

1. Right mandible from Mosbach, SMF PA/F 8718; a: occlusal view; b: buccal view; c: lingual view.
2. Left mandible from West Runton, BM 6089; a: occlusal view; b: buccal view.
3. Part of left humerus from Mosbach, NHM 1956/296; a: posterior view; b: medial view.


1a
1b
1c
2a
2b
3a
3b
1cm

From Süßenborn a part of a mandibular ramus with the alveoles of P_4, M_1 and M_2 of *Lutra* is known. It was described by Soergel (1926). Kurtén (1969) described it as *L.* cf. *simplicidens*. *L. simplicidens* is the only *Lutra* species known from the Middle Pleistocene of Europe, but the fossil does not allow specific determination due to its incompleteness.

The humerus is known by a specimen from the West Runton Freshwater Bed and a specimen from Mosbach (Pl. 1). The WRFB specimen is a left one of which the distal part is lacking (BM 17895; Savin coll. 1115). It differs clearly from *L. lutra* and since *L. simplicidens* is known from the same locality by a lower jaw, it seems reasonable to refer the humerus to this species. The only other Pleistocene otter known from Western and Central Europe is *Cyrnaonyx antiqua*, but the humerus of this species is known from Tornewton Cave and differs very much from this specimen. The part which is preserved is 45.1 mm long. The humerus is more curved than in *L. lutra*, the deltoid tuberosity is larger and the deltoid ridge shows a strong lateral curve, causing a lateral expansion of the deltoid tuberosity. In both characters the specimen resembles *Sardolutra ichnusae*. The Mosbach humerus, a left one with the distal part lacking (NHM 1956/296) is referred to this species for exactly the same reasons as the WRFB specimen. The humerus is also more curved dorsoventrally than in *L. lutra*, just like the WRFB specimen. The trochanter minor is somewhat more prominent than in *L. lutra*. The ulna is known from a specimen from Voigtstedt, described by Thenius (1965). As main difference with *L. lutra* he mentioned the more curved olecranon and the laterally more compressed diaphysis.

The radius, known from Hundsheim and Voigtstedt, was described by Thenius (1948, 1965). According to him, it differs from *L. lutra* in having a more strongly bent diaphysis, the less pronounced capitulum, the in dorsal view more slender diaphysis and the strongly developed bony ridge for muscle attachment. The curved diaphysis, the robust distal part and the bone ridge are also present in *Sardolutra*.

The femur was described from Hundsheim by Thenius (1948). It is short and stout in comparison with *L. lutra*, with robust trochanters and an in dorsoventral direction rather flattened diaphysis. The trochanter minor is situated more medially than in the extant species and the trochanter major is broader. The femur resembles that of *Sardolutra ichnusae*, which is also short and stout. The trochanter major does, however, not rise as high in that species.

The calcaneum and the astragalus are known from Voigtstedt and described by Thenius (1965). According to him, the calcaneum is rather large and can be distinguished from *L. lutra* by the more developed peroneal tubercle, which is grooved, and the cuboid facet having a median expansion.

A caudal vertebra from the West Runton Freshwater Bed (BM 17893; Savin coll. 1056) probably also belongs to this species, as it is clearly lutrine and no other otters are known from these beds. It is 20.0 mm long.

Jánossy (1986, p. 99) mentioned three specimens of *Lutra* sp. (aff. *simplicidens* Thenius) from Rock Shelter 1, layer 8, of Uppony (Hungary). According to the author, it is of older Middle Pleistocene age. Unfortunately, the specimens are only mentioned in a faunal list and no details were given.

Systematic remarks — *L. simplicidens* clearly differs from *L. lutra* in its postcranial skeleton, as was already pointed out by Thenius (1965). The mandible and the lower dentition show only minor differences with *L. lutra*. In the M_1, a number of consistent differences can be seen:

Lutra simplicidens	*Lutra lutra*
talonid less broad than trigonid	talonid broader than trigonid or equally broad
talonid flat, sloping down from the hypoconid to the inner edge	talonid concave
hypoconulid absent	hypoconulid present
metaconid larger	metaconid smaller
inner cingulum less developed; often extending paraconid	inner cingulum more developed, extending backward to the basis of the metaconid

The ratio of Wtal/Wtri for M_1 is 0.97 for the East Runton specimen, 0.96 for the Cromer specimen, 0.96 for the Mosbach specimen and 0.97 for the Voigtstedt specimen. In eight Recent *L. lutra* specimens it varied from 1.03 to 1.28 (mean 1.11), while in subfossil specimens I observed values as low as 1.00.

All *Lutra* material from the Pleistocene of the European mainland which was complete enough to allow a specific determination, appeared to be *L. simplicidens*. Pasa (1947) described a mandible from the Pleistocene of Soave (Verona) as *L. lutra*. He mentioned that the M_1 talonid is narrower than the trigonid. It is therefore possible that the specimen is a *L. simplicidens* too. On the other hand Pasa stated that the tooth is very slender and elongated, which would point in the direction of a non-lutrine mustelid. With its length of 12 and width of 5.3 mm the tooth is smaller than any *Lutra* known to me. Unfortunately, Pasa (op. cit.) did not illustrate this specimen, nor did he give a detailed description.

L. simplicidens shows many resemblances to *L. euxena*, *L. trinacriae* and *Sardolutra ichnusae*, though there are many differences also. This is pointed out more in detail in the remarks to those species.

Stratigraphic remarks — The Central European localities are of Middle Pleistocene age. Voigtstedt and Süßenborn can be placed in the Late Biharian, for which *Mimomys savini*, found in both faunas, is a typical species. These localities can be correlated with the Cromerian Complex of the Dutch sequence. In the Mosbach-2 fauna and in Hundsheim, *Arvicola cantiana* is found and these faunas must therefore be younger. The transition from *Mimomys savini* to *Arvicola cantiana* is placed at the end of the Cromerian in the British stratigraphy by Stuart & West (1976) and by Stuart (1982). This would place Mosbach and Hundsheim in the Elsterian of the Dutch sequence, since the Cromerian can probably be correlated with Interglacial IV of the Dutch Cromerian Complex (West, 1980). Fejfar & Heinrich (1983), however, place the transition to *A. cantiana* at the end of the Elster Complex and they consider these faunas to be correlated to the Holstein Complex.

Stuart (1981) showed that the Voigtstedt fauna can be correlated with the Cromerian fauna from West Runton. The otter remains from West Runton were found in the Upper Freshwater Bed, which is type Cromerian (see Stuart, 1975).

The fauna from East Runton is older than that of West Runton. It is certainly not Cromerian in the restricted sense as used in the British stratigraphy (Sutcliffe & Kowalski, 1976). The deposits are partly pre-Pastonian, partly maybe Pastonian (Mayhew & Stuart, 1986). Having in mind the age of the other known *L. simplicidens* specimens, Pastonian is the most plausible age for the East Runton otter specimen. Zagwijn (1975) correlated the Pastonian with Interglacial III of the Cromerian Complex. Zagwijn (1979) stated that a detailed correlation is not possible at the moment but that the Pastonian-Beestonian-Cromerian is equivalent to the upper part of the Cromerian Complex.

Summarizing, it can be concluded that *L. simplicidens* is known from the Middle Pleistocene, the oldest specimen possibly being Pastonian (Cromerian Complex), the youngest Elsterian or Holsteinian.

Lutra euxena (Bate, 1935)

Synonyms — *Nesolutra euxena* Bate, 1935; *Lutra euxena*, in Thenius, 1951, 1962 (partim).

Holotype — Subadult right humerus, stored in the British Museum (Natural History), Dep. of Palaeontology, London, M 15443.

Type locality — Tal Gnien, near Imkabiba, southwest of Valetta, Malta.

Other localities — None.

Stratigraphic occurrence — Pleistocene.

Geographic distribution — Malta.

Measurements — See Tables 6, 11-13.

Original diagnosis — 'Humerus without sharp keel on anterior aspects of shaft, but with external supra-condyloid ridge much produced and extending for a considerable distance up the shaft, which is slender and proximally bowed forwards. Radius with muscle ridges very strongly marked; metacarpals flattened and expanded, without ridge on palmar aspect. Tibia with shaft very slender compared with proximal end and cnemial crest sharply defined.' (Bate, 1935, p. 248).

Material — All material is from the type locality and stored in the BM. Right humerus (holotype, M 15443), distal part of right humerus (M 15444), right radius (M 15445), left ulna fragment (M 15446), right tibia fragment (M 15448), second right metacarpal (M 15447), second right metatarsal (M 15449), right upper canine (M 15450), right I^3 (M 15451) (Fig. 8).

Description — Bate (1935) gave a detailed description of the material. Here, the main characters will be pointed out and some additional observations will be made.

The holotype humerus (BM M 15443) is of a subadult animal. The proximal epiphysis is lacking. The suture of the distal epiphysis is visible. The shaft is curved at a more proximal point than in *L. lutra*. The anterior border of the shaft is not keeled. The distal part of the humerus is much wider than in *Lutra* and the ectepicondylar ridge runs much more proximally on the shaft. The distal humerus fragment (BM M 15444) is also very wide (see Table 12). In some respects, the humerus resembles that of *Potamotherium valletoni*: in this species there is also a wide ectepicondyle and a large ectepicondylar ridge, but the humerus is more curved than in *Lutra* (Savage, 1957), while in *L. euxena* it is less curved.

The right radius (BM M 15445) is also of a young animal, the distal epiphysis is lacking. The bony ridge on the shaft is strongly developed. The bicepital pit is less developed than in *L. lutra*. Of the ulna, only a proximal fragment is present (BM M 15446). The same is true for the tibia (BM M 15448).

The second metacarpal (BM M 15447) is somewhat shorter than in *Lutra lutra* and rather broad. The second metatarsal (BM M 15449) on the contrary is very slender.

The canine (BM M 15450) and the incisor (BM M 15451) resemble those of *Lutra*.

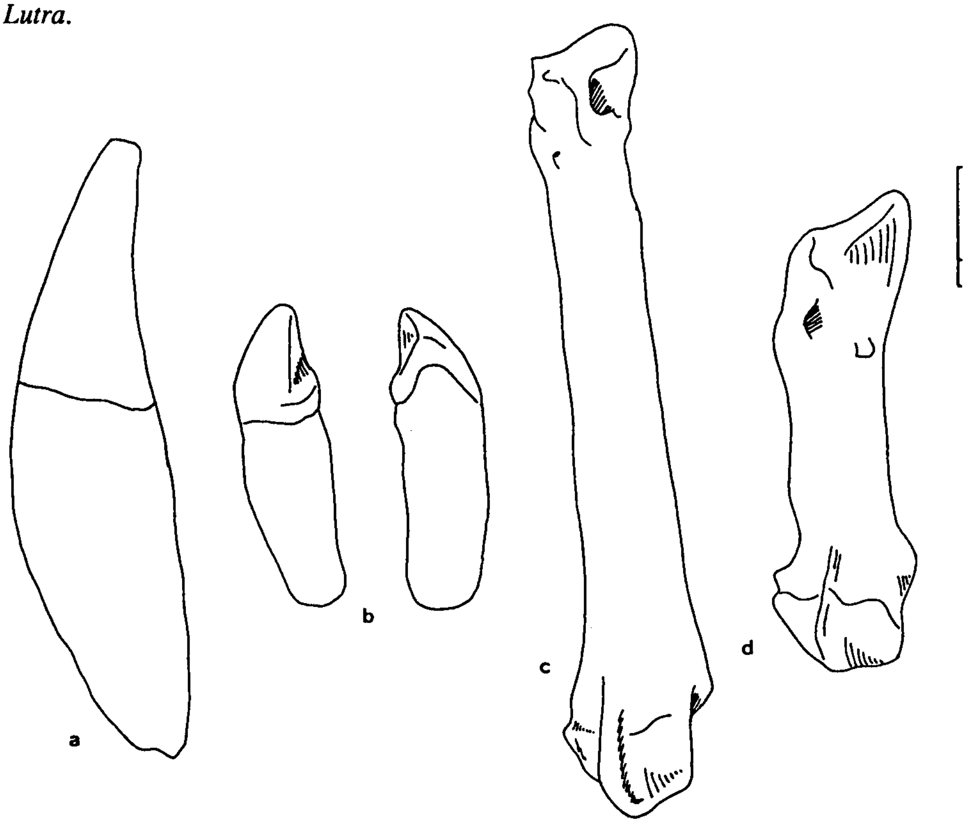


Fig. 8. *Lutra euxena*, Tal Gnien, Malta; a: right upper canine (M 15450); b: right I^3 (M 15451); c: second right metatarsal (M 15449); d: second right metacarpal (M 15447). All specimens are from the BM collection; scale = 5 mm.

Systematic remarks — The radius of *L. euxena* shows similarities to a lutrine radius from Hundsheim, as was pointed out by Thenius (1948). Thenius described that radius and a femur from the same site as *Nesolutra* sp. Later, he included the Hundsheim otter in *L. euxena* and transferred the species to *Lutra* (Thenius, 1951). After having studied more material of the same species than the remains from Hundsheim and after having discovered a mandible in Hundsheim, Thenius (1965) came to the conclusion that he had been wrong after all, and he created a new species, *Lutra simplicidens*, for his material from Central Europe, since the lower dentition clearly is *Lutra* and there are differences with *L. euxena* in the postcranial remains. Thenius (1965) pointed out that the differences between his new species and *L. euxena* are such, that a specific identity is impossible. As pointed out above, he also reassigned *L. euxena* to its original genus.

Stratigraphic remarks — Bate (1935) stated that the material from Tal Gnien probably is Early Pleistocene in age. Malatesta (1977) supposed, that the material probably is younger. According to Bate (1935), three other mammal species were found at Tal Gnien: *Crocidura* cf. *russula*, *Elephas mnaidriensis* and *Leithia melitensis*. Further, *Palaeocygnus falconeri*, a giant tortoise and a frog or toad were mentioned by her. Bate (op. cit.) noted, that precise dating was impossible, but she assumed an Early Pleistocene or even Pliocene age. This was, however, only based on the fact, that the fauna consists of extinct species only.

The Tal Gnien fauna and thus the otter, may very well be younger. The fact that the species probably evolved from *L. simplicidens*, as will be pointed out later, would suggest a Middle Pleistocene or younger age. Indeed, a Late Pleistocene age would be in accordance with the assumption that *E. mnaidriensis* faunas on Sicily are of Late Pleistocene age and younger rather than older than *E. falconeri* faunas (Burgio et al., in press; see also stratigraphical remarks under the next species). Burgio & Fiore (1988) pointed out, however, that no elements, allowing a confirmation of the specific determination of *E. mnaidriensis* from Tal Gnien, are known to exist now. Apart from *E. mnaidriensis*, the fauna from Tal Gnien resembles the Spinagallo 'Stage' of Kotsakis (1978). Recently, also a giant tortoise has been found in association with *E. falconeri* on Sicily (Burgio & Fiore, 1988), which makes the resemblance between the Spinagallo 'stage' and the Tal Gnien fauna even greater. Thus, *L. euxena* from Malta and *L. trinacriae* from Sicily may well be contemporaneous, according to the scheme of Burgio et al. (in press) Middle Pleistocene.

Lutra trinacriae (Burgio & Fiore, 1988)

Synonyms — *Nesolutra* sp., in Esu et al., 1986; Pennacchioni & Cassola, 1986; *Nesolutra trinacriae* Burgio & Fiore, 1988.

Holotype — Almost complete skeleton, preserved in the Geological Museum G.G. Gemmelaro of the University of Palermo, PS 1 to PS 25.

Type locality — Poggio Schinaldo Cave, Palermo (Sicily).

Other localities — None.

Stratigraphic occurrence — Middle or Late Pleistocene.

Geographic distribution — Sicily.

Measurements — See Tables 5, 6, 11, 13, 15.

Original diagnosis — 'Lutrina di taglia intermedia fra *Lutra lutra* e *Nesolutra ichnusae*. Il cranio si presenta tozzo e largo con profilo dorsale piatto e ventrale parallelo; il muso è troncato con grandi fosse nasali; i processi post-orbitali risultano corti e gli zigomi robusti e alti; la constrizione post-orbitale è marcata; la cassa cerebrale è rigonfia con foramen magnum molto largo; le bulle uditive sono di forma triangolare e allungata. Formula dentaria: 3/3 1/1 4/3 1/2.

La rimanente parte dello scheletro post-craniale presenta delle caratteristiche peculiari che denunciano una maggiore specializzazione rispetto a *L. lutra*. In particolare l'omero si presenta tozzo e marcatamente ricurvo dorso ventralmente con una cresta epicondiloidea molto espansa.

Il radio è caratterizzato da diafisi chiaramente curvata, epifisi distale espansa e forti inserzioni muscolari. La tibia presenta diafisi allungata, cresta tibiale incurvata lateralmente molto prominente e tagliente e fosse per l'inserzioni muscolari molto sviluppate.' (Burgio & Fiore, 1988).

(Lutrine, of intermediate size between *Lutra lutra* and *Nesolutra ichnusae*. The skull is squat and broad with a flat dorsal surface, parallel to the ventral plane; the muzzle is truncated with large nasal fossae; the postorbital processes are short and the zygomatic arcs strong and high; the postorbital constriction is marked; the braincase swollen with a large foramen magnum; the tympanic bullae have an elongated and triangular shape. Dental formula: 3/3 1/1 4/3 1/2. The remaining part of the postorbital skeleton shows some peculiar characteristics which indicate a greater specialization as compared with *L. lutra*. In particular, the humerus is clearly squat and markedly curved dorsoventrally with a large epicondylar crest. The radius is characterized by a clearly curved diaphysis, a large distal epiphysis and strong muscular insertions. The tibia has an elongated diaphysis, a very prominent and blade-shaped, laterally curved tibial crest and well developed fossae for the muscular insertions.)

Material — Only the holotype is known.

Description — The holotype was described and illustrated by Burgio & Fiore (1988). Professor Burgio and Dr. M. Fiore from Palermo and Professor A. Malatesta from Rome kindly sent me information and photographs of the specimen.

The skull is rather flat, according to Burgio & Fiore (1988). It is somewhat less arched than in *Sardolutra ichnusae*. The muzzle is somewhat broader. The skull is more elongated than in *S. ichnusae*. The intertemporal region is relatively longer than in *S. ichnusae*. The postorbital constriction is much wider than in *L. lutra*. The jugal width is greater than in the Sardinian species. The mandible resembles *S. ichnusae* very much.

The most striking difference with *S. ichnusae* in the upper dentition is the presence of P^1 on the left side. It is relatively smaller than in *L. lutra*. On the right side the tooth is absent in the holotype, it is not clear whether it has fallen out during the animal's life or whether it never grew at all (Burgio & Fiore, 1988). P^2 and P^3 are two-rooted and monocuspid. P^4 resembles *L. lutra* and *S. ichnusae*. The talonid has about the same relative size. The size difference between the paraconid and the metaconid is less marked than in *S. ichnusae* (Burgio & Fiore, op. cit.). The M^1 touches the metacone of the carnassial and bears a clearly visible hypocone (Burgio & Fiore, 1988). The lower premolars are two-rooted. P_4 has an accessory cuspid. The lower carnassial has a wider talonid than in *L. lutra*, according to Burgio & Fiore (1988). According to my measurements, almost the opposite is true. The talonid and the trigonid are equally wide (6.3 mm). In *L. lutra*, the talonid is generally wider than the trigonid. As stated above, I found a Wtal/Wtri ratio varying from 1.00 to 1.28 for *L. lutra*. On the talonid, no clear hypoconulid can be distinguished. In this respect, the species resembles *L. simplicidens*.

The sacrum is more elongated and narrower than in *S. ichnusae* and the spines of the second and third sacral vertebra are not fused as in the Sardinian species (Burgio & Fiore, op. cit.).

The humerus has its pectoral ridge curved medially and the deltoid ridge curved laterally, as is the case in *L. simplicidens* and also in *S. ichnusae*. As in these two species, the shaft is more curved dorsoventrally than in *L. lutra*. The ectepicondylar ridge is much expanded. It is more expanded than in *L. euxena* and it does not run as high on the shaft as in that species. As far as can be judged from the photographs in Burgio & Fiore (1988), the ectepicondylar ridge is even more expanded laterally than in the Sardinian species. The distal epiphysis is wider than in *L. euxena* and in *S. ichnusae* (Burgio & Fiore, op. cit.). Unfortunately, the distal part of the humerus of *L. simplicidens* is unknown. The shaft of the humerus is anteriorly only slightly keeled, much less than in *L. lutra*.

Burgio & Fiore (1988) noted, that the radius is more robust than in *L. lutra*, but not as robust as in *S. ichnusae*. They further noted that the radius is more curved in lateral view than in *L. lutra*, the distal epiphysis is more expanded, the bicepital pit is more marked, the pronator teres tubercle is more prominent and the posterior side of the shaft bears a well marked crest. In all these characters, the radius resembles that of *L. simplicidens*, that of *L. euxena* and that of *S. ichnusae*. Burgio & Fiore (1988) noted some differences with *L. euxena*, but they correctly point out that the latter is a juvenile specimen and this may explain some of the differences, such as the less-developed bicepital pit.

The ilium is more expanded and the acetabulum of the pelvis larger than in *S. ichnusae*, according to Burgio & Fiore (1988). The relative length of ilium and ischiopubis resembles the Sardinian species. They noted that the femur is straight and longer than in *S. ichnusae*, but shorter and stouter than in *L. lutra*. They also noted that the trochanter major is somewhat less prominent, and the notch medially to the trochanter less deep than in *S. ichnusae*, though both are more developed than in *L. lutra*. Burgio & Fiore (op. cit.) concluded from the preserved part that the tibia is longer than in both *S. ichnusae* and *L. lutra*. They noted the same for the fibula, which is not fused to the tibia proximally. The metatarsals are longer but less robust than in the Sardinian species (Burgio & Fiore, 1988).

Systematic remarks — Originally, the species was described as a *Nesolutra*. This genus is considered a junior synonym of *Lutra* in this paper, as is explained in the systematic remarks to the genus *Lutra*. Because of the resemblance to *L. simplicidens* and the relatively small differences with other *Lutra* species in general, the species is included in this genus.

Esu et al. (1986) already noted, that the Sicilian otter is related to the Sardinian *S. ichnusae*. They noted a great resemblance in the structure of the limb bones, but quite some differences in cranial morphology. In the section on *Sardolutra ichnusae*, it is explained that the two species cannot be congeneric. Also the resemblance to *L. euxena* is large, but there are still some differences, excluding specific identity, especially in the structure of the humerus and the radius: the humerus has a larger deltoid tuberosity, a wider distal epiphysis, and a more expanded ectepicondylar ridge, running less high on the shaft, and the radius has a more developed bicepital pit and is curved at a more proximal point.

Stratigraphic remarks — According to Esu et al. (1986), five other mammal species were found in the Poggio Schinaldo cave: *Crocidura esui*, *Elephas falconeri*, *Praemegaceros* cf. *carburangelensis*, *Leithia melitensis*, and *L. cartei*, apart from birds, reptiles, fishes and molluscs. The otter fossil was found in a layer with only *Leithia melitensis* (Burgio, pers. comm.) Esu et al. (op. cit.) referred the fauna to the Spinagallo Stage, which is the second youngest of the five mammal stages (in fact, those stages are faunal units and not stages), distinguished in the Quaternary of Sicily by Kotsakis (1978). In Esu et al. (1986) the first two of those faunal stages were considered to be identical. The Spinagallo Stage was correlated with middle Pontinian deposits by Kotsakis (1978), which means a Würmian (Weichselian) age. However, the mammal biostratigraphy, proposed by Kotsakis (1978) needed reconsideration, as was suggested by Esu et al. (1986). In 1988, Burgio et al. presented a revised biostratigraphy of Sicily. Based among other things on absolute datings by amino-acid racemization, they concluded that faunas with *Elephas falconeri* are older than those with *Elephas mnaidriensis* (Burgio et al., in press; Kotsakis, pers. comm.). The *E. falconeri* fauna, as found in Spinagallo, is now considered to be of Middle Pleistocene age, while the fauna with *E. mnaidriensis*, which is contemporaneous with *Hippopotamus pentlandi*, is of Late Pleistocene age. These new data suggest a Middle Pleistocene age for *L. trinacriae*.

Lutra bravardi Pomel, 1843

Synonyms — ? *Lutra clermontensis* de Blainville; *Aonyx bravardi*, in Pohle, 1919 and many later authors.

Holotype — Right maxilla with I^3, C, P^1, P^2, P^3, P^4 and M^1, figured by Pomel (1843) and, reversed, by Gervais (1859). It is unknown where the holotype is now. Apparently, already Pohle (1919) was unable to trace the holotype.

Type locality — Perrier-Etouaires.

Other localities — A possible record from Kislång.

Stratigraphic occurrence — Late Ruscinian, MN zone 16A.

Geographic range — Perrier-Etouaires (France).

Measurements — See Table 3.

Original diagnosis — Pomel (1843) did not give a formal diagnosis. He gave a detailed description and figured the holotype [op. cit., pp. 169-170; pl. 3 (p. 155), fig. 1, 2].

Emended diagnosis — Otter with P^2 and P^3 more robust than in *L. lutra*. P^4 with triangular outline, talon somewhat larger than in *L. lutra*, with inner edge of the talon converging backward to the trigon as a straight line. M^1 larger than in *L. lutra* and with more expanded talon.

Description — Since the present whereabouts of the holotype is not known, we have to base ourselves completely on the description and on the drawings in Pomel (1843) and in Gervais (1859, pl. 27, fig. 6). For some reason Gervais' figure shows the specimen reversed. The short description of Gervais (op. cit., p. 243-244) does not add any new information.

Pomel (1843) stated that the distance between I^3 and C sup. is smaller in *L. bravardi* than in *L. lutra* and concluded from this that C inf. was smaller also. Pohle (1919) pointed out that this conclusion needs not be correct. P^2 and P^3 are more robust, more blunt and have a much better developed cingulum according to Pomel's description. P^4 has a triangular outline, as pointed out by Pomel (op. cit.). From his description and from the figure in Gervais (1859) it can be concluded that the talon is somewhat larger than in *L. lutra*. It leaves the parastyl free, but extends more backward, the inner edge converging as a straight line to the trigon. The talon is by no means as much expanded as in some other lutrine genera, such as *Lutrogale*, *Amblonyx* or *Aonyx* (see Table 3). M^1 has a more quadrangular shape than in *L. lutra* and the talonid is larger. From Pomel's description it can be concluded that the cingulum at the basis of the metacone was much more developed than in *L. lutra*.

Systematic remarks — Pomel (1843) and Gervais (1859) included the species in the genus *Lutra*. Pohle (1919) transferred it to the genus *Aonyx* because of the broad M^1, notwithstanding the small talon of P^4. This classification was followed by most authors since Pohle. Indeed, M^1 is larger than in *Lutra lutra*. All aonychoid forms

(*Aonyx*, *Amblonyx*, *Cyrnaonyx*) have, however, a P^4 talon which is much larger and much more expanded than in *L. bravardi*. In those forms, its posterior border normally touches the anterior border of M^1. In aonychoid forms, the upper carnassial is much broader relative to its length. The P^4 talon of *L. bravardi* is even smaller than in many extant *Lutra* species (especially the New World species), in *Lutrogale* or in *Pteronura*. Further, there are extant *Lutra* species which have a broader M^1 than *L. lutra* (e.g. *L. provocax*, *L. canadensis*). Considering the dimensions of M^1 in all extant forms within the genus *Lutra*, there is no reason to exclude *L. bravardi* from that genus because of its M^1. The shape of P^4 of *L. bravardi* also reminds one of *Paralutra jaegeri*, but *P. jaegeri* has an M^1 with a characteristic posterolingual expansion which is absent in *L. bravardi*.

Kurtén (1968) also classified the species as *Aonyx* and suggested that *'Aonyx' reevei* possibly is the same form. The broad, sea-otter-like lower carnassial of *Enhydra reevei* (as this species is classified in this paper) could, however, never give a good occlusion with the upper dentition as figured by Gervais (1859) and Pomel (1843). Both forms are not even related morphologically.

It is clear that *L. bravardi* is quite unlike *Aonyx* and as far as can be judged from the available descriptions and figures, it falls well within the range of the genus *Lutra*.

An M^1 described by de Blainville (1841) as *Lutra clermontensis* was already referred to *L. bravardi* by Gervais (1859). It was claimed to be from Clermont but Gervais expressed his doubts about this, not knowing any specimen found near Clermont.

Pohle (1919) suggested that a lower jaw from the Red Crag in the UK, described by Newton (1890) as *Lutra dubia*, might belong to this species too. The species *dubia* was later transferred to the genus *Mionictis* by Thenius (see Ginsburg, 1968), but the specimen of Newton is in fact a lower jaw of *Enhydrictis ardea*. Kurtén (1968) and Heintz et al. (1974) mentioned a tibia from Saint-Vallier, which is in the museum at Basel (no. SV 306). They attribute it to *L. bravardi*, but with doubts. The only reason to refer the tibia to this species can be the fact that Etouaires and Saint-Vallier do not differ much in age (according to Heintz et al., 1974), Saint-Vallier is slightly younger than Etouaires). It is better to classify the tibia as 'lutrine', as long as no postcranial material is found together with clearly identifiable material of *L. bravardi* at the same site.

Stratigraphic remarks — Heintz et al. (1974) gave a faunal list of Perrier-Etouaires in their critical revision of the faunal lists of the main Villafranchian deposits in France. They concluded that the 'Zone des Etouaires' is younger than assumed by some authors and than suggested by some absolute datings, such as 3.4 Ma for Etouaires. Chaline & Laurin (1986, p. 206) reviewed several published datings. Basing themselves on those results and on the polarity of the deposits, they concluded an age of approximately 2.5 Ma and they placed Etouaires at the end of the Gauss Normal Epoch. They also correlated this locality with the Reuverian. Contradictory to the latter, they placed Etouaires in the Praetiglian and not in the Reuverian in their fig. 5. Since they placed the lower border of the Praetiglian at the border of the Gauss and the Matuyama Epoch, this contradicts also to their statement that Etouaires should be placed at the end of the Gauss Epoch. It seems clear that an error was made in preparing the figure and that Chaline & Laurin (1986) consider the site to be of Late Reuverian age.

Concluding, Perrier-Etouaires can be correlated with the uppermost Reuverian. This correlates to the Upper Ruscinian or MN zone 16A.

The species is also reported from Kislång (Hungary) as *Lutra* cf. *bravardi* in a faunal list by Jánossy (1986, p. 45). No further information is available concerning the specimen or specimens. Since Kislång is Upper Villányian (MN 17, see e.g. Jánossy, 1986; Reumer, 1984) this record would be considerably younger than the holotype.

Lutra affinis Gervais, 1859

Holotype — Lower mandible with M_1. Its location is unknown.

Type locality — Montpellier, 'dans les sables marins de l'époque pliocène' according to Gervais (1859).

Other localities — None.

Stratigraphic occurrence — Pliocene.

Geographic range — Montpellier (France).

Original diagnosis — 'Assez semblable à la Loutre ordinaire; le bord inférieur de sa mandibule est cependant plus rectiligne et sa carnassière inférieure a son talon un peu moins allongé.' (Gervais, 1859, p. 244).

Description — Gervais (1859) did not give any details. Apart from the diagnosis he stated: '(...) la dent carnassière est la seule qui y soit conservée. On y voit d'ailleurs les alvéoles des autres molaires, qui sont au même nombre que celles du *Lutra vulgaris* et ont une disposition peu différente. La longueur totale des cinq molaires était de 0,027. La carnassière seule a 0,011.' (op. cit., p. 244).

Systematic remarks — The species is very doubtful. The description of Gervais (1859) is quite insufficient and does not give any details. Gervais did not figure the specimen either. No later author gave any information other than what could be drawn from Gervais' original description, nor did anyone give an illustration. Apparently nobody has studied the actual specimen after Gervais. Unless the holotype will turn up somewhere, it will be impossible to decide whether this species is a valid species and whether it really is a *Lutra*.

Lutra bressana Depéret, 1893

Holotype — Unknown.

Type locality — Bresse.

Stratigraphic occurrence — ? Villanyian.

Geographic distribution — Bresse (France).

Original diagnosis — Depéret, 1839.

Description — According to Malatesta (1977), only some bones of the hind limb are known, which are much larger than in *L. lutra*. The tibia is notably curved and rather twisted, being similar to *Nesolutra*, according to Malatesta (op. cit.).

Systematic remarks — Since it is so incompletely known, it is impossible to evaluate the status of this species.

Stratigraphic remarks — Nowadays, a large number of sites yielding mammal fossils, which together are called Bresse, are known. The age of the Bresse marl complex is between 2.5 and 1.5 Ma, some other deposits (the Tournus Marls and the Trevoux-Reyrieux Sands) are older (between 3 and 2.5 Ma) according to Chaline (1984). The rodents from different sites suggest correlations ranging from the uppermost Reuverian to the Eburonian (Chaline, op. cit.). The lutrine fossil might thus be of Early Pleistocene age.

Lutra sp.

Locality — Hoxne, UK.

Stratigraphic occurrence — Hoxnian.

Material — Left P^4 (BM, Hoxne coll. 4936), left calcaneum (BM, Hoxne coll. 4682), right calcaneum (BM, Hoxne coll. 5185).

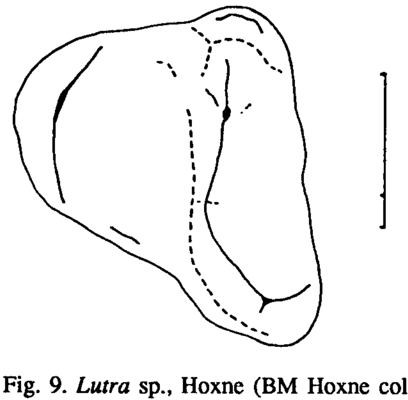


Fig. 9. *Lutra* sp., Hoxne (BM Hoxne coll. 4936), left P^4, occlusal view; scale = 5 mm.

Measurements — See Table 3.

Description — The left P^4 (Fig. 9) is clearly a *Lutra*. It is a not very worn specimen. The large paraconid and the smaller metaconid form a sharp cutting edge. A parastyl is present. The talon is concave, basin-shaped. The edge of the talon is somewhat higher than a Recent *L. lutra* specimen (BM, mammal dept., 58.5.4.147) used for comparison. In fact, no significant morphological differences with *L. lutra* can be seen. Calcaneum 4682 is somewhat smaller than 5185.

Systematic remarks — The upper carnassial is very much like that of *L. lutra*. The yet unknown upper dentition of *L. simplicidens* would be expected to differ very little or not at all from that of *L. lutra*. Since no *L. lutra* remains from the Middle Pleistocene of Europe are known, the possibility that the Hoxne specimens represent *L. simplicidens* deserves serious consideration. At the moment, it is better not to refer this material to any of the two species.

Stratigraphic remarks — The fossils were found in the Hoxnian stratotype and so they are clearly of Hoxnian age.

Genus *Sardolutra* gen. nov.

Type species — *Nesolutra ichnusae* Malatesta, 1977.

Diagnosis — Lutrine, with short and broad skull; muzzle broad; intertemporal region short and broad, hardly constricted; dental formula 3/3 1/1 3/3 1/2; P^1 lacking; P^4 with small talon not covering the entire lingual side of the tooth; M_1 *Lutra*-like, with talon and trigon equally broad and without strongly developed external cingulum. Second and third sacral spine fused. Humerus more curved than in *L. lutra*, not keeled, with wide distal part; radius with robust distal part; femur short and stout; tibia and fibula proximally fused. Baculum very large, much larger than in *Lutra* or even in *Enhydra*, ending in a blade-like process from which two smaller processes are protruding.

Stratigraphic occurrence — Probably Upper Pleistocene or Holocene.

Geographic occurrence — Sardinia.

Systematic remarks — The type species, which is the only species of the genus, has originally been described by Malatesta (1977) as a *Nesolutra*, of which *N. euxena* Bate, 1935 is the type. This view was followed by all other authors including myself. *Nesolutra* was thus thought to include three species: *N. euxena*, *N. ichnusae* and *N. trinacriae* Burgio & Fiore, 1988. From a comparison between *N. ichnusae* and *N. euxena* it was difficult to draw conclusions, since the latter is so incompletely known. The discovery of the holotype of *N. trinacriae* made a better evaluation of the characters possible. The species have many characters in common, such as the short and broad skull, the morphology of the humerus, the radius and the femur and many characters in the dental morphology. All common characters are, however, also shared with *Lutra simplicidens*, the supposed common ancestor (see the chapter on Phylogeny) or can easily be explained as resulting from similar ecological circumstances. The Sicilian and the Maltese form differ too little from *Lutra* to place them in a separate genus as was explained above. The Sardinian form is, however, a more derived form, differing in a number of aspects from both *Lutra simplicidens* (as far as this species is known) and *L. trinacriae*. The fused tibia and fibula, the fused sacral spines, the very large and peculiarly shaped baculum and the lack of P^1 suffice to justify generic separation.

Sardolutra ichnusae (Malatesta, 1977)

Synonyms — *Nesolutra ichnusae* Malatesta, 1977.

Holotype — Skeleton, preserved in the Department of Earth Sciences of the University of Rome.

Type locality — Grotta di Nettuno, Capo Caccia, Sardinia.

Other localities — None.

Stratigraphic occurrence — Probably Upper Pleistocene or Holocene.

Geographic distribution — Sardinia.

Measurements — See Tables 5-6, 11-17.

Original diagnosis — 'Lutrine of slightly smaller size than *Lutra lutra*; neck short; foot very long; tail long. Skull short and broad, with dorsal surface almost straight; muzzle high and short; postorbital processes slight; postorbital constriction almost lacking; zygomatic arc strong and wide; braincase little more swollen than in *Lutra*; mastoid and paraoccipital processes short; palatine wide and short; bullae slightly prominent, anteriorly elongated. Dental formula 3/3 1/1 3/3 1/2; P^4 resembling that of *Lutra*, but the difference between paracone and metacone is less marked, the cusps more obtuse, the talon broader but less prominent on the lingual side; M^1 lingual side rounded; paracone and metacone forming a scarcely notched ridge. The borders of the external cusps of P^4 and M^1 touch each other, leaving an ample room on the lingual side, where the paracone and metacone of M_1 fit. Lower premolars shorter and broader than in *Lutra*. M_1 similar to the equivalent of *Lutra*, but shorter, with low and obtuse cusps and a narrower talon. Fibula more or less perfectly fused to the tibia; astragalus with an astragalian canal.' (Malatesta, 1977, p. 177-178)

Material — Only the holotype is known.

Description — Malatesta (1977) gave a good and very complete description. The main characters are mentioned in the diagnosis, and I will not redescribe the material here. Some additional observations which I made on the postcranial skeleton will suffice. The second and eleventh thoracic vertebra are heterostrophic. The twelfth thoracic vertebra has its spine directed anteriorly.

The humerus of *S. ichnusae* is more curved than that of *Lutra lutra*. The deltoid tuberosity on the humerus is much more expanded than in *L. lutra*. The deltoid ridge is not straight, but shows an outward curve to enlarge the attachment area for the muscles on the deltoid tuberosity. The pectoral ridge shows a medial curve, which has a similar effect. The shaft of the humerus is not keeled anteriorly and resembles *L. euxena* in this respect. The scar of the m. teres major is situated at a relatively more distal point than in *L. lutra*. The radius is robust and more curved than in *L. lutra*. It shows a more developed bicepital pit than *L. lutra* according to Malatesta (1977). The attachment area for the m. extensor metacarpi is more marked than in *L. lutra*. There is a strongly developed bone ridge for attachment of the pronator teres.

The femur is short and stout. The trochanter major is very pronounced.

The baculum is very peculiar. It is relatively larger than in *Enhydra lutris* (Malatesta, 1977), which has the largest baculum of all extant lutrines both in relative and absolute sense (see Fig. 10). The distal part of the baculum of *S. ichnusae* has a very complicated structure and is unlike the baculum of any extant species. It ends in a large, blade-like process, from which two smaller processes are protruding (see Malatesta, 1977, fig. 22).

Systematic remarks — *S. ichnusae* shows many similarities to *Lutra simplicidens*. Thenius (1948, 1965) mentioned many characters for the latter which are also found in the former: The short and strongly curved radius with its robust distal epiphysis, the

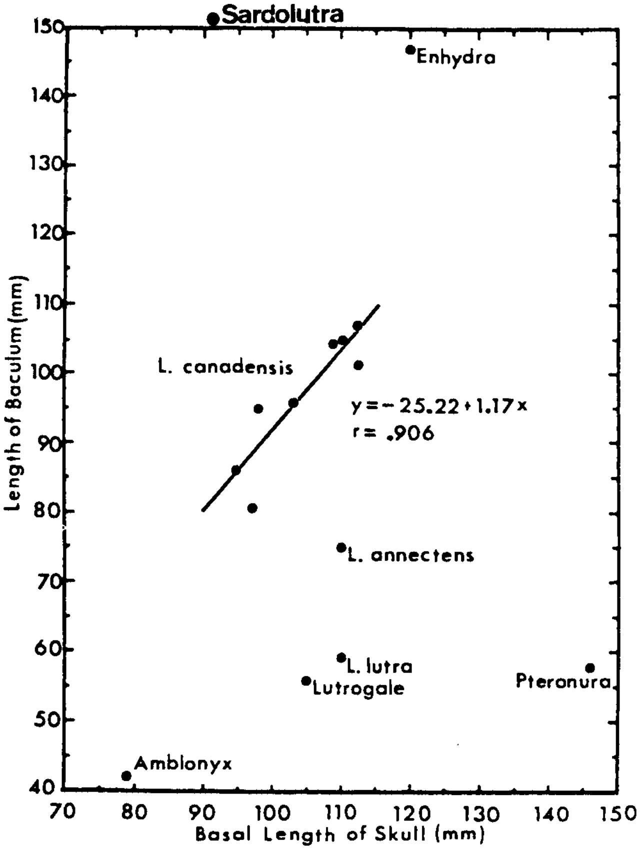


Fig. 10. Length of baculum relative to basal length of skull in adult otters. Adapted from van Zyll de Jong (1972).

rather curved olecranon, the large peroneal tubercle of the calcaneum. The radius even resembles *L. euxena* and *L. trinacriae*. The figure in Thenius (1948) shows that the femur of *L. simplicidens* has a very pronounced and more medially situated trochanter minor when compared to *L. lutra*, which is reminiscent of *S. ichnusae* and of *L. trinacriae*. Thenius (1965) supposed, basing himself on the large calcaneum, that the foot of *L. simplicidens* was rather large. A large foot is certainly characteristic for *S. ichnusae* (Malatesta, 1977). The typical expansion of the deltoid tuberosity on the humerus is also found in *L. simplicidens* and in *L. trinacriae*. Differences in the postcranial skeleton between the *S. ichnusae* and *L. simplicidens* are the proximally more slender radius shaft of *L. simplicidens*, which has a smaller caput; the ulna which is more compressed laterally in *L. simplicidens* (see Thenius, 1965, pl. 2 and Malatesta, 1977, fig. 13); the trochanter major of the femur rising higher in *S. ichnusae* and the astragalian canal being present in this species. The condition of the tibia and fibula is unknown in *L. simplicidens*, but it is not fused in any other *Lutra* species. *S. ichnusae* and *L. simplicidens* also show similarities in the lower dentition (the upper dentition of the latter is unknown). Both species have rather broad premolars and an M_1 with a more developed metaconid. In *S. ichnusae*, however, a hypoconulid is present, which is not the case in *L. simplicidens*. The resemblances between the two species are remarkable. The differences between *S. ichnusae* and the genus *Lutra* are so many that generic separation is fully justified, as was already shown by Malatesta (1977), but of the mainland forms within the genus *Lutra*, *L. simplicidens* clearly is the species which has most characters in common with *Sardolutra*.

Stratigraphic remarks — In the Grotta di Nettuno no other mammal remains have been found. The otter skeleton was laying on, and partly embedded in, a sand bed (Malatesta, 1977). According to Malatesta (ibid.), the skeleton is probably not older than the last Tyrrhenian transgression. The fossil therefore is not older than Würm/ Weichselian.

Genus *Lutrogale* Gray, 1865

Synonyms — *Lutra* Brisson, 1762 (partim); *Isolalutra* Symeonides & Sondaar, 1975.

Type species — *Lutra perspicillata* Geoffroy, 1826.

Original diagnosis — Gray (1865).

Emended diagnosis — Otter with highly arched skull, with eyes set more forward and more laterally than in *Lutra*; rostrum shorter than in *Lutra*; intertemporal region broad; mastoid processes well developed. Dentition robust. P^4 with triangular contour, broad, with large talon covering more than two-third of the length of the trigonid. M^1 large. Second and twelfth thoracic vertebra heterostrophic. Baculum slender, ending in a knob-like, bilobed distal process. Pelage smooth, feet large, third phalanges of fingers and toes free from webbing. Tail a bit flattened.

Stratigraphic occurrence — Pleistocene to Recent.

Geographic range — Pleistocene: SE Asia, Crete; Recent: S and SE Asia.

Systematic remarks — Many authors consider *Lutrogale* not to be a separate genus but include it in *Lutra* (e.g. Pohle, 1919; Harris, 1968; Corbett & Hill, 1986). The skull is, however, quite different from *Lutra*. An analysis of cranial and dental characters of most extant species by van Zyll de Jong (1972) shows that *L. perspicillata* is clearly separated from the cluster of *Lutra* and *Lontra* (a genus in which van Zyll de Jong (1973) placed the New world *Lutra* forms) species. The dentition shows aonychoid characters.

There are also other important differences with *Lutra*. The baculum differs very much from the massive baculum of *Lutra* (van Bree, 1968; van Zyll de Jong, 1972; Davis, 1978). The latter has a large and sharply curved process, which sharply contrasts with the slender process of *Lutrogale*. In both forms the distal process is bifurcated but in *Lutrogale* the asymmetry between both branches is larger. Only the baculum of *Lutra maculicollis* shows some resemblance to that of *Lutrogale*. The generic separation is supported by the place of the posterior heterostrophic vertebra and other characters of the postcranial skeleton (see Willemsen, 1980). Davis (1978) also pointed out some differences in behaviour.

In the diagnosis, the well developed mastoid processes of *Lutrogale* are mentioned. Pohle (1919) stated that *Lutrogale* has less developed mastoid processes than *Lutra*, but Willemsen (1980) showed, that the opposite is true.

Lutrogale cretensis (Symeonides & Sondaar, 1975)

Synonyms — *Isolalutra cretensis* Symeonides & Sondaar, 1975.

Holotype — Nearly complete skeleton, preserved in the Geological Institute of the University of Athens, coll. 2/1974.

Type locality — Liko Cave, bed Liko a, 4 km north of Georgioupolis, Crete.

Other localities — None.

Stratigraphic range — Late Pleistocene.

Geographic range — Crete.

Measurements — See Tables 4 and 16.

Original diagnosis — Symeonides & Sondaar (1975), p. 12.

Emended diagnosis — Rather robust *Lutrogale*. Dental formula 3/3 1/1 4/3 1(2)/2.

Lower canine in occlusion directed parallel to sagittal plane of skull. P^4 relatively broader than in *L. perspicillata*. M^2 may be present. Ilium longer relative to ischiopubis than in *L. perspicillata*. Femur more robust than in *L. perspicillata*.

Material — Nearly complete skeleton (holotype, GIA 2/1974), left mandible (IvAU LiBa 1), two left M_1 (IvAU LiBa 2 and LiBa 4), left femur (IvAU LiBa 3).

Description — The holotype was described in detail by Symeonides & Sondaar (1975) and by Willemsen (1980). I will not repeat those descriptions here in detail but only give a short description, pointing out the main characters. The skull is large and highly arched. The intertemporal region is broad and the mastoid processes are prominent. The morphology is much like in *L. perspicillata*. The mandible is robust and large.

The dentition resembles *Lutrogale perspicillata*. The talon of P^4 is large and the tooth is slightly broader than in average *L. perspicillata*. In this respect it is comparable to *L. palaeoleptonyx* (see Fig. 11 and Willemsen, 1986). The most peculiar aspect in the dentition is the fact that on the right side the alveole for M^2 is present. The lower carnassial is much like in *L. perspicillata*.

In the axial skeleton, the second and the twelfth thoracic vertebra are heterostrophic, as in the type species. The sacrum consists of two vertebrae. The first sacral spine is directed anteriorly, the second posteriorly. The pelvis differs from that of the type species in the relative length of ilium and ischiopubis. In *L. cretensis* the ilium is relatively longer. The ratio of ilium length and ischiopubis length is 1.34, which is significantly more than in *L. perspicillata*. The limb bones are large and

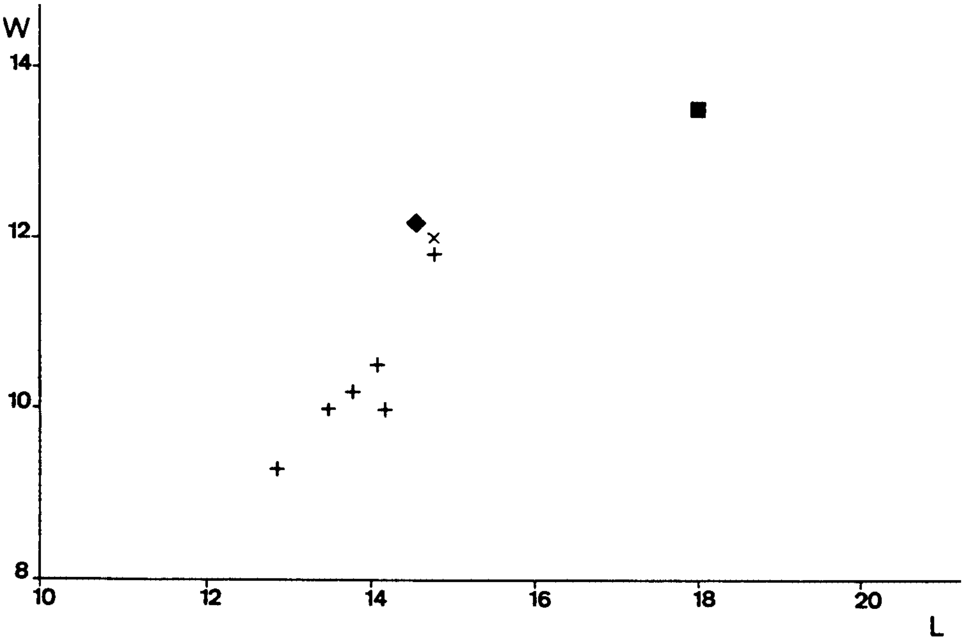


Fig. 11. P^4 length and width of *Lutrogale perspicillata* (+), *L. cretensis* (triangle), *L. palaeoleptonyx* (×) and *L. robusta* (square).

robust. On the humerus, the pectoral ridge and the deltoid tuberosity are less pronounced than in *L. perspicillata*. The femur is very robust, the neck is relatively thicker and the condyles are broader than in the type species. The attachment area for the mm. glutei on the trochanter major is also larger.

In a later excavation in the same deposits by a team from the Institute of Earth Sciences in Utrecht some more material was discovered which I will describe here.

A left mandible (IvAU LiBa 1) has about the same size as the holotype. Only P_3 and P_4 are present. Both teeth are monocuspid, though P_4 has a slight accessory cuspid at the posterior side of the main cuspid. This accessory cuspid is less developed than in the holotype. A small talonid is also present in this tooth.

Two isolated left M_1 (IvAU LiBa 2 and 4) were also found. They are very much like the M_1 in the holotype. Paraconid and protoconid are about equally large, the metaconid is somewhat smaller. Talonid and trigonid are equally wide. The labial edge of the talonid is in fact formed by the hypoconid. As in the holotype, no hypoconulid is present. An external cingulum is present, starting at the anterior side of the paraconid almost disappearing at the posterior part of the protoconid and clearly visible again along the talonid.

An isolated left femur (IvAU LiBa 3) was also found. It is shorter and more slender than the holotype femur. The condyles are relatively broad and the neck is massive compared to *L. perspicillata*. In the holotype the attachment area for the mm. glutei on the trochanter major is larger than in *L. perspicillata*, in this specimen this is not the case.

Systematic remarks — Symeonides & Sondaar (1975) created a new genus, *Isolalutra*, for this species. They compared the fossil with *Lutra lutra* but not with *Lutrogale perspicillata* and they suggested that *Lutra* might be ancestral to the Cretan genus. In Willemsen (1980), the many resemblances to *Lutrogale perspicillata* were pointed out, and a phylogenetic relationship between this species and the Cretan fossil was suggested. Willemsen (1980) maintained the genus *Isolalutra*, though with some doubts. Comparison with many other extant and extinct species, however, have lead to the conclusion that the differences between *Lutrogale* and *Isolalutra* are too small to justify generic separation. The differences between *L. cretensis* and *L. perspicillata* are: the direction of the lower canine; the presence of the M^2 alveole in the Cretan species (which could be an anomaly, since it is present on one side only); the number of sacral vertebrae, which is known to be variable to some extent in extant species (normally there are 3, but sometimes a number of 2 or 4 sacral vertebrae occurs); the direction of the second sacral spine and the relative length of ilium and ischiopubis. Willemsen (1980) also mentioned the place of the lesser sigmoid notch on the ulna, but the difference between the two species is so small that it probably falls within the intraspecific variation. The ilium length is in fact the most important character. It is clear that the differences between the two species are so small that the Cretan otter must be included in the genus *Lutrogale*.

Stratigraphic remarks — *L. cretensis* is only known from the type locality, Liko Cave on the island Crete. The cave is situated in Miocene limestones at the coast near the village Likotenaria, c. 4 km north of Georgioupolis. The cave is filled with red fossiliferous clay. The otter fossils were found in the upper layer in the rear part of the cave, called Liko Ba. Liko Cave can be correlated to the *Mus minotaurus* subzone of the *Mus* zone in the biostratigraphy of de Vos (1984). The *Mus minotaurus* subzone is the youngest of the four biostratigraphical units recognized by de Vos (1984) in the Pleistocene of Crete. The fauna from this locality contains *Mus minotaurus*, *Crocidura zimmermanni*, *Candiacervus cretensis*, *C. rethymnensis*, two other *Candiacervus* species and a large number of birds (de Vos, 1984; Reumer, 1986; Weesie, in press). *Mus minotaurus* is a Late Pleistocene species which survived till historical times (Mayhew, 1977), *Crocidura zimmermanni* is an extant species already present in the Pleistocene (Reumer, 1986) and the *Candiacervus* species are Pleistocene. From the available data, a Late Pleistocene age for the Liko cave fillings can be concluded.

Genus *Algarolutra* Malatesta & Willemsen, 1986

Synonym — *Cyrnaonyx* Helbing, 1935 (partim).

Type species — *Cyrnaonyx majori* Malatesta, 1978.

Original diagnosis — As for the type species, given by Malatesta (1978, p. 114-115).

Emended diagnosis — Upper carnassial (P^4) with remarkably large talon, its anterior border forming a very obtuse angle with the labial border; the posterior border swollen in the middle; paracone strong and raising straight, not inward bent as in *Lutra*; protocone narrow and elongated, high on the hollow surface of the talon and extended in a ridge along the posterior border of the tooth; M^1 short and broad, with large parastyle; lingual side longer than labial side; protocone preceded by a protoconule; protocone and protoconule blunt, cusp-like, not elongated; low and crest-like hypoconid; strong cingulum; lower carnassial (M_1) with trigonid almost as large as talonid; talonid hardly broader than trigonid; paraconid short and stout; protoconid and metaconid rather diverging, the latter being lower; protoconid long, with hind side double-keeled, posterior border of the talonid much elevated and hypoconid ridge almost reaching the height of the metaconid; cingulum scarcely developed.

Stratigraphic occurrence — Late Pleistocene.

Geographic distribution — Sardinia, Corsica.

Systematic remarks — The type species was described by Malatesta (1978) as new type species of the genus *Cyrnaonyx* Helbing, 1935. This was, however, not in accordance with the International Code on Zoological Nomenclature. According to the rules, *Lutra antiqua* de Blainville, 1841 remains type species of *Cyrnaonyx* and therefore, Malatesta & Willemsen (1986) proposed the genus *Algarolutra* for the species *majori*. *Algarolutra* differs from other genera by its aberrant M^1. All known lutrines except *Enhydra* and *Enhydriodon*-like forms have an elongated, crest-like protocone.

It is clear, that *Algarolutra* does not resemble the Enhydrini in any other respect, so it cannot be included in one of the genera in this group either. M_1 has the narrow talonid, the crest-like hypoconid and the small cingulum of the Lutrini. P^4 has a rather large talonid, but its dimensions fall within the range for *Lutra* so the genus can be included in the Lutrini.

Algarolutra majori (Malatesta, 1978)

Synonyms — *Cyrnaonyx antiqua*, in Helbing (1935) (partim); *Lutra lutra*, in Malatesta, 1970; *Cyrnaonyx majori* Malatesta, 1978.

Holotype — Left P^4, M^1 and M_1 (probably from one individual), preserved in the Museum of the Department of Earth Sciences of the University of Rome, 1944-1946.

Type locality — Grotta di Dragonara, near Alghero, NW Sardinia.

Other localities — Grotta del Margine, Corsica.

Stratigraphic occurrence — Late Pleistocene.

Geographic distribution — Sardinia, Corsica.

Measurements — See Table 6.

Original diagnosis:— Malatesta (1978), p. 114-115.

Emended diagnosis — As for the genus.

Material — Left P^4, M^1 and M_1 from Grotta di Dragonara, Sardinia (holotype, UR 1944-1946); right P^4 and M_1 from Grotta del Margine, Corsica (coll. UCBL).

Description — The holotype teeth were described by Malatesta (1978). The P^4 shows a large, expanded talonid, almost covering the entire lingual side of the trigonid (Fig. 12). The tooth is broad. The paracone is much higher than the metacone. Its tip is broken off.

The M^1 is broad and has a large talon (Table 6). The parastyl is larger than in *Lutra*, resembling the situation in *Amblonyx* and *Aonyx*. The metastyl is very small. The protocone is not elongated, as it is in all other Lutrini and Aonyxini. Labially of the protocone, a protoconule is present. Protocone and protoconule are less conically-shaped than in the specimen from Grotta del Margine. The hypocone is low and elongated, forming the posterolingual edge of the talon, and proceeds anteriorly as a cingulum around protocone and protoconule. The cingulum is rather wide at the anterolingual edge. The hypocone is divided by a notch.

M_1 has a relatively narrow talonid (Table 6). In the trigonid, the paraconid is

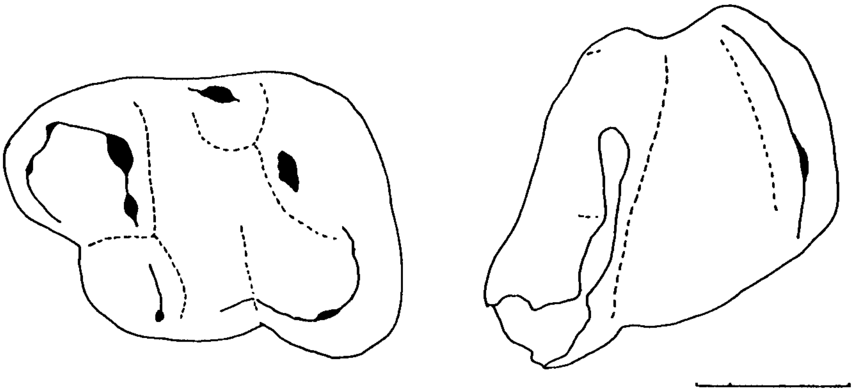


Fig. 12. *Algarolutra majori*, right P^4 and M^1 from Grotta del Margine, Corsica; scale = 5 mm.

the largest cuspid, but the protoconid is the highest. The metaconid is the smallest cuspid and placed more backwards than the protoconid, as in *Lutra*. The hypoconid is elongated and crest-like. The outer edge of the talonid is formed by the hypoconid and the hypoconulid. Between the protoconid and the hypoconid, an accessory cuspule is present, as in *Lutra*. The external cingulum of the talonid is only weakly developed. The tooth is two-rooted.

The P^4 and M^1 from Grotta del Margine, Corsica, (Fig. 12) were described for the first time by Helbing (1935). The teeth are somewhat larger than the specimens from Sardinia. Of the P^4, the parastyl is broken off as well as the anterolabial root. The paracone is high and steep. The metacone is much lower. The talon is very large, as was already noted by Helbing (1935). The posterolingual edge of the talon is not straight but shows a slight expansion. The M^1 is broad (Table 6). Its parastyl is large and the metastyl is very small compared to *Lutra*. In this respect, the tooth resembles the aonychoids. The protocone is not elongated but has the form of a blunt, conically shaped cusp. Its posterolingual side is trenchant, but at its labial side it slopes down gently. Anterolabially of the protocone, a smaller protoconule is present (Fig. 12). The hypocone is low, forming the posterolingual edge of the talon. The talon is expanded posterolingually. There is a cingulum anteriorly and lingually to the protocone and the protoconule, but it is less developed than in the Sardinian specimen.

Systematic remarks — There are slight differences between the specimens from Sardinia and from Corsica: the teeth from Corsica are slightly larger and the M^1 from Corsica has a protocone and a protoconid which are more conically-shaped than in the tooth from Sardinia. In the latter, a slight tendency towards elongation is visible. In the Sardinian M^1 the cingulum is more developed. The differences are small, however, and probably due to intraspecific variation.

Stratigraphic remarks — The specimens from Corsica were found in Pleistocene sediments in the Grotta del Margine (Helbing, 1935). A better age estimate than 'Pleistocene' cannot be given.

The teeth from Dragonara Cave on Sardinia come from a layer, overlying Tyrrhenian-2 beach-gravel (Malatesta, 1978). The stratigraphy of Dragonara Cave is described in detail by Malatesta (1970). Fossils of mammals and birds were found in a clayey layer. The fossils must be younger than the Tyrrhenian-2 deposits, which can be correlated with the Eemian. The fauna is a typical Late Pleistocene one, containing *Nesiotites similis, Cynotherium sardous, Vulpes vulpes, Sus scrofa, Megaceros cazioti, Prolagus sardus, Tyrrhenicola henseli, Rhagamys orthodon,* and possibly *Ovis musimon* (Malatesta, 1970).The so-called *Tyrrhenicola* fauna appeared on Sardinia in the Middle Pleistocene, replacing the older *Nesogoral* fauna. Species like *M. cazioti* and *C. sardous* became extinct shortly after the beginning of the Holocene. Thus, the fauna can be dated as probably Weichselian.

Tribus Aonyxini Sokolov, 1973

Type genus — *Aonyx* Lesson, 1827.

Diagnosis — Lutrine with body somewhat less elongated than Lutrini, head short, fingers without or with short nails. Facial part of the skull short and broad, postorbital constriction broad. Dentition more robust than in the Lutrini, teeth broad. P^4 with large talon; with shearing blade; protocone elongated and forming the anterolingual cingulum of the talon; no hypocone. M_1 with talonid broader than trigonid; hypoconid present as a real cuspid; entoconid if present elongated and smaller than hypoconid; outer cingulum of the talonid strongly developed.

Genus *Cyrnaonyx* Helbing, 1935

Synonyms — *Lutra,* in de Serres et al. (1839), de Blainville (1841), Harlé (1910); *Aonyx,* in Kurtén (1968) and many others.

Type species — *Lutra antiqua* de Blainville, 1841.

Original diagnosis — Helbing (1935) did not give a formal diagnosis, but he gave a detailed description of his material.

Proposed diagnosis — Otter, with dorsoventrally flattened skull; with eyes set dorsally as in *Lutra*; muzzle short and broad; intertemporal region much broader than in *Lutra,* almost as in *Aonyx,* but more elongated than in *Aonyx*; mastoid processes more prominent than in *Lutra.* Mandible with two mental foramina. Dentition robust; dental formula 3/3 1/1 4/3 1/2; P^4 broad and with large talonid, almost covering the entire lingual side of the trigonid. Lower premolars robust and broad. M_1 robust and broad, with broad talonid, which is lingually more expanded than in *Lutra,* hypoconid well developed, hypoconulid present, talonid with strongly developed external cingulum, expanding more than in *Lutra* and *Aonyx.*

Stratigraphic occurrence — Holsteinian to Eemian/Weichselian.

Geographic distribution — Central and Western Europe.

Systematic remarks — The genus *Cyrnaonyx* was established by Helbing (1935) as a monospecific genus for *Lutra antiqua.* Apart from the holotype of this species , which he described and figured in detail, and some other mandibles, he referred a P^4 and an M^1 from Grotta del Margine, Corsica, to this species. He explicitly based his new genus on the characters of the Corsican material. Symeonides & Sondaar (1975) were the first to question the conspecificity of the Corsican material and *Lutra antiqua,* stating that: '... the proportions and the bunodont character of the upper molars make it very improbable that a functional occlusion was possible with the type specimen from Lunel-Viel. Therefore the fossil from Corsica must belong to a different and most probably new species.' (loc. cit., p. 20).

This conclusion was supported by Malatesta (1977, 1978) and by Willemsen (1980, 1984). The conclusion is confirmed by the upper dentition of *Cyrnaonyx antiqua* from Tornewton Cave, described in this paper, which is very different from the Corsican material (see Figs. 12 and 15).

Malatesta (1978) described a new species for a lutrine from Sardinia which he called *Cyrnaonyx majori,* and included the Corsican material in this species. He made clear in his paper, that he did not mean to include his new species in the same genus as *L. antiqua.* Malatesta argued, that Helbing (1935) established his genus *Cyrnaonyx* because of the characters of the Corsican teeth, that the Corsican otter was wrongly included in *L. antiqua,* but still is the type species of *Cyrnaonyx.* Malatesta (op. cit.) proposed *C. majori* as new type species for the genus instead of *L. antiqua,* which he referred to *Aonyx.* Initially, the present author followed Malatesta in this solution (Willemsen, 1984). However, Malatesta and Willemsen (1986) recognized, that this is not in accordance with the International Code of Zoological Nomenclature, since the type of a genus is always a species and not a specimen, and thus *L. antiqua* remains the type species of *Cyrnaonyx,* even if the Corsican teeth are no longer included in the species. Therefore, Malatesta & Willemsen (1986) established the genus *Algarolutra* for the species *majori.*

Several authors have included *C. antiqua* in the genus *Aonyx* (e.g. Kurtén, 1968; Malatesta, 1978; Pennacchioni & Cassola, 1986). Indeed, there are many aonychoid characters, such as the short and broad skull, the broad snout, the broad intertemporal region, the robust dentition and the structure of the M_1. Figures. 13 and 14 show, that P^4 and M_1 dimensions are comparable to *Amblonyx cinerea,* though especially M_1 tends to be slightly larger. On the other hand, there are also a number of differences with *Aonyx,* justifying generic separation. Differentiating characters with respect to the genus *Aonyx* are the fact that the skull is flattened, the dorsally set eyes, the intertemporal region which is longer, and the broader external cingulum of the M_1 talonid. The differences in skull morphology also point to a way of life which is quite different from *Aonyx,* as will be shown in the chapter on functional morphology.

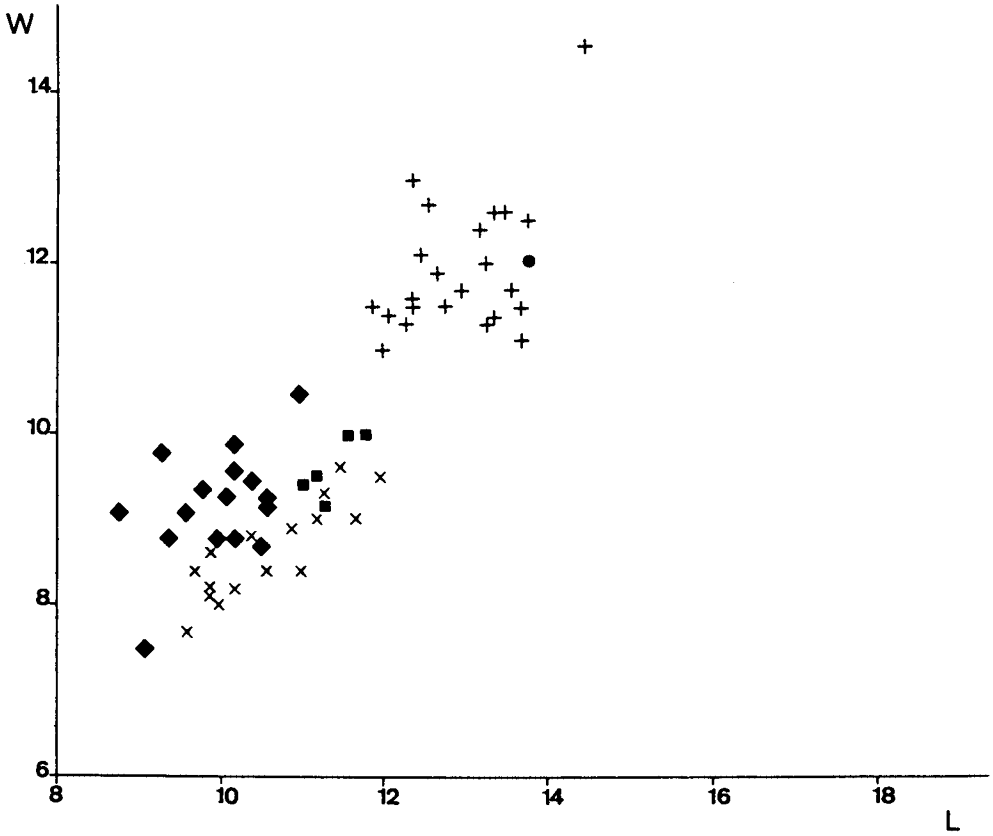


Fig. 13. Scatter diagram of P^4 length and width of *Cyrnaonyx antiqua* (square), *Aonyx capensis* (+), *Amblonyx cinerea* (x) and *Aonyx congica* (triangle). Measurements partly from Pohle (1919).

Cyrnaonyx antiqua (de Blainville, 1841)

Synonyms — *Mustela lutra*, in de Serres et al. (1839); *Lutra antiqua* de Blainville, 1841; *Lutra canadensis*, in Harlé (1910); *Aonyx antiqua*, in Kurtén (1968) and many later authors.

Holotype — Right mandible with P_3, P_4 and M_1, preserved in the Laboratory of Palaeontology of the University of Languedoc, Montpellier, coll. LUV 68.

Type locality — Lunel-Viel, France.

Other localities — Roter Berg near Saalfeld, Weimar-Ehringsdorf (GDR), Tornewton Cave (UK), Maasvlakte (Netherlands), Carrière d'Aurensan, Montsaunès? (France), Verona? (Italy).

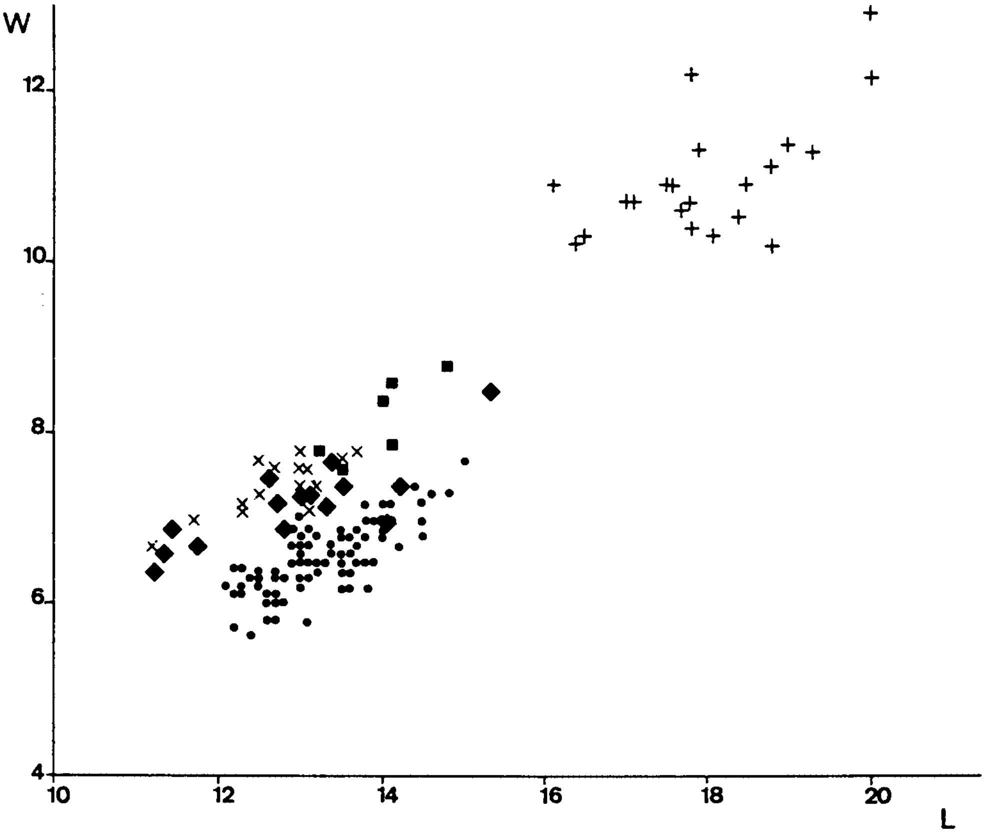


Fig. 14. Scatter diagram of M_1 length and width of *Cyrnaonyx antiqua* (square), *Aonyx capensis* (+), *Amblonyx cinerea* (X) and *Aonyx congica* (triangle) and *Lutra lutra* (dot). Measurements partly from Pohle (1919).

Stratigraphic occurrence — Holsteinian to Eemian/Weichselian.

Geographic distribution — Central and Western Europe.

Measurements — See Tables 7-9.

Original diagnosis — De Blainville (1841).

Emended diagnosis — As given above for the genus.

Material — Lunel-Viel: right mandible with P_3, P_4 and M_1 (holotype, LPM LUV 68); Carrière d'Aurensan: mandible with P_4 and M_1; Roter Berg: left mandible with M_1 (MNB MB Md 8069); Weimar-Ehringsdorf: left M_1; Maasvlakte: left mandible with P_3, P_4, M_1 (Ke RM 226); Tornewton Cave: skull (BM M 34370), two skull fragments (BM M 34376, M 34377), C sup. (BM M 34375), 3 right P^4 (BM M 34373, M 34374,

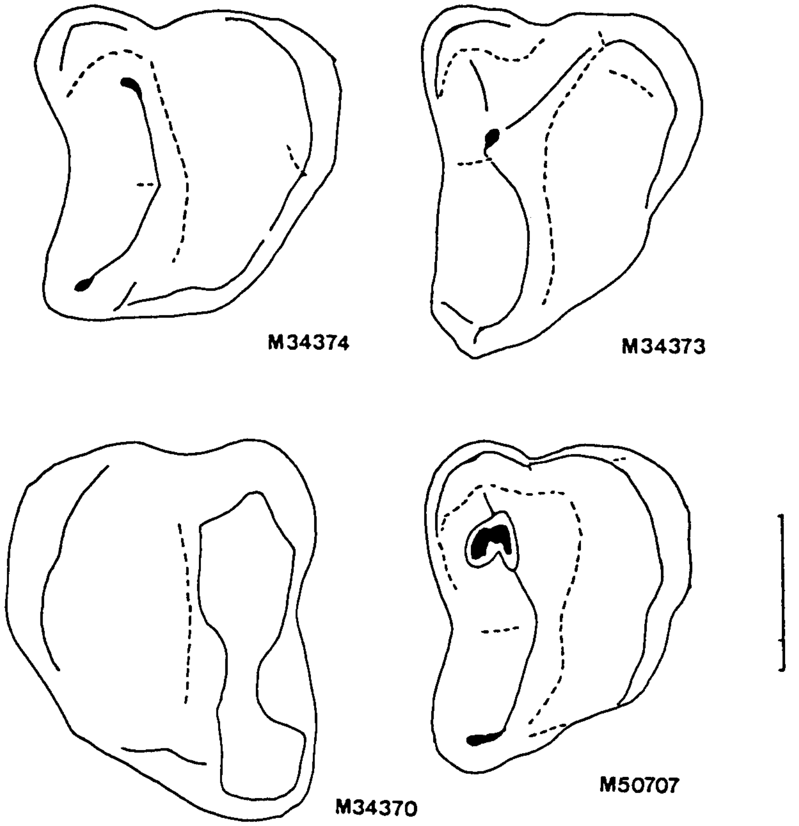


Fig. 15. Four P^4 of *Cyrnaonyx antiqua* from Tornewton Cave from the BM collection; scale = 5 mm.

M 50707), right mandible with almost complete dentition (BM M 34371), mandibular fragment with left M_1 and M_2 (BM M 34372), P_2 (BM M 50709), left M_1 (BM M 50708), atlas (BM M 34378), epistrophaeus (BM M 34379), cervical vertebra (BM M 34380), sacrum (BM M 34384), caudal vertebra (BM M 34381), right humerus fragment (BM M 34382), right tibia (BM M 34386); Montsaunès: right M_1 fragment?; Verona: left P^4?

Description — The holotype from Lunel-Viel (LPM LUV 68) was described by de Serres et al. (1839), de Blainville (1841), Harlé (1910) and in great detail by Helbing (1935). The mandible is very robust. There are two mental foramina, situated under the P_2 and the P_4 respectively. The teeth are not very worn. P_3, P_4 and M_1 are present. P_2 is situated very obliquely, as can be seen from the alveoles. The posterior part of P_4 is much broader than in *Lutra*. In the M_1, the paraconid is relatively larger than in *Lutra* and the metaconid is more closely connected to the other two cuspids of the trigonid than in *Lutra*. It is much smaller than the other two cuspids. In *Lutra*, the metaconid is situated more backwards and is more isolated. The talonid is very broad,

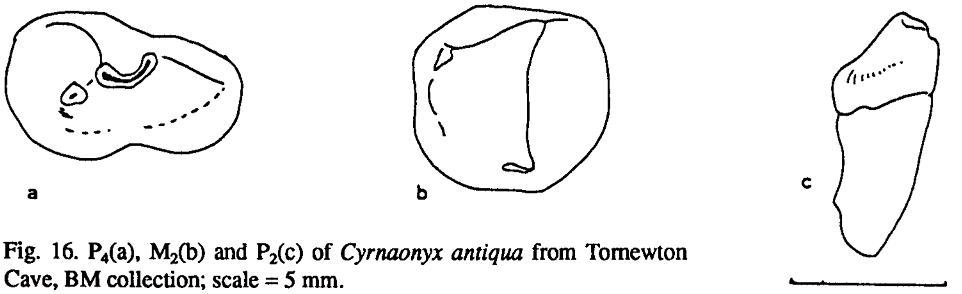


Fig. 16. P_4(a), M_2(b) and P_2(c) of *Cyrnaonyx antiqua* from Tornewton Cave, BM collection; scale = 5 mm.

considerably broader than the trigonid; its outer cingulum is strongly developed and the lingual edge shows an expansion. The hypoconid is larger than in *Lutra*. Anterior to it, a small accessory cuspid, closely connected to the protoconid, is present as in most otters. Posteriorly, a small hypoconulid can be seen. The talonid shows a lingual expansion, though not as extreme as in the Saalfeld specimen. A cingulum is present at the inner side of the paraconid and at the entire outer side of the tooth. The external cingulum of the talonid is very much broader than in *Lutra* and even broader than in *Aonyx*.

Two other specimens from France were also described by Helbing (1935): a mandible with P_4 and M_1 from Carrière d'Aurensan in Bagnières de Bigorres, Hautes-Pyrénées and an anterior half of a right M_1 from Montsaunès. The latter is, according to Helbing (op. cit.), considerably larger than the other specimens and it has an extra cuspule between metaconid and paraconid. From the description, it is not clear whether this specimen really should be referred to *C. antiqua*. The Carrière d'Aurensan specimen resembles the Lunel-Viel specimen very much according to Helbing (1935). Harlé (1910) noted this similarity too.

From The Netherlands, a left mandibular ramus with P_3, P_4 and M_1 is known from the Maasvlakte (Ke RM 226). Willemsen (1984, p. 14) mentioned this species from the North Sea. This was a confusing error, since it was this Maasvlakte specimen which was meant. The alveoles of the canine and of P_2 and M_2 are present. The mandibular ramus is stout, it is higher than the length of M_1. There are two mental foramina, situated under P_2 and under P_4 respectively. The alveoles show that P_2 was two-rooted. It was situated very obliquely with respect to the longitudinal axis of the ramus. The teeth show large wear facets. The P_3 is more robust than in *Lutra*. A posterior accessory cuspid is present. The P_4 is also more robust than in *Lutra*. The tooth is surrounded by a clear cingulum, which is only lacking at the posterior part of the lingual side. The posterior part of the tooth is relatively much broader than in *Lutra*. In the M_1, the paraconid and the protoconid show large wear facets. At its base, the metaconid is not free from the protoconid. The metaconid is the smallest of the three cuspids in the trigonid. It is situated less backward with respect to the other two than in *Lutra*. The talonid is broader than the trigonid and it is relatively broader than in *Lutra*. The hypoconid is completely worn and can be seen as a wear facet on the talonid only. It is difficult to distinguish because of the black colour of the tooth. The hypoconulid cannot be distinguished, probably because it is also worn completely. The external cingulum of the talonid is larger than in *Lutra* or *Aonyx*, but it is relatively

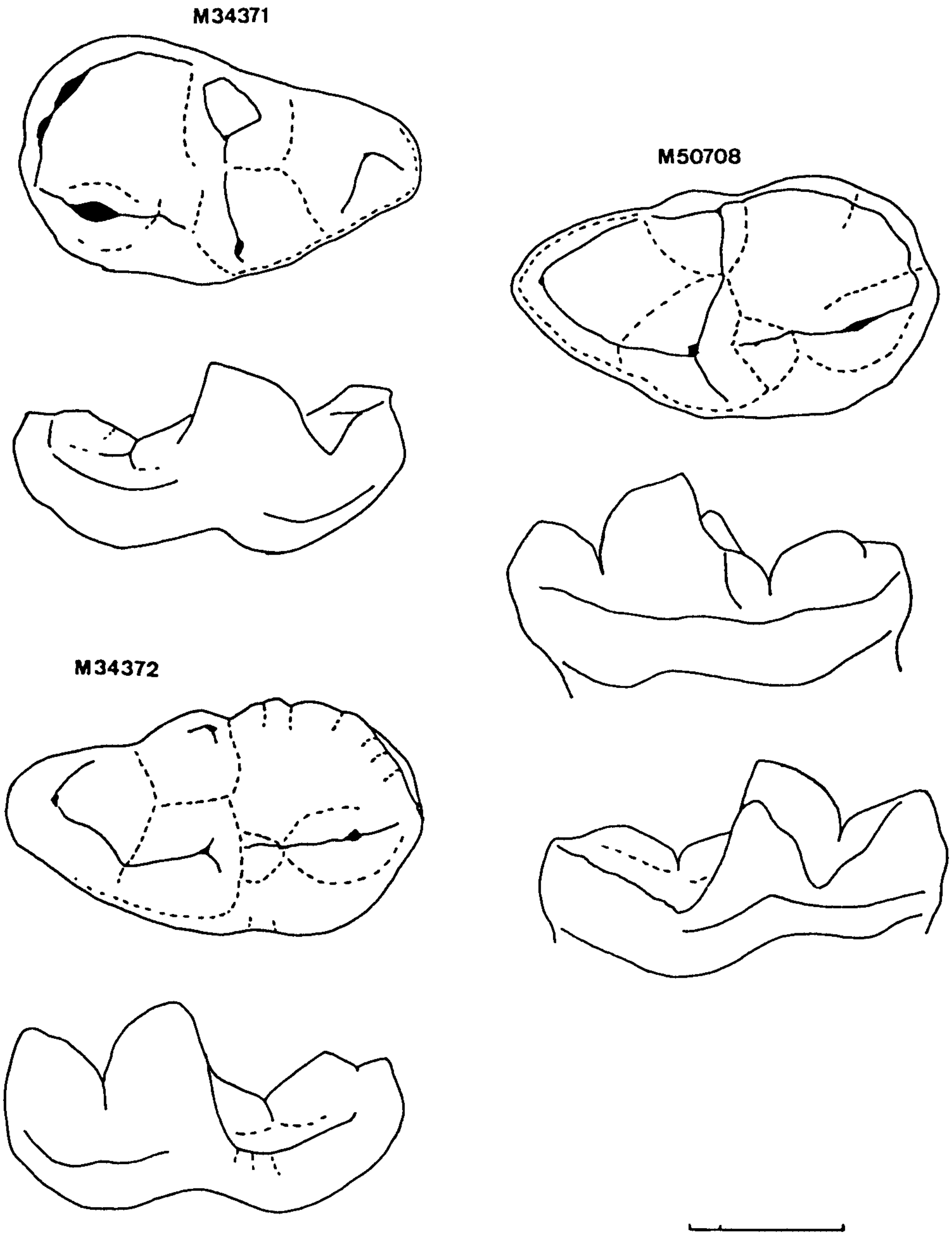


Fig. 17. M_1 of *Cyrnaonyx antiqua* from Tornewton Cave, BM collection. Occlusal, buccal and labial view; scale = 5 mm.

somewhat less prominent than in the specimens from Tornewton Cave.

From Roter Berg near Saalfeld (Thuringia), a left mandibular ramus with M_1 was described by Helbing (1935). The specimen was very well illustrated by Heinrich & Fejfar (1988). Of the teeth, only the M_1 and the basal part of the crown of the P_4 are preserved. The mandible is only slightly higher than the length of M_1. There are two mental foramina. The M_1 has two main roots and a small third root under the protoconid. In the M_1, the paraconid and the protoconid show wear facets. The metaconid is smaller and not worn. The metaconid is not free from the protoconid at its base, and it is situated less backward than in *Lutra*. The trigonid is surrounded by a cingulum, which is, however, absent along the metaconid. The talonid is broader than the trigonid. It has a broad external cingulum, as in *Aonyx* and *Amblonyx*, but not as broad as in the Tornewton Cave specimens. The hypoconid shows a narrow wear facet over its entire length. Between the protoconid and the hypoconid there is a small cuspule as in most lutrines. A small hypoconulid is present. Posterolingually on the talonid, an elongated wear facet is present, representing the entoconid. The talonid shows a lingual expansion, which is much more marked than in the other specimens of this species.

From the Lower Travertine of Weimar-Ehringsdorf a left M_1 is known. It was found in 1982 and described shortly by Heinrich et al. (1986). A more elaborate description and illustration of the specimen was given by Heinrich & Fejfar (1988). Among other things, they mentioned the fact that the tooth is broader than in *Lutra*, the large metaconid, the broad talonid, the presence of a hypoconid, a hypoconulid and an accessory cuspule between the protoconid and the hypoconid. From the wear facet they concluded, that a functional entoconid was present. The tooth has three roots, and no inner cingulum is present. Heinrich & Fejfar (1988) as well as Heinrich et al. (1986) refer the specimen to the species *antiqua* only provisionally, noting differences with the Saalfeld specimen. In fact, when taking all known specimens into consideration, the Saalfeld specimen is the most aberrant one and the Weimar-Ehringsdorf specimen resembles the holotype so much that the two are without doubt conspecific.

The most complete material of *Cyrnaonyx antiqua* was found in Tornewton Cave, Devon, UK, in 1960 and some additional material in 1968 (see Pls 2-5 and Figs. 15-17). The presence of the species was mentioned by Sutcliffe & Zeuner (1962) and many later authors, but so far the specimens have not been described properly.

The skull (BM M 34370): In the maxilla, the right P^2 and P^4 are present, the other teeth are lacking. The basicranial part of the skull is lacking too. The skull is relatively shorter and broader than in *Lutra lutra*. The snout is rather short and very broad. The nasal opening is very wide. the skull is flattened dorsoventrally to a degree, comparable to *L. lutra* and not high arched as in *Aonyx*. In lateral view, the sagittal line is not arched but rising slightly in a backward direction. The eyes are set rather dorsally, as in *Lutra*. The angle between the orbital planes (angle of forward vision, see Savage, 1957) is about 100°. The sagittal crest is developed only weakly. The palatum is a lot broader than in *Lutra*. The interorbital width is greater than in *L. lutra*, the postorbital constriction is much broader than in *Lutra* but not as broad as in *Aonyx*. The intertemporal width is smaller than the interorbital width. The intertemporal region is relatively more elongated than in *Aonyx*. The intertemporal region is longer than wide; in *Aonyx* it is wider than long. The mastoid processes are more prominent than in *L. lutra*. The infraorbital foramen is oval in shape. The anterior edge of the orbita is situated above the P^3.

Only two teeth are present in the skull, the others are represented by their alveoles, in which in some cases the roots are still present. The alveoles show that I^3 was much larger than the other two incisives. The small, single-rooted P^1 was situated almost medially of the canine. Part of the crown of the left P^2 is present. This tooth is larger and broader than in *Lutra*. P^2 and P^3 are two-rooted. The left P^4 is present, but the crown is damaged (Fig. 15). The paracone and the metacone are broken off. A small parastyl is present. The talon is large and concave, covering the entire lingual side of the trigone. The tooth is three-rooted. The part of the skull, bearing the M^1 is partly broken off on both sides.

Two small fragments, probably from the same skull, are also preserved: a fragment with the right bulla (BM M 34376) and a fragment with the right part of the condyle (BM M 34377). The tympanic bulla is broader relative to its length than in *L. lutra*, the external auditory meatus extending more laterally. Thus, the angle between the anterior and the posterior border of the tympanic is sharper.

Three isolated P^4 are preserved, all right ones (BM M 34373, M 34374, M 50707). M 34374 is the only specimen of this species not found in the so-called Otter Stratum but in the Glutton Stratum. In all three, the talon is large, covering the entire lingual side of the trigon (Fig. 15, Table 8). The broad talon is concave and is surrounded by a well-developed cingulum. All three specimens show three roots and in all three a parastyl is present. The paracone is higher than the metacone. Both cusps form a cutting edge, sloping down from the paracone, backwards to the metacone. In M 34373, the edge slopes down and runs horizontally over some distance towards the metacone, in M 34374 the ridge is concave, rising again towards the metacone.

In the right mandible (BM M 34371), the complete dentition except I_1 and M_2 is present. The angular process is relatively lower than in *L. lutra*. There are two mental foramina, one under P_2/P_3 and one under the P_4. The height of the mandibular ramus exceeds the length of the carnassial both in this specimen and in a left mandibular fragment. No P_1 is present. Of the canine and the P_2, the tip of the crown is missing. The P_2 is small and single-rooted. An isolated P_2, which is also preserved (BM M 50709), does not differ from the specimen in M 34371. All premolars are more robust than in *Lutra*. P_3 and P_4 have a more developed cingulum and P_4 also has a posterior accessory cuspid which is larger than in *Lutra* (Fig. 16). The carnassial is much more robust and broader than in *Lutra* (Fig. 17, Table 9). The cuspids show large wear facets, but it can be seen that the paraconid is the largest cuspid. The metaconid is much smaller than the other two cuspids in the trigonid. It is closely connected to the protoconid at its base and placed on one line with it, and not more backward as in

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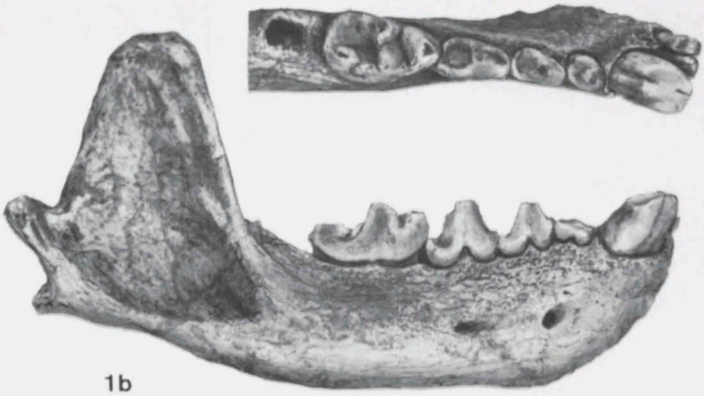
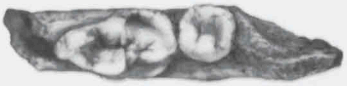
Plate 2

Cyrnaonyx antiqua (de Blainville, 1841)
1. Right mandible from Tornewton Cave, BM M 34378; a: occlusal view; b: buccal view.
2. Fragment of left mandible from Tornewton Cave, BM M 50709; a: occlusal view; b: buccal view.
3. Left mandible from the Maasvlakte, Ke RM 226; a: occlusal view; b: buccal view.


1a
1b


2a


2b


3a


3b
2 cm

Lutra. A cingulum is present, starting at the internal posterior basis of the paraconid, surrounding this cuspid, posteriorly continuing along the protoconid and along the talonid. The talonid is very broad. There is a large hypoconid, much larger than in *Lutra.* Between the protoconid and the hypoconid there is the small cuspule, which is present in most lutrines. A hypoconulid is present. The extreme width of the talonid (which is wider than the trigonid) is caused by the lingual expansion of the talonid (which is, however, not as large as in the Saalfeld specimen) and by the extremely broad external cingulum. This external cingulum is even broader than in *Aonyx,* and in the three Tornewton Cave specimens it is broader than in the specimens from Saalfeld, Weimar-Ehringsdorf and from The Netherlands. In the lingual edge of the talonid, two wear facets can be seen.

There is also a left mandibular fragment with M_1 and M_2 (BM M 34372). In this case too, the ramus is higher than the length of the carnassial. The M_1 is not very worn. The overall structure is the same as in M 34371. The paracone and the metacone are subequal in height, though the former is somewhat higher. Also in this specimen, the hypocone is large and the external cingulum of the talonid is very broad. The lingual edge of the talonid is crenelated. The M_2 is approximately circular. It is large and the cuspids are more pronounced than in *Lutra.* Between the two main cuspids, there is a concave ridge running transversely.

The third M_1, an isolated left one (BM M 50708), shows the same morphology as the carnassial in M 34371.

The atlas (BM M 34378): The transverse processes are broken off. The anteroposterior length of the neural arch is less than in a *L. lutra* specimen used for comparison. The anteroposterior width of the cotylar processes (anterior to the foramen obliquus) is less than in *Lutra.* The tubercle on the anterior edge of the neural arch is more developed than in my *L. lutra* specimen and the cervicospinal canal is narrower.

The epistrophaeus (BM M 34379): A large part of the spine is broken off. The anterior tip of the spine, where the m. rectus posticus minor is attached, is somewhat higher than in my *L. lutra* specimen. The odontoid process is larger. The spine and the transverse processes of another cervical vertebra (BM M 34370) are broken off. It resembles the sixth cervical vertebra in *L. lutra.*

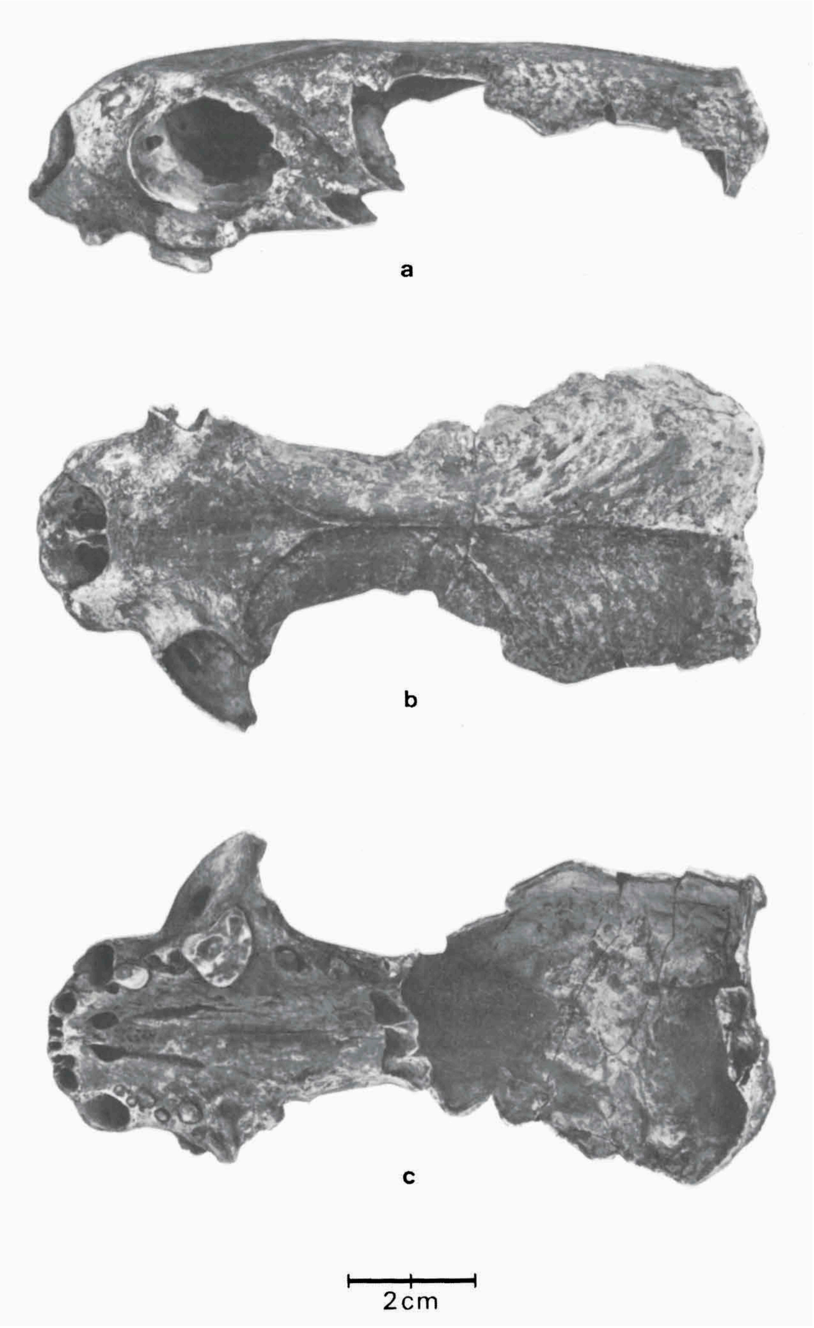
The sacrum (BM M 34384) consists of three fused vertebrae. It is shorter and broader than in *L. lutra.* One caudal vertebra (BM M 34381) is preserved, which resembles the fourth caudal vertebra in *L. lutra.*

The proximal part of a right humerus (BM M 34382) is also preserved. The size and the curvature of the shaft resemble *L. lutra.* The attachment area for the m. subscapularis is somewhat shorter than in *L. lutra.* The attachment areas for the m. deltoideus and the m. pectoralis are considerably smaller than in *L. lutra.*

Of the right tibia, only the diaphysis is preserved (BM M 34386).

Plate 3

Cyrnaonyx antiqua (de Blainville, 1841). Skull from Tornewton Cave, BM M 34370; a: lateral view; b: dorsal view. c. ventral view.


a
b
c
2cm

Systematic remarks — The holotype was described as *Mustela lutra* by de Serres et al. (1839). They acknowledged differences with the extant common otter, but they did not refer the fossil to a new species. According to de Blainville (1841), de Serres has separated the Lunel-Viel otter from *Lutra lutra* as *L. antiqua*. However, Helbing (1935, p. 571) was not able to trace this in any of de Serres publications, 'trotz eifrichem suchen'. Therefore, de Blainville is considered to be the author of the species. Harlé (1910) included the specimen in *Lutra canadensis*, but Helbing made clear that the species has affinities to the aonychoid group.

Pasa (1947) described some Pleistocene material from Verona: a canine, a maxilla fragment and a left P^4. Pasa (op. cit.) quoted Stehlin, who pointed out in a letter to Pasa: 'La prémolaire supérieure n'est pas suffisament pareille à celle de *Cyrnaonyx antiqua* pour lui être attribuée avec assurance.' However, Stehlin of course compared the specimen to the P^4 from Grotta del Margine, wrongly included in *C. antiqua* by Helbing (1935) and now referred to *Algarolutra majori*. The real P^4 of *C. antiqua* was not known at that time. As far as can be judged from the description and the illustration in Pasa (1947), there is a great resemblance to the specimens from Tornewton Cave and the upper carnassial can probably be referred to *C. antiqua*.

Stratigraphic remarks — The cave fauna from the type locality has been described by many authors. Bonifay & Bonifay (1965) considered the faunas from Lunel-Viel to date from the late Mindel-Riss or from the earliest Riss, but they added that the impression they got from the faunas did correspond most to the interglacial. A Mindel-Riss (= Holsteinian) age is also stated by many later authors (e.g. Kurtén, 1968; Guérin, 1980).

The Saalfeld specimen belongs to a collection of fossils which was collected at the end of the 19th century. The fossils were collected partly in fissure fillings and partly in the beds, covering those fillings (Heinrich, pers. comm.). The fauna, listed by Mania & Toepfer (1973), probably is a mixed fauna, containing both Eemian and Weichselian elements (Dietrich, 1968), though these authors stated, that a Brörup Interstadial age is not impossible. Heinrich (pers. comm.) found, that *Arvicola terrestris* from Roter Berg is of a type which is characteristic for the Early Weichselian in Central Europe, but since the Roter Berg 'fauna' is a mixed assemblage, it is unclear to which extend this can be taken as indicative for the age of the *C. antiqua* specimen. The age of the otter fossil cannot be determined more exactly than Eemian or Early Weichselian.

The age of the Lower Travertine of Weimar-Ehringsdorf, in which the lower

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Plate 4

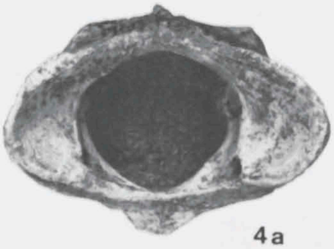
Cyrnaonyx antiqua (de Blainville, 1841)
1. Part of right humerus from Tornewton Cave, BM M 34382; a: lateral view; b: anterior view.
2. Fragment of right tibia from Tornewton Cave, BM M 34386.
3. Epistrophaeus from Tornewton Cave, BM M 34379; a: lateral view; b: dorsal view.
4. Atlas from Tornewton Cave, BM M 34378; a: anterior view; b: dorsal view.
5. Cervical vertebra from Tornewton Cave, BM 34380; dorsal view.
6. Caudal vertebra from Tornewton Cave, BM M 34381; dorsal view.

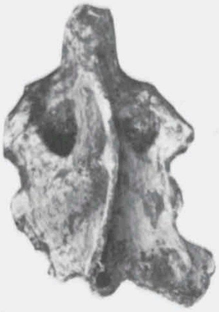

1a


1b


2


3a


4a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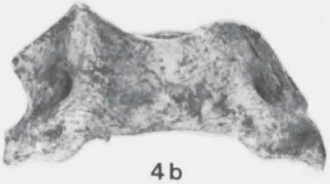
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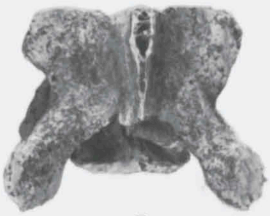
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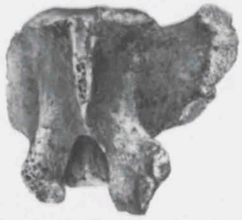
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carnassial described by Heinrich & Fejfar (1988) was found, is not clear either. All estimates fall within the Saalian/Eemian (Heinrich & Fejfar, 1988). Heinrich (pers. comm.) is of the opinion, that the fauna should be placed in a warm period within the Saalian, rather than in the Eemian. Fejfar & Heinrich (1983) gave a radiometrical date of 262 000 years BP for this site, which would be in accordance with an Early Saalian interstadial.

Excavations in Tornewton Cave have been carried out since more than a century (see Walker & Sutcliffe, 1968). Tornewton Cave has a complex stratigraphy, described by Sutcliffe & Zeuner (1962) and by Sutcliffe & Kowalski (1976). All material of *C. antiqua* was found in the so-called Otter Stratum, except for one P^4 (BM M 34374), which was found in the Glutton Stratum. The Glutton stratum contains a clearly glacial fauna. It is the oldest fossiliferous deposit in the Main Chamber of the cave, older than the Reindeer Stratum (Devensian), the Hyaena Stratum (tentatively referred to the Ipswichian by Sutcliffe & Kowalski, 1976), and the Bear Stratum. From the Glutton Stratum an *Arvicola* is known, which is intermediate between *A. cantiana* and *A. terrestris* (Sutcliffe & Kowalski, 1976). This points to a Wolstonian age. The Otter Stratum cannot be linked directly to the main sequence of the cave stratigraphy, since it is not found in the Main Chamber but in a small chamber, called Vivians Vault. The deposits show similarities to the deposits of the Glutton Stratum (Sutcliffe, pers. comm.). According to Sutcliffe & Kowalski (1976), the Otter Stratum consists of a mixture of broken stalagmite blocks in an earthy matrix. The rodent fauna is a mixture of two originally separate layers, with remains from a warm period, probably the Ipswichian, dominating. Remains of *Ursus arctos* are abundant, suggesting, that bears used the cave as a lair. Therefore, the Otter Stratum probably is older than the Hyaena Stratum (in the main sequence the Bear Stratum, a deposit with abundant bear fossils, is underlying the Hyaena Stratum, on top of the Glutton Stratum). Further, Sutcliffe & Kowalski (1976) mentioned that *Arvicola* from the Otter Stratum is also intermediate between *A. cantiana* and *A. terrestris*, but slightly more advanced than the form from the Glutton Stratum. Concluding, the Otter Stratum is probably somewhat younger than the Glutton Stratum but also of Wolstonian age. In terms of continental stratigraphy, the otter fossils are of Saalian age.

The Maasvlakte faunal assemblage is a mixed assemblage, containing fossils from three periods (Vervoort-Kerkhoff & van Kolfschoten, 1988). The fossils have been found in sands which have been dredged in the so-called Rijnmond area, and which have been used to create the Maasvlakte. Within the fossil assemblage a group of dark, heavi-

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Plate 5

Cyrnaonyx antiqua (de Blainville, 1841)
1. Upper canine from Tornewton Cave, BM M 34375.
2. P^4 from Tornewton Cave, BM M 34373; a: buccal view; b: occlusal view.
3. P^4 from Tornewton Cave, BM M 34374; a: buccal view; b: occlusal view.
4. Skull fragment with right bulla from Tornewton Cave, BM M 34376.

Limnonyx sinerizi Crusafont Pairò, 1950
5. Part of right mandible from Can Ponsich, IPS 2058; a: occlusal view; b: lateral view.

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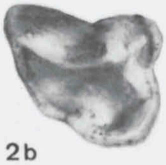
2a



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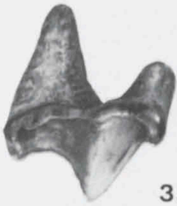

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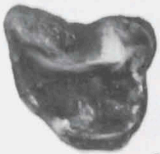

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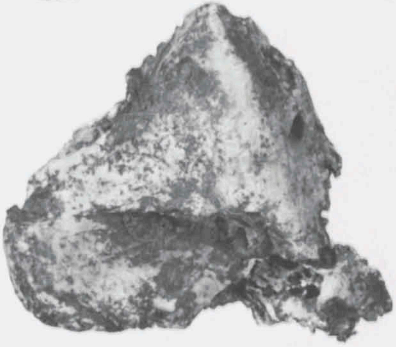

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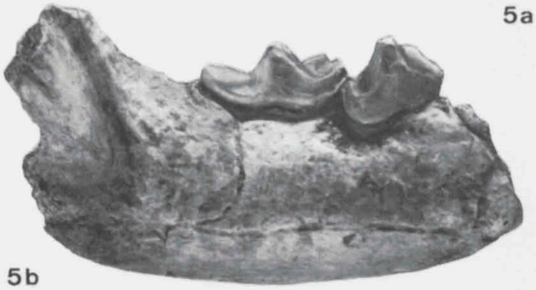

5b

1cm

ly mineralized specimens and two groups of less mineralized specimens can be recognized. One of the two latter groups consists of Holocene species from a temperate climate (fauna III in Vervoort-Kerkhoff & van Kolfschoten, 1988). The other consists of species which indicate glacial conditions and can be referred to the Weichselian (fauna II). The fossils in this group are slightly more mineralized than the fossils in the Holocene group. The group of heavily mineralized fossils contains several Early Pleistocene species, such as *Trogontherium cuvieri*, *Ursus* aff. *deningeri*, *Cervalces latifrons*, *Dicerorhinus etruscus brachycephalus*, and *Sus scrofa mosbachensis* (fauna I). On the basis of the faunal assemblage and of the geology of the Rijnmond area, this group is referred to the Bavelian (van Kolfschoten, pers. comm.). The *C. antiqua* specimen from the Maasvlakte is a rather well mineralized specimen. It is clearly much more mineralized than the *Lutra lutra* mandibles from the same site, which are referred to the Holocene group. Van Kolfschoten therefore places it in the Bavelian fauna (pers. comm.). All remains of the species from other sites, however, can be referred to an interval which includes the Late Holsteinian to the Eemian or the Early Weichselian. Thus, a Weichselian age for the Maasvlakte specimen would fit very well from this point of view. If one assumes a Bavelian age for the Maasvlakte specimen, it would be at least 400 000 years older than the oldest of the other specimens. The degree of mineralization indeed seems to support this view. In view of the usual uncertainties with dredged assemblages and the above mentioned disagreement with the age of the other *C. antiqua* specimens, a Bavelian age of the Maasvlakte specimen remains uncertain.

Genus *Megalenhydris* Willemsen & Malatesta, 1987

Type species — *Megalenhydris barbaricina* Willemsen & Malatesta, 1987.

Original diagnosis — 'Lutrine, much larger than *Lutra* and even larger than *Pteronura*. The dentition is very robust, aonychoid. The talon of P^4 is more expanded than in *L. lutra* L., 1758, and is more like the talon in *Amblonyx cinerea* Illiger, 1815. The talonid of M_1 is large and broad. The mandible is very robust, its height being greater than the length of the M_1. At least the first five caudal vertebrae are flattened dorsoventrally.' (Willemsen & Malatesta, 1987, p. 85)

Stratigraphic occurrence — Unknown.

Geographic distribution — Sardinia.

Systematic remarks — The type species is the only species known.

Megalenhydris barbaricina Willemsen & Malatesta,1987

Holotype — Partly preserved skeleton, including a left mandible with dentition, P^4 and M^1, a humerus and part of the axial skeleton, stored in the Museo Civico di Archeologia e Speleologia, Nuoro, Sardinia.

Type locality — Ispiginoli, near Dorgali, Sardinia.

Other localities — None.

Stratigraphic occurrence — Unknown.

Geographic distribution — Sardinia.

Measurements — See Table 6.

Original diagnosis — As for the genus.

Material — The holotype is the only specimen known.

Description — A detailed description will not be given here, since the holotype was described in detail recently (Willemsen & Malatesta, 1987). I will, however, mention some main characters and make some additional observations. The dentition is robust. P^4 has a large talon, almost covering the entire lingual side of the trigonid (Table 6). P^4 is relatively broader than in *Lutrogale* or *Pteronura* and comparable in its dimensions to *Aonyx capensis*. M^1 has a relatively larger talon than *Lutra*. The lower premolars are rather broad, P_4 is much larger than P_2 and P_3. Willemsen & Malatesta (1987) stated that the talonid of the lower carnassial is broader than in *L. lutra*. In fact, this is not true. The M_1 looks very robust and the lingual expansion of the talonid, which is more pronounced than in *Lutra*, is rather striking (see Willemsen & Malatesta, 1987, pl. 1). The talonid width, however, is only 9.1 mm; the trigonid width 9.2 mm (Willemsen & Malatesta, 1987 and Table 6), the index Wtal/Wtri = 0.99. In eight Recent *L. lutra* specimens it varied between 1.03 and 1.28, in subfossil specimens values as low as 1.00 were noted. The value of the index compares very well to *Sardolutra ichnusae* (1.00), the holotype M_1 from Dragonara Cave of *Algarolutra majori* (1.00) and to *Lutra simplicidens* (0.96-0.97; n = 3) The W/L index for the M_1 of *M. barbaricina* is 0.52, which falls within the range of *Lutra* (*L. lutra*: 0.44-0.54, mean 0.49, n = 95; in some other species the index is even larger) and in the lower part of the range of *Aonyx congica* (0.50-0.61, mean 0.56, n = 14). It is clear from those comparisons that nor M_1 as a whole, nor the talonid is relatively broader than in *Lutra*. The visual robustness of the tooth and the fact that the talonid indeed expands more lingually than in *L. lutra* can be misleading in this respect. The talonid does not have a very pronounced outer cingulum. The outer cingulum is not developed as strongly as in *Aonyx capensis* or in *Cyrnaonyx antiqua*. The outer edge of the talonid is formed by the hypoconid, no hypoconulid is present. The inner edge of the talonid is smooth. There is a marked cingulum around the paraconid.

The left humerus is robust. The attachment areas for the m. pectoralis and the m. deltoideus on the shaft and for the m. supraspinatus and the m. pectoralis on the trochanter major are larger than in *Lutra* (Willemsen & Malatesta, 1987). It can be added that the shaft is somewhat less curved than in *L. lutra*. The ectepicondylar ridge is more expanded than in *L. lutra*. The distal epiphysis is much narrower than in

Sardolutra in relation to the humerus length.

The first five caudal vertebrae, which can be studied with some difficulty, since they are embedded in the sediment and encrusted with calcite, are strongly flattened dorsoventrally, a character not seen in any other lutrine.

Systematic remarks — Willemsen & Malatesta (1987) stated that the dentition is aonychoid. Indeed, this is true in the sense that it is heavy and robust, the P^4 talon is large and the M_1 talonid shows a lingual expansion. As is clear from the description above, the overall structure of the M_1 is not *Aonyx*-like, however: the external cingulum is not developed as strongly as in *Aonyx* and related forms, the hypoconid is not a real cuspid but is ridge-like, forming the outer edge of the talonid, the inner edge shows no cuspids, no hypoconulid is present. The tooth seems lutroid, but the talonid has a lingual expansion which is uncommon in lutroid species.

The upper carnassial, however, is clearly aonychoid. Though a large talon is found in some Lutrini also (*Lutrogale, Pteronura*), P^4 is relatively much broader in *Megalenhydris* than in any Lutrini, having similar dimensions as *Cyrnaonyx antiqua*. The M^1 talonid is also large and reminiscent of aonychoid forms.

Taking all characters in account, I tentatively classify the species as belonging to the Aonychini.

Stratigraphic remarks — The holotype was found in the abyssal cave Ispiginoli, near the village of Dorgali. The skeleton was embedded in clay and covered with calcite. No other fossils were found in the cave. It is clear, that in such circumstances not much can be said about the stratigraphic position or the age of the specimen. Willemsen & Malatesta (1987) presumed a Late Pleistocene or Holocene age. This is quite possible, but a greater age cannot be excluded either.

Tribus Enhydrini Gray, 1865

Type genus — *Enhydra* Fleming, 1822.

Diagnosis — Large lutrine, with rather short skull. Teeth very large and robust, with low, blunt cusps. No shearing blades are present. P^4 with protocone and hypocone present as large, conical cusps. M_1 very broad, with large and broad talonid, hypoconid present as a blunt cuspid, entoconid large, blunt.

Genus *Enhydra* Fleming, 1822

Synonyms — *Mustela* L., 1758 (partim); *Lutra* (partim), in many early authors; *Pusa* Oken, 1816; *Latax* Gloger, 1827.

Type species — *Mustela lutris* L., 1758.

Original diagnosis — Fleming (1822).

Emended diagnosis — Large otter, with relatively short, dorsoventrally flattened tail. Head large, blunt; neck short, stout. Skull flattened, very broad, facial part short, muzzle short and broad. Dental formula: 3/2 1/1 3/1 1/2. Dentition very robust, teeth broad, cusps blunt. P^4 short and broad, with large talon, protocone absent, hypocone large. M^1 very broad, much expanded at the lingual side, with low cusps. M_1 very broad and with low, blunt cusps. Legs relatively short, femur short and stout, proximal digits of the hind feet shorter than the distal ones.

Stratigraphic occurrence — Quaternary and still extant.

Geographic distribution — Pleistocene: eastern North Pacific coast and United Kingdom. Recent: eastern and western North Pacific coast.

Systematic remarks — Repenning (1976) has shown that the inner cusp of P^4 probably represents the hypocone of the ancestors of the sea otter rather than the protocone. See also the chapter on phylogeny.

Enhydra reevei (Newton, 1890)

Synonyms — *Lutra reevei*, in Newton, 1890 and others; *Latax reevei*, in Pohle (1919); *Aonyx reevei*, in Kurtén (1968) and others; *Enhydriodon reevei*, in Repenning, 1976.

Holotype — Right M_1, stored in the Norwich Castle Museum, Norwich (UK), 548.

Type locality — Bramerton, East Anglia (UK).

Other localities — None.

Stratigraphic occurrence — Late Tiglian-Early Eburonian.

Geographic distribution — East Anglia coast (UK).

Measurements — See Table 10.

Original diagnosis — Newton (1890, p. 446) did not give a formal diagnosis but a description and an illustration of the holotype.

Proposed diagnosis — Otter, with very broad M_1, almost as in *E. lutris*; outline showing strong bilateral symmetry; cusps low and blunt; paraconid situated anterior to metaconid and protoconid on the longitudinal axis of the tooth, somewhat smaller than the other two cusps; protoconid and metaconid about equally large; talonid broad, almost quadrangular; hypocone large and blunt; talonid posterolingually surrounded by a strong, blunt crest; external cingulum of the talonid very broad.

Material — Right M_1 (holotype, NCM 548), right M_1 (SM X.17989), both from Bramerton.

Description — Unfortunately, the holotype, seems to be missing. During a study visit to the Norwich Castle Museum in 1984, only the empty box could be found. The curator at the time, Ms D.H. Smith, made a strong effort to find it, but without succes. Mr P. Lambley of the same museum told me, that he had gone into the matter earlier and that the fossil seemed to be missing for several years already. Later efforts to locate the fossil did not succeed either and in 1987 the present curator, Dr A.J. Stuart, informed me that it is still missing, but that there is some hope that it will turn up again during a reorganisation which will be undertaken in the near future. The Museum could, however, provide some very good photographs and in the British Museum (Natural History) in London there is a cast of the specimen (BM M 4118), on which I base my description.

The fossil consists of the crown only. It is completely unworn. According to Newton (1890), the fossil consists of the enamel cap, supported by a layer of dentine. The shape of the tooth is largely bilateral symmetrical. The sides are parallel. The cuspids of the trigonid are very low and blunt. The paraconid is somewhat smaller than the other two cuspids, which are about equally large. The talonid has an almost quadrangular shape. The hypoconid is present as a large, blunt cuspid, posterolingually merging into the strong, blunt entoconidal crest, which surrounds the talonid basin posteriorly and lingually. At the posterolingual side of the hypoconid a small hypoconulid, closely linked to the hypoconid, can be distinguished. Labially to the hypoconid there is a very broad cingulum.

There is some confusion about the dimensions of the tooth. According to Newton, the length is 20 mm, the width 10 and the height 4 mm. Pohle (1919) pointed out that the length of the figure in Newton (1890, pl. 18, fig. 2a), which is stated to be of natural size, is 16 mm, while the width indeed is 10 mm. The cast (BM 4118) has a length of 15.7 mm and a width of 10.3 mm (Table 10). Probably, the length of the original specimen indeed is only about 16 mm.

The second specimen, also a right M_1, was found by Mr P. Cambridge (Norwich) in Blake's Pit at Bramerton, and is now in the Sedgwick Museum in Cambridge (SM X.17989). The specimen is very worn by use. The crown is in fact completely worn away, only its basis is present. The talonid is slightly damaged. The tooth is two-rooted. The anterior root is rather short and broad.The posterior root is broken off. The tooth is very broad (Table 10, Fig. 18). The cuspids are worn away, but it can be seen that the paraconid was smaller than the protoconid and the metaconid. It is situated at the longitudinal axis of the tooth. The tooth shows the same degree of bilateral symmetry as the holotype, the sides being almost parallel. The talonid is short and very broad.

Systematic remarks — Newton (1890) described the species as *Lutra reevei*. He noted, however, similarities to *Lutra cinerea* (nowadays *Amblonyx cinerea*) and to *Lutra hessica* (Newton, 1891). Pohle (1919) included the species in the genus *Latax*, which is a junior synonym of *Enhydra*. He considered *E. reevei* to be intermediate between *L. hessica*, which he included in *Aonyx*, and *E. lutris*. Repenning (1976) rightly reject-

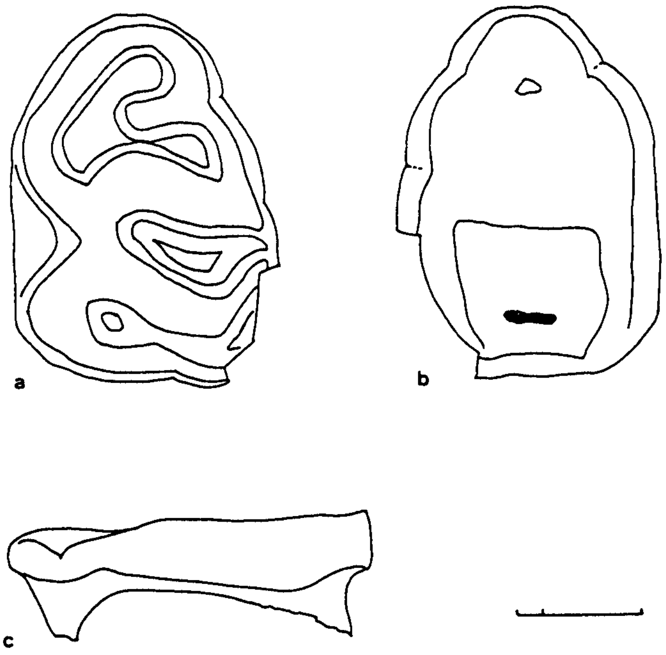

Fig. 18. Right M_1 of *Enhydra reevei* from Bramerton, SM X.17989, occlusal view (a), view from below (b), and buccal view (c); scale = 5 mm.

ed a relationship between *E. reevei* and *L. hessica*. The structure of the M_1 is quite different.

Kurtén (1968) included *E. reevei* in the genus *Aonyx*, without giving his reasons for this. His assignment was followed by many later authors (e.g. Stuart, 1974, 1982; Mayhew, 1979; Pennacchioni & Cassola, 1986). I do not follow this classification. The M_1 of *E. reevei* is much broader than those of *Aonyx* (see Fig. 19). In *Aonyx*, the paraconid is the largest cuspid and it is situated lingually with respect to the longitudinal axis of the tooth. The talonid is elongated and not short as in *E. reevei* and it is not nearly as broad as in *E. reevei*. The sides of the tooth are not parallel in *Aonyx* and it shows no bilateral symmetry. Further, the cuspids are much higher in *Aonyx*, even in *A. capensis*. In short, there are too many differences between *E. reevei* and *Aonyx* to include the species in that genus. Kurtén (1968) also suggested, that *Lutra bravardi* might be identical with *E. reevei*. In the section on *L. bravardi* I point out that this cannot be true.

Repenning (1976) suggested that *E. reevei* should be included in *Enhydriodon*. He pointed out, that the morphology of the M_1 is intermediate between *Enhydriodon lluecai* and *Enhydra lutris*. Since *E. reevei* cannot be considered to be ancestral to *E. lutris* (Mitchell, 1966), and North American *Enhydriodon* forms offer a more plausible origin for sea otters, Repenning (1976) considered *E. reevei* to have developed from European *Enhydriodon* independently and therefore he did not include it in the genus *Enhydra*.

Morphologically, the two specimens of *E. reevei* are quite different in compari-

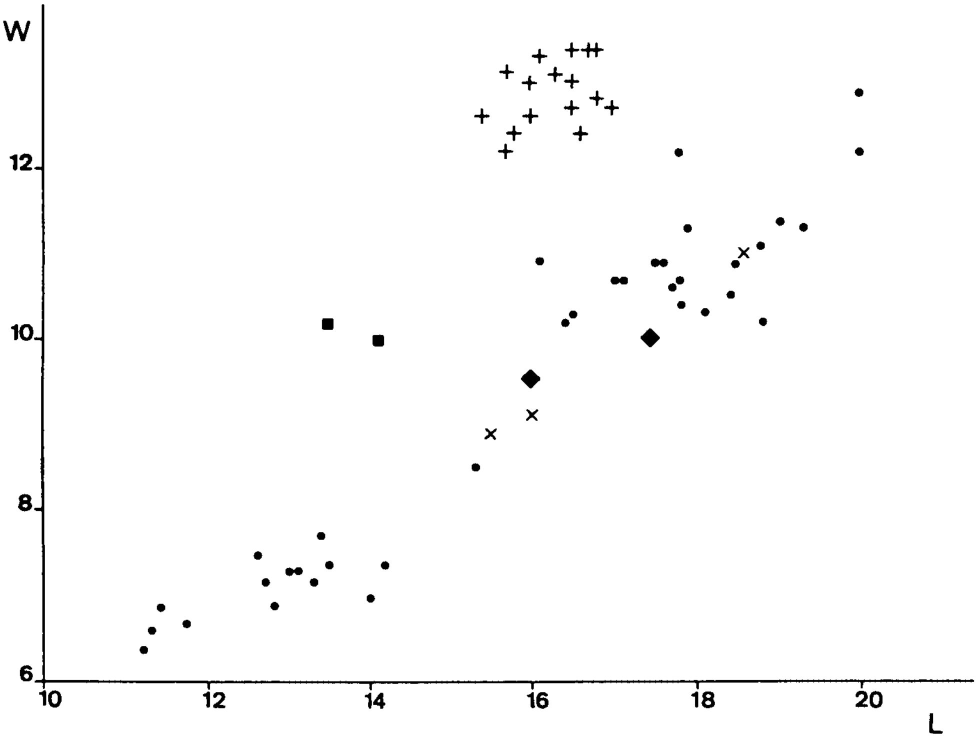

Fig. 19. Scatter diagram of M_1 length and width of *Enhydra reevei* (square), *E. lutris* (+), *Sivaonyx bathygnathus* (×), *Enhydriodon* spp. (triangle) and *Aonyx* spp. (dot). Measurements partly after Pohle (1919) and Pilgrim (1931).

son with *Enhydriodon*. The cuspids are lower and the tooth is much broader. Fig. 19 shows that the dimensions of the tooth are much more like *Enhydra lutris* than like *Enhydriodon* and related forms. The width of M_1, the short and broad talonid, the bilateral symmetry, the position and the small size of the paraconid are characters which are strongly reminiscent of *Enhydra lutris*. In *Enhydriodon lluecai* from Spain and in *E.* cf. *lluecai* from California the paraconid is situated lingually with respect to the longitudinal axis. In *Enhydra reevei* it is on this axis and in *E. lutris* it is even somewhat labially to this axis. The resemblances between *Lutra reevei* and *Enhydra lutris* are such, that *L. reevei* must be included in the genus *Enhydra*. Theoretically, an independent origin of *E. reevei* from the *Enhydriodon* stock as conceived by Repenning (1976) cannot be excluded, and in that case it would have to be placed in a separate and new genus, since there are too many differences with *Enhydriodon* to include it in that genus. I think, however, that the morphological resemblances between *E. reevei* and *E. lutris* are so striking, that a close relationship between both lineages is much more probable. This will be discussed in more detail in the chapter on phylogeny.

There are some differences between *E. lutris* and *E. reevei* also. The paraconid is not only situated somewhat more buccally in *E. lutris*, it is also relatively smaller. The metaconid is larger in the extant species, extending backward. The hypoconid and the entoconidal ridge are more developed and there is no real basin on the talonid as in *E. reevei*. In *E. lutris*, M_1 is larger and still broader than in *E. reevei*.

Stratigraphical remarks — Both specimens of *E. reevei* were found at Bramerton. Bramerton in fact consists of two localities, some 200 m apart, called Bramerton Common and Blake's Pit respectively. The stratigraphy of both pits was described by Funnell et al. (1979). In the lower part of Blake's Pit, the type Bramertonian was defined. The warm aspect of the fauna was confirmed at the re-excavation of this section (Cambridge, 1979). In the Bramertonian section, pollen samples, molluscs and foraminifera indicate a temperate climate. On top of the Bramertonian, a shell bed (the Upper Shell Bed, USB) is found, the samples from which indicate a cooler climate (Mayhew & Stuart, 1986). In the lower 4 m of the section an *Alnus-Quercus-Carpinus* Pollen Assemblage Zone was recognized, at 5 m (the level of the USB) a *Pinus*-Ericales-Gramineae Pollen Assemblage Zone, based on a single sample (Funnell et al., 1979). The mollusc fauna from the USB in Blake's Pit contains certain northern elements. The shells of *Nucella* have an elongate form, as those found in estuaries today (Cambridge, 1979). Pollen and molluscs thus also indicate that the USB was deposited in a cool phase.

According to Mayhew & Stuart (1986), the lower 3-4 m of the Common section are Bramertonian, with a cooler phase starting at 4.5 m. According to Cambridge (pers. comm.), however, the Bramertonian is not present in the Common Section. According to him, the whole Common section in fact is younger than the type Bramertonian and the Lower Shell Bed in both pits cannot be correlated. The cool phase after the Bramertonian cannot be correlated with the pre-Pastonian, as was pointed out by Mayhew & Stuart (1986).

The vertebrate fossils from Bramerton were listed by Mayhew (1979). Of the material in old collections, such as the *E. reevei* holotype, it is not known from which of the two sections they came. According to Mayhew & Stuart (1986), material labelled 'Lower Shell Bed', as is the case with our holotype, is almost certainly of Bramertonian age. If it came from Blake's Pit, this is clear, but if the material came from the Common Pit, this is only true if one assumes the lower part of this section to be Bramertonian. Otherwise, it would have to be placed in the subsequent cool phase. Thus, the *E. reevei* holotype has to be dated as Bramertonian or the subsequent cool phase.

The stratigraphic position of the second specimen is known much better. It was found by Mr P. Cambridge in the Upper Shell Bed in Blake's Pit, so it can be dated at the beginning of the cool phase following the Bramertonian.

The small mammals from The Lower Shell Bed in Blake's Pit (type Bramertonian) support a correlation with the late Villanyian and with the Tiglian-C (Mayhew, 1979). The USB in this pit, where the second specimen was found, can thus be correlated with a cool phase in the Late Tiglian or the onset of the Eburonian.

Functional morphology and ecology

Functional morphology and comparison with extant species can give important clues about the ecology of extinct species. The comparative functional morphology of some lutrines is discussed in detail in Savage (1957) and in Willemsen (1980). Otters show a number of clear adaptations to a semiaquatic way of life. Swimming puts some very specific demands on the anatomy. Otters can swim in different ways. When swimming slowly, *Lutra* propells itself by dog-paddling with all four legs. When swimming at high speed under water, the main propulsive power comes from a vertical undulating movement of the body, especially the hind part and the tail. The hind feet are held along the body, the soles facing dorsally, and thus enlarge the area used for propulsion. In *Pteronura brasiliensis* and *Enhydra lutris*, this area is even more enlarged by the remarkable flattening of the tail. In *Enhydra lutris*, the hind legs are not held rigidly along the body but give additional thrust by kicking upward at the end of each stroke (Chanin, 1985). This species is the only one using this method of swimming at the surface too (Chanin, op. cit.). At the surface, it also often propells itself lying on its back and moving its tail and its hind legs. This way of swimming is not known in other otters.

Adaptations in the fore limb

All extant otters are semiaquatic to some extent and the skeleton shows clear adaptations to such a way of life. Adaptations to an aquatic way of life are evident especially in the limb bones. The demands of swimming are very different from those of terrestrial locomotion. In the fore limb, the humerus usually shows clear adaptations in aquatic mammals. In pinnipeds and also in the highly aquatic extinct mustelid *Potamotherium* the humerus is short and stout and strongly curved. The strong curvature gives the bone strength to withstand the strains of strong flexing. Strong flexing is important in swimming, especially at lower speed, and is facilitated among other things by powerful pectoralis and deltoideus muscles.

A humerus which is more curved than in *L. lutra* is found in *Lutra simplicidens*, *Sardolutra ichnusae* and *Lutra trinacriae*. These species also show much expanded attachment areas for the pectoralis and the deltoideus muscles on the shaft and the morphology of the humerus suggests a higher degree of aquaticy than in *L. lutra*. *Cyrnaonyx antiqua* has smaller attachment areas for the pectoralis and the deltoideus muscles than *L. lutra* and a slightly less curved humerus, which suggests a lower degree of aquaticy. *L. euxena* also has a less curved humerus, but the specimen is difficult to interpret, since it is of a young animal. The humerus of *Megalenhydris* is less curved too, but has relatively somewhat larger areas for the pectoralis and the deltoideus. This seems contradictory, but the species is much larger than the other species and we must remember that larger animals, all other things being equal, must have more powerful muscles. So in this case the somewhat larger muscles do not necessarily point to a more aquatic way of life.

In swimming, a powerful rather than a fast adduction of the humerus is important. This is influenced by the place where the m. teres major is attached on the shaft. The in- and out-lever of the force executed by this muscle (I_i and I_o respectively) are determined by this place. When the attachment area is situated more distally, the ratio I_o/I_i becomes smaller and the movement is more powerful but slower (Hildebrand, 1974; Willemsen, 1980). In cursorial mammals this ratio is large and in diggers and swimmers it is small (Hildebrand, 1974). In Table 19, the ratio is given for some lutrines and for the terrestrial *Martes martes*. It is clear, that in all otters the ratio is smaller than in the marten. It is also clear from the table that *Lutrogale* and *Amblonyx* are less adapted to swimming than *L. lutra* when we look at the teres major, while the adaptation is stronger in *Sardolutra ichnusae*.

Some otters, notably *Sardolutra ichnusae* and *Lutra trinacriae*, show a large ectepicondylar supinator wing, compared to *L. lutra*. The supinator wing carries the anconeus muscle on the posterior surface and the extensor muscles of the lower arm on its border. Strong lateral development of this wing, combined with well developed grooves for the extensor muscles on the radius, as is seen also in these two species and also in *Lutra euxena* and in *L. simplicidens* (the condition of the supinator wing is not known in the latter) suggests strong extensors of the hand. A combination of strong fore-arm flexion and strong lower arm extension is characteristic for a type of limb movement, important in both digging and dog-paddle swimming. This combination is found in *S. ichnusae*, *L. trinacriae* and *L. simplicidens*, as far as the relevant bones are known, and also in *Potamotherium*. The ectepicondylar wing is not expanded so much laterally in *L. euxena* (though the lateral expansion of the distal part of the humerus as a whole is more than in *L. lutra*) and the flexor muscle attachment areas (pectoralis and deltoideus) on the shaft are much smaller. However, again we have an immature specimen only. A fossorial adaptation in this species, as suggested by Bate (1935) is not evident. The demands of dog-paddling and burrowing on the fore limb are in many respects the same. The only character in the fore limb indicating a digging adaptation exclusively is the presence of a strong metacromion and acromion on the scapula (Malatesta, 1977). In *L. ichnusae* and *L. trinacriae* these structures are not particularly strong developed. The adaptations, as seen in the above-mentioned species, have clearly to be interpreted as aquatic adaptations, though otters of course burrow holes too. The demands of swimming probably formed the main selective force leading to the mentioned adaptations.

Symeonides & Sondaar (1975) suggest that *Lutra euxena* shows a more terrestrial adaptation, resembling *Lutrogale cretensis*. The available material, however, shows a somewhat stronger aquatic adaptation in *L. euxena* than in *L. lutra*, and there are no resemblances to *Lutrogale*.

The most aquatic extant otter, *Enhydra lutris*, does not show the above-mentioned lateral expansion of the ectepicondylar wing. Apparently, this cannot be considered a general characteristic for all aquatic species but only one of several possible solutions to the demands of aquatic life.

Adaptations in the hind limb

The hind limb shows more clear adaptations to an aquatic way of life. Aquatic carnivores move their legs backwards and upwards, the soles facing upwards. This is facilitated by a shortening of the femur and by a reduction of the sacropelvic angle. When the sacropelvic angle, i.e. the angle between the ventral surface of the sacral centra and the line from the anterior tip of the pubic symphysis through the centre of the sacral facet on the ilium, is reduced, the acetabulum is brought upwards, towards the level of the sacrum. In *Lutrogale* and in *Amblonyx*, this angle is larger than in *L. lutra*, which is a more terrestrial adaptation compared to *Lutra*. In *Sardolutra ichnusae* the sacropelvic angle is smaller than in *L. lutra* and in some other aquatic carnivores, such as *Potamotherium* and the pinnipeds, it is still smaller (see Table 20).

In aquatic mammals, the ilium tends to be short and the ischiopubis long. In terrestrial carnivores, the situation is the reverse. The function of these morphological differences is explained in detail in Willemsen (1980). To the ischiopubis, the adductors of the femur and the flexors of the tibia (mm. gracilis, adductor, semitendinosus, semimembranosus and biceps femoris) are attached. An extensive ischiopubis gives attachment to large adductors and flexors. A much expanded ischium indicates a strong development of those muscles. The powerful backward swing of the leg, which is very important in swimming, is largely accomplished by this muscle complex. Also, when the ischium is elevated, the distance between origin and insertion of the muscles is enlarged, causing a greater rotation angle resulting from the same relative contraction.

To the ilium, another set of adductors of the femur, viz. the mm. glutei, is attached. The moment arm of the glutei is much shorter than that of the ischiopubic muscle complex, indicating an adaptation to speed rather than power, which is particularly important in terrestrial locomotion. The glutei are the 'high gear' muscles. Species, in which terrestrial locomotion is important, tend to have well developed glutei.

The relative development of the ilium and the ischiopubis is expressed in the ratio of ilium length to ischiopubis length. I investigated this ratio for a number of extant aquatic and semiaquatic mammals (see Table 21). In phocids, the ratio is smallest, in otariids, which are able to walk on land better than phocids, it is somewhat larger. In *Potamotherium*, the ratio is still larger, but smaller than in lutrines. Within the lutrines, there is some variation. Some lutrines have a ratio which is not much larger than in *Potamotherium*, in other species it is almost as large as in the terrestrial *Martes*. *L. lutra*, *Enhydra lutris* and *Lutrogale perspicillata* have a ratio between 1.00 and 1.25. In *Amblonyx* the ratio is rather large (c. 1.25) and in *Aonyx* it is largest of all extant lutrines. *Lutrogale cretensis* has a ratio of 1.34, which compares very well to 1.35 in an *Aonyx* specimen and which points to a more terrestrial way of life than extant *Lutrogale perspicillata*. In *Sardolutra ichnusae* it is 1.06, which is comparable to *Enhydra* and to the lower part of the range of *L. lutra*. In *S. ichnusae*, the ischium is much expanded, indicating a strong development of the ischiopubic muscle complex. This condition suggests very good swimming abilities. For *L. trinacriae* a more expanded ilium than for *L. lutra* is mentioned by Burgio & Fiore (1988). It is not clear what they mean exactly by this, but as far as can be judged from their figure, the relative length of the ilium is about the same as in *S. ichnusae*.

As we saw above, the back-swing of the leg needed in swimming is facilitated by a shortening of the femur. In aquatic carnivores, the femur is short and stout and the foot is large. In the most aquatic extant otter, *Enhydra lutris*, the femur is much shorter than in *Lutra*. A similar development is seen in *Potamotherium* (Savage, 1957). Both *Lutra simplicidens*, *L. trinacriae* and *Sardolutra* have a short and stout femur, compared to *L. lutra*. In *S. ichnusae*, the relative size of the femur is comparable to *Potamotherium* (Malatesta, 1977). In *L. trinacriae* the femur is intermediate in this respect between *L. lutra* and *S. ichnusae* (Burgio & Fiore, 1988).

In aquatic carnivores, the femur tends to have a broad distal condylar part and it tends to be flattened anteroposteriorly. This is very clear in *Phoca*, much less in *Lutra*, and *Potamotherium* is intermediate. In comparison with *L. lutra*, both *L. simplicidens*, *L. trinacriae* and *Sardolutra* have a broad condylar region. In *L. trinacriae* it is even somewhat broader than in *S. ichnusae*, according to Burgio & Fiore (1988). A wide distal part of the femur is of course reflected in a wide proximal condylar part of the tibia, as is indeed found in *S. ichnusae*. *L. euxena* also has a broad proximal articular part in the tibia, which suggests a similar adaptation in the femur. A short, stout femur with broad distal condyles is also found in *Paralutra jaegeri* (Viret, 1951; Malatesta, 1977), which suggests a highly aquatic way of life for this species too.

In some species (*S. ichnusae*, *L. simplicidens* and *L. trinacriae*) the trochanter minor extends more medially than in *L. lutra*. To this trochanter, the iliopsoas muscle, which originates at the ventral border of the ilium, inserts. There might be a correlation between the more inward position of the trochanter minor and a more horizontal position of the femur in swimming, but then it is strange that *Enhydra* does not show this adaptation (Malatesta, 1977).

In *S. ichnusae*, tibia and fibula are fused. Malatesta (1977) suggested that this too is an adaptation to aquatic life. Two highly aquatic carnivores, *Otaria* and *Phoca*, show a proximal fusion of these two bones. Probably this construction gives the leg more rigidity, important in powerful flexions of the lower leg. This character is unique among lutrines, as far as the relevant bones are known. Of *L. trinacriae*, it is known that the bones are not fused proximally (Burgio & Fiore, 1988). The condition of the distal part is unknown.

Aquatic mammals show shortening of the proximal bones of the hind leg, together with an enlargement of the foot bones. A large, webbed foot gives more propulsive power. Pinnipeds have a very large foot. In *Enhydra* the foot is much larger than in other lutrines. *Sardolutra* is intermediate between *Enhydra* and *Lutra*. *Lutrogale* also has a larger foot than *Lutra*, but the proximal bones of the leg are not shortened.

The tail

A unique character of *Megalenhydris barbaricina* are its flattened caudal vertebrae. A flattening of the tail is found in *Enhydra lutris*, *Pteronura brasiliensis* and to some extend in *Lutrogale perspicillata*. *Enhydra* and *Lutrogale*, however, do not have flattened vertebrae; the caudal vertebrae of *Pteronura* were not available for study. It is clear, that *Megalenhydris* had a flattened tail. A flattening of the tail enlarges the area used for propulsion in fast swimming by vertically undulating the body. Large feet further enlarge this area. The clear flattening of the tail in *Megalenhydris* indicates that it was a very good swimmer.

The baculum

The baculum of *Sardolutra ichnusae* is very large. Large baculums are found in monogamous pinnipeds which mate in sea, and in *Enhydra*. *Enhydra* also mates in sea (many other otter species often mate in the water, but in that case not in the open sea). It appears that marine carnivores who always mate in the open sea have large baculums, facilitating copulation in this environment. The baculum of *S. ichnusae* is relatively much larger than that of *E. lutris*, which has the largest baculum of all extant lutrines (see Fig. 10). This character supports the conclusion of Malatesta (1977) that *S. ichnusae* had a marine way of life. It probably mated in the sea also.

Conclusions on the functional morphology of the locomotory system

Concludingly, it can be said that *Lutra simplicidens*, *L. trinacriae*, *L. euxena* and *Sardolutra ichnusae* show stronger aquatic adaptations than *L. lutra*. This is evident from the structure of the limb bones, as shown above. *S. ichnusae* probably was marine, in how far this is true for *L. trinacriae* or *L. euxena* is not clear, though the strong aquatic adaptations of *L. trinacriae* would fit very well with a similar way of life. *L. euxena* remains a problem because of the incompleteness of the material.

Megalenhydris probably was a rather aquatic lutrine; the flattened tail indicates that it was a very good swimmer.

Lutrogale cretensis shows more terrestrial adaptations than both *Lutra lutra* and *Lutrogale perspicillata*, though not to the extent seen in *Aonyx*. *L. perspicillata* combines a number of adaptations to terrestrial locomotion (e.g. the position of the teres major and the sacropelvic angle) with clear aquatic adaptations (e.g. the ratio of ilium and ischiopubis length, the large feet and the somewhat flattened tail, facilitating fast underwater swimming).

The evidence for *Cyrnaonyx antiqua* is somewhat contradictory: the skull shows clear adaptations to aquatic life (see next section), resembling those found in *Lutra*, but the humerus does not show any evidence for the strong pectoralis and deltoideus muscles. Since the fore limb after all only plays a minor role in swimming, the skull characters are conclusive in this case and *Cyrnaonyx* probably was a stream dweller like *Lutra*.

Skull form

Lutra lutra is, among other things, characterized by its rather flat skull, with its eyes set rather dorsally. A similar condition is found in a number of other *Lutra* species. *Sardolutra ichnusae*, *L. trinacriae* and even more strongly in *Cyrnaonyx antiqua*, also show dorsoventral flattening and dorsally set eyes. The same is found in the extinct mustelid *Potamotherium*. Some other lutrines have high arched and narrow skulls with laterally set eyes. This is found in e.g. *Amblonyx*, *Aonyx*, *Lutrogale* and to a lesser degree in *Pteronura* and in *Lutra maculicollis*. Also *Enhydriodon sivalensis* has a high and narrow skull. Dorsoventral flattening of the skull is found in many unrelated aquatic mammals and can be regarded as an adaptation to an aquatic way of life. On the other hand, the opinion that a high arched and narrow skull indicates a less aquatic way of life is not tenable. Van Zyll de Jong (1972, p. 62) pointed out that dorsoventral flattening of the skull is not a general rule among aquatic mammals. For example, many pinnipeds do not have flattened skulls. According to van Zyll de Jong (op. cit.), the adaptive significance of the two skull types is not clear, but he mentioned that dorsoventral flattening is only found in species which live in streaming water and feed on fast moving prey. This seems to be true at least for the extant otter species.

Dorsoventral flattening of the skull enlarges the overlap between the two orbital planes (the angle of forward vision; see Savage, 1957 and Willemsen, 1980) and thus enlarges the field of binocular vision (which is directed upward). Probably, this is most important for stream-dwelling and fish-eating otters which often approach their prey from beneath. *Lutra lutra*, when chasing its prey, mostly approaches the prey from beneath (Erlinge, 1968). This obviously gives the otter the best view of the fish and probably reduces the chance for the otter of being seen by the fish. Otters, which feed on prey which is not very motile, such as *Aonyx* and *Amblonyx*, clearly do not need a large and upwards directed field of binocular vision. They search for prey on the bottom of streams and waters. In these species the tactile senses in the hand are important in foraging. This can be seen from the cranial endocast (Radinsky, 1968; Willemsen, 1980). Radinsky (1968) studied endocranial casts of several otter species. In *Amblonyx*, *Aonyx* and *Enhydra* the primary somatic sensory area for the fore limb is more developed than in *Lutra*, which is related to the importance of the hand in searching for shellfish. Also in *Lutrogale*, this area is larger than in *Lutra*. In *Lutra* and *Pteronura*, the primary somatic sensory area for the head is larger than in the other forms, which can be explained by the highly sensitive vibrissae, which are important in detecting moving prey in the water (Fig. 20). Indeed, *L. lutra* is known to depend on its eyes and, especially in deeper or in turbid water, where the sight is bad, on its vibrissae. This was shown experimentally by Green (1977). He removed the vibrissae of otters. The hunting success in clear water was hardly affected, but in darkened water the hunting success was considerably less. About *Aonyx capensis*, Mason & Macdonald (1986, p. 181) stated: 'Its long vibrissae may help it to find prey in murkey water.' This may play some role indeed, but the vibrissae are less important than in *Lutra* and the tactile sense of the hand is much more important, as is shown by the size of the respective primary somatic sensory areas found by Radinsky (1968).

Pteronura brasiliensis, which is known to be a fish-feeder mainly, though crabs are also frequently taken (Duplaix, 1980; Mason & Macdonald, 1986), does not have a flattened skull and dorsally set eyes. A problem is posed by *Cyrnaonyx antiqua*. This species has a remarkably flattened skull and a large overlap between the orbital planes. Its dentition, however, clearly shows strong adaptations to shellfish rather than fish, as we will see below. A similar combination of characters (flat skull and robust dentition) is found in *Lutra provocax*, which indeed is known to feed on crustaceans almost exclusively (Mason & Macdonald, 1986). This species, however, probably evolved rather recently from other *Lutra* species in the New World which fed on motile prey to a large extent (presumably from *L. longicaudis* or its ancestor). Similarly, we may assume that *C. antiqua* also descended from a species feeding on fast-moving prey. There is, however, no evidence for this.

We may conclude that dorsally set eyes and a large overlap of the orbital planes (both facilitated by dorsoventral flattening of the skull) probably evolved as an adaptation to catching motile, swimming prey, but this adaptation is not present in all species feeding on such prey and some species with this adaptation are secondarily specialised on less motile prey.

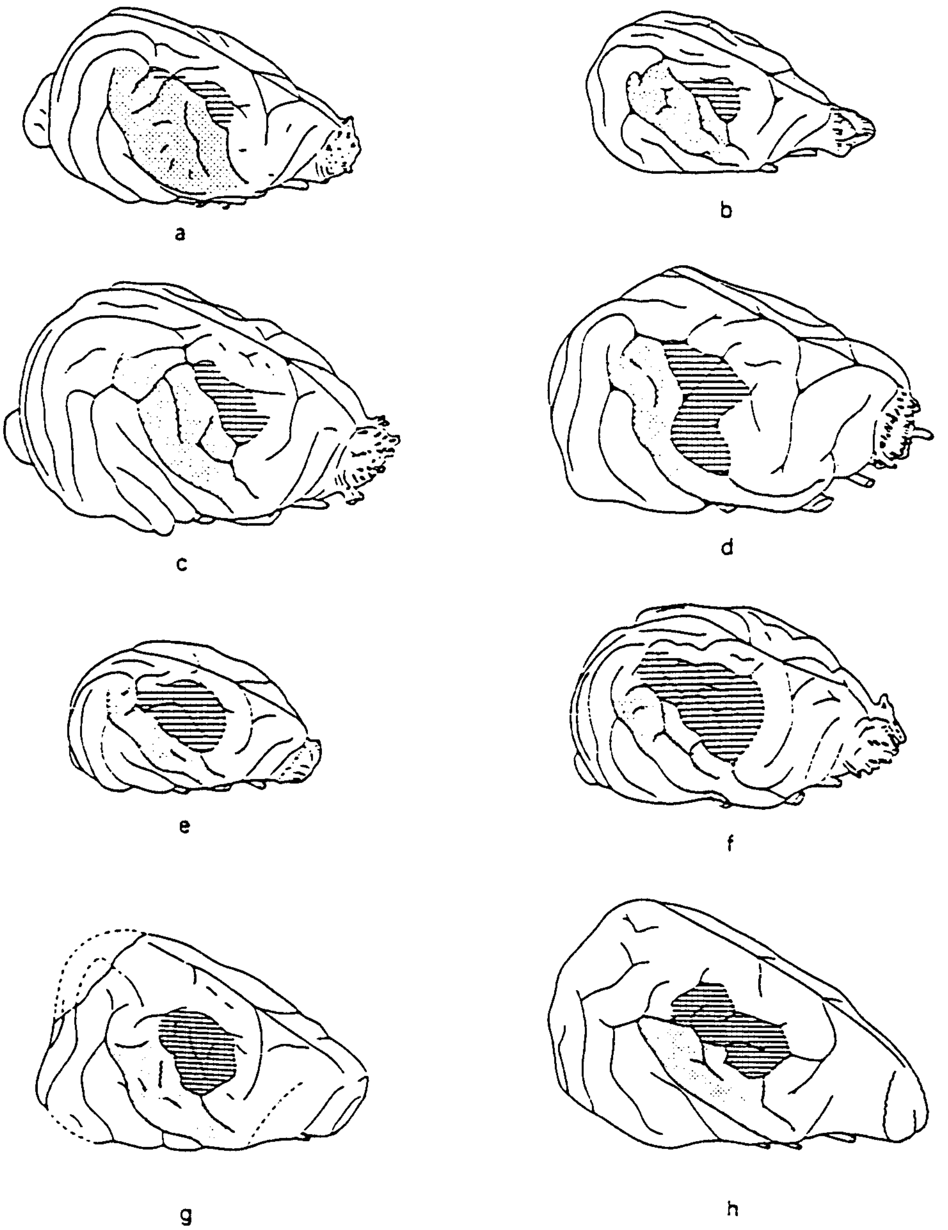

Fig. 20. Endocranial casts of some lutrines, partly after Radinsky (1968). The primary somatic sensory area of the head (stippled) and of the fore limb (striped) are indicated; a = *Lutra canadensis*; b = *Lutra lutra*; c = *Pteronura brasiliensis*; d = *Enhydra lutris* e = *Amblonyx cinerea*; f = *Aonyx capensis* g = *Lutrogale cretensis*; h = *Lutrogale perspicillata*. Not to scale. From Willemsen (1980).

Dentition types and feeding habits in extant lutrines

The main adaptations to feeding habits that can be studied in fossils, are found in the dentition. Of course, an interpretation of the adaptations in fossils is largely based on actualistic principles. Therefore, it was necessary to study the dentition of many extant otter species. The two extreme types are fish specialists and invertebrate (largely shellfish) specialists. *L. lutra* is a typical fish-eater. Fish comprises about 80-95% of its diet; the other 5-20% consists of crustaceans, birds, mammals and amphibians (Chanin, 1985; Erlinge, 1968, 1971; Erlinge & Jensen, 1981; Harris, 1968; Mason & Macdonald, 1986). However, we must keep in mind that otters are very opportunistic in their feeding habits: the diet can be influenced to a high degree by the local circumstances. This is shown by many studies of the diet of *L. lutra* in different areas and different habitats. In most cases, frequencies of different kinds of prey were determined by spraint analysis. In some cases, fish comprises a much lower percentage of the diet. In one study in Portugal, the fish frequency was 44.9% and amphibians counted up to 31.3%, in a Greek study amphibians made up 20.9% (Mason & Macdonald, 1986). In other less extreme cases invertebrates counted up to 20% or birds to 10% (Mason & Macdonald, op. cit.). In the river Klingavälsån (Sweden), where a dense crayfish population is found, crayfish formed 36% of the diet (Erlinge, 1967). Diet composition may also vary seasonally with the availability of certain prey species. In summer, when some fish species may be more difficult to catch, other animal species are more heavily depredated. This was clearly demonstrated by the Klingavälsån study of Erlinge (1967): during the summer months, when the crayfish were most active, crayfish predation was much higher than the annual mean of 36% (Fig. 21). Thus, we see that the composition of the diet of *L. lutra* may vary considerably, according to the circumstances. In most cases, however, fish is the main food of this species. Erlinge (1968) examined the food preference of *L. lutra* in captivity. He showed, that motile prey (fish) was preferred above less motile prey (crayfish and frogs). This preference was found both for hunting and actual eating.

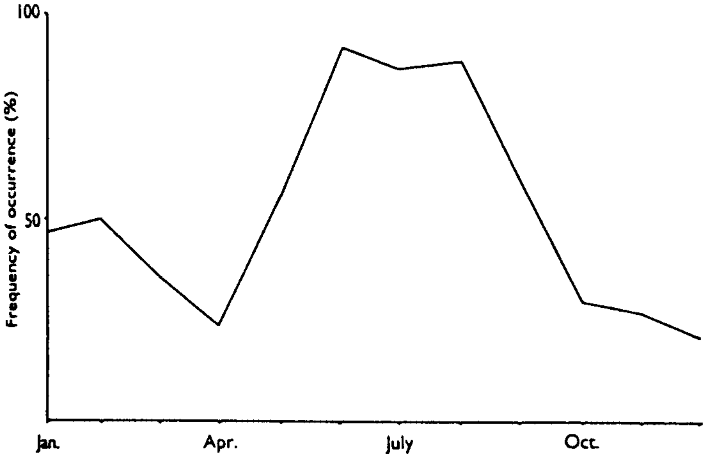

Fig. 21. Seasonal variation in predation on crayfish by *Lutra lutra* in the river Klingavälsån (Sweden). From Erlinge (1967).

Summarizing, we may say that *L. lutra* preys mainly on motile fish. The teeth of *L. lutra* have sharp cusps and cutting ridges and they are not very robust. P^4 has a small talon and M_1 a small talonid. In the latter, the hypoconid is present as a sharp ridge.

Near the other end of the scale is *Aonyx capensis*. Its diet normally consists of 60-70% crustaceans, 3-8% fish and the remaining percentage other vertebrates (Chanin, 1985; Mason & Macdonald, 1986). An exception is formed by a population of *A. capensis* living in a coastal area in South Africa, where the diet consists of 50% fish and 40% crustaceans (Mason & Macdonald, 1986), but this fish belongs almost exclusively to one, non-motile species, the suckerfish *Chorisochismus dentex*. The dentition is robust, the cusps are blunt, the talon of P^4 and the talonid of M_1 are very large and the hypoconid in M_1 is a real cuspid. In *Amblonyx cinerea* and in *Aonyx congica*, these dental characters are less extreme. The cusps are less blunt and the shearing blades better developed than in *A. capensis*. *Amblonyx* feeds on small crabs, molluscs and small fish. The ecology of *Aonyx congica* is virtually unknown. The 'invertebrate specialist' type of dentition is often called 'aonychoid' because it is typically found in *Aonyx*. But it is found outside the Aonyxini too. Extant *Lutra provocax* clearly has a dentition of this type, being very robust and with blunt cusps. This species feeds on crustaceans and bivalves exclusively (Mason & Macdonald, 1986).

Some otters, e.g. *Lutra canadensis*, have an intermediate kind of dentition: robust, broad teeth, but sharp shearing blades are present. This type of dentition may be regarded as dual purpose dentition, adapted both for crushing and cutting (van Zyll de Jong, 1972). This is clear when we look at the diet of these species. In *Lutra canadensis*, fish comprises 40-90% (in one population only 15%) and crustaceans up to 50% of the diet (Mason & Macdonald, 1986). *Lutrogale* also has such an intermediate type of dentition.

The most aberrant dentition among extant lutrines is found in *Enhydra lutris*, which feeds on invertebrates exclusively. Bivalves form an important part of the diet, ranging from 30 to 80% in frequency, but sea urchins may also count up to 80% (see Harris, 1968; Mason & Macdonald, 1986). The teeth are very large and robust and all cusps are large, blunt, and very low. It is a type of dentition completely adapted to crushing. No shearing blades, formed by the carnassials in other species, are present and the dentition is completely insuitable for catching fish.

Thus, several types of dentition can be distinguished, related to the feeding habits of the species, within the Lutrinae. Summarizing, we have the following types:

1. Relatively slender teeth, sharp cutting blades, talon of P^4 and M^1 and talonid of M_1 relatively small. 'Fish specialist' dentition. Species, which feed on motile prey, viz. fish mainly. Example: *Lutra lutra*.
2. Robust teeth, talon of P^4 large, talonid of M_1 may be broader, but external cingulum not broadened. Sharp cutting ridges are present. 'Dual purpose' dentition. Species, which feed on fish, but invertebrates (crustaceans) forming an important part of the diet too. Examples: *Lutra canadensis*, *Lutrogale perspicillata*.
3. Very robust teeth, rather bluntly cusped. Ridges present, but not very sharp. Talon of P^4 and M^1 large, talonid of M_1 broad and with broad external cingulum. 'Aonychoid' dentition. Species, feeding mainly on invertebrates (mostly shellfish). Examples: *Aonyx capensis*, *Lutra provocax*.

4. Very robust and broad teeth, with very low and blunt cusps. No ridges present. Species, feeding on invertebrates exclusively, with a large percentage of bivalves. Example: *Enhydra lutris*. Of course, there is no sharp distinction between those types. Intermediate types may occur.

Dentition types and their functional interpretation

In this section the dentition types of the fossil forms will be examined and conclusions on their feeding habits will be drawn.

The dentition of *Lutra simplicidens* resembles that of *L. lutra* very much. There are only minor differences to be found in the lower dentition (the upper dentition is unknown). The teeth are slender, the carnassial talonid is not broadened. This species clearly shows the first type, the fish specialist type of dentition. The diet of *L. simplicidens* was probably comparable to that of *L. lutra*, fish being the main food source. This species, having even stronger aquatic adaptations in the skeleton than *L. lutra*, probably chased its prey in a similar way as the extant species. But like *Lutra lutra*, it may partly have switched to other types of prey when the circumstances would make this profitable.

Sardolutra ichnusae and *L. trinacriae* also show a dentition of the fish specialist type. Their diet probably also consisted mainly of fish. Its hunting behaviour probably was similar. Angelelli (in press) studied the endocranial cast of *S. ichnusae*. The primary somatic sensory area for the head is relatively larger than in *L. lutra* and that for the hand is very small. The relative sizes of the two areas resemble *L. canadensis*. This points to highly sensitive vibrissa, which is in accordance with the assumption that the animal preyed on highly motile fish. The way of life of *S. ichnusae*, and maybe also of *L. trinacriae*, may have resembled that of the present coastal populations of *L. lutra*.

Lutra bravardi has a narrow P^4 with a small talon. Though the M^1 is slightly broader than in *L. lutra*, it probably preyed mainly on fish too. *Lutrogale cretensis* resembles *L. perspicillata* very much, as far as its dentition is concerned. The dentition shows both fish specialist and invertebrate specialist characters and like *L. perspicillata*, its dentition can be considered dual purpose (type 2). *L. perspicillata* feeds on both fish and shellfish. According to Wayre (1978) the food consists of 15 to 30 cm large fish, with crabs being important in coastal areas. The same was probably true for *L. cretensis*. Willemsen (1980) showed that the morphology of the endocranial cast also points to a more important role of bottom dwelling non-motile prey (presumably shellfish) in the diet of *Lutrogale* than in *Lutra* (Fig. 20). In both *Lutrogale* species, the primary somatic sensory area for the hand is larger than in *Lutra*. Possibly *L. cretensis* also took small mammals, which were abundant on Pleistocene Crete (Symeonides & Sondaar, 1975). *Lutra lutra* is known to take land vertebrates if it can, and *L. cretensis* was clearly more suited for this than *Lutra* with its terrestrial adaptations. Though it is quite possible, that small mammals and birds formed a considerable part of the diet, there is no reason to suppose that they formed the main part of the diet.

Invertebrates probably were important in the diet of *Algarolutra majori* too. In this species, P^4 and M^1 are broad, both have a large talon and on the M^1 the protocone is present as a large, rather blunt cusp, the protoconule as a similar smaller cusp. On the other hand, M_1 does not have a broad talonid, the hypoconid is not cusp-like and in

P^4 the paracone is rather high. In this case, we have a dual purpose dentition too.

The dentition of *Megalenhydris* shows dual purpose characters too. P^4 has a large talon, but the cusps are high. M^1 is large, M_1 is broad but the talonid does not show the broad external cingulum of the aonychoid type and the hypoconid is a ridge, forming the outer edge of the talonid. A similar combination of characters (large, high cusps, large P^4 talon, non-aonychoid M_1) is found in *Pteronura brasiliensis*, which feeds on large fish mainly, though crabs are also frequently taken (Duplaix, 1978; Mason & Macdonald, 1986). *Megalenhydris* probably preyed on large fish, supplemented frequently with crustaceans and incidentally other vertebrates. It is quite possible that the three Sardinian species lived at the same time, viz. the latest Pleistocene. Different habitats, different feeding specializations and maybe also different behaviour probably helped to avoid competition. *Pteronura* lives in the same habitat as *Lutra longicaudis*. The latter seems to feed on smaller fish and is nocturnal, so that competition is avoided. In a similar way, *Megalenhydris* could prey on much larger fish than *Algarolutra* or *Sardolutra*. Of the latter two, *Algarolutra* fed on shellfish also and maybe they lived in different habitats. *Sardolutra* was marine, the habitat of *Algarolutra* is not clear.

Cyrnaonyx antiqua clearly has an aonychoid dentition (type 3). The teeth are robust and broad, P^4 has a large talon, M_1 is particularly broad and its hypoconid is present as a cuspid rather than a ridge. The dentition is, however, not as robust and the cusps not as low and blunt as in *Aonyx capensis*. The dentition resembles that of *Aonyx congica* and *Amblonyx cinerea*. *Amblonyx* feeds on shellfish and small fish (Mason & Macdonald, 1986). The diet of *Aonyx congica* is unknown. The very broad external cingulum of the M_1 talonid as compared to *Amblonyx* may point to a greater importance of shellfish. The dorsally set eyes could be important in catching fish, as explained above, but this character is also found in the exclusively shellfish-feeding *Lutra provocax*. In the latter case, this character is explained by its fish-feeding ancestors (*L. longicaudis* or a similar form). In the case of *Cyrnaonyx* this character may indicate an ancestor more specialized on fish too.

Enhydra reevei is characterized by a very broad M_1 with very low and blunt cuspids, as in *E. lutris* (the fourth type of dentition as defined in the preceding section). Since it has been found in estuarine deposits at Bramerton, it may have lived in estuaries and coastal areas. Its feeding habits probably resembled those of the extant sea otter, the diet consisting of invertebrates exclusively. Related Miocene and Pliocene forms of the genus *Enhydriodon* had a similar dentition (robust, low cusps, no shearing blades) and probably similar feeding habits.

Phylogeny and palaeobiogeography

THE LUTRINI

The origin of the Lutrinae

In the past, many authors considered *Potamotherium* Geoffroy, 1833 to be a lutrine, as we saw in the chapter on taxonomy. Since the oldest *Potamotherium* finds are Late

Oligocene, thus older than any lutrine, *Potamotherium* has long been considered to be very near the ancestral stock of the Lutrinae (see e.g. Pohle, 1919). Savage (1957) demonstrated that *Potamotherium* shows a number of specialized characters, which make it impossible to accept it as general ancestor for the subfamily. He and many others (e.g. Thenius, 1949, 1969; Romer, 1966; Fahlbusch, 1967; Ginsburg, 1968; van Zyll de Jong, 1972; Willemsen, 1980, 1984) still considered *Potamotherium* to be a lutrine. This was doubted by other authors and de Muizon (1982) made perfectly clear that *Potamotherium* has strong affinities with the Phocidae. Savage (1957) already noted similarities to the Phocidae and he as well as several other students supposed, that the Phocidae might have originated from a *Potamotherium*-like form (see Repenning et al., 1979; de Muizon, 1982). It is probable, that *Potamotherium* represents an independent mustelid line, showing convergences with the lutrines in several respects, due to a similar ecology. De Muizon (1982) noted certain synapomorphies of the phocids, *Potamotherium* and the Enhydrini as opposed to the other mustelids and suggested a relationship. The fossil evidence, however, suggests that the Enhydrini originated from Early Miocene lutrines, as we will see below, and a common lutrine ancestor for *Potamotherium* and the Enhydrini can be rejected on the basis of the great age of *Potamotherium* and the many morphological differences. The synapomorphies mentioned by de Muizon (1982), the large ectotympanic and the reduced tympanic, the reduced suprameatic fossa and the reduced or lost postglenoid foramen, can be explained as parallelism and convergence. As de Muizon (op. cit.) pointed out himself, a reduction of the postglenoid foramen and a reduction of the tympanic are also found in other carnivores, as diverse as Hyaenidae, Otariidae and Ailuropoda (postglenoid foramen reduction) and Mustelinae and Melinae (tympanic reduction). A reduction of the suprameatic fossa may be functionally related to hearing under water or the reduction of water pressure (de Muizon, 1982) and the reduction of this fossa may have happened independently in the Enhydrini and in the *Potamotherium*-Phocidae, due to the aquatic environment. It should be noted that the reduction is much more evident in the latter group. The dentition of *Potamotherium* is quite unlike the lutrines. The main differences are the relatively short M^1 with a small talon and a completely different structure of the trigon; the rather slender M_1 with a very small metaconid and a very small and narrow talonid; the presence of an M^2. The skull also differs in some respects from the Lutrinae, such as the structure of the auditory region (de Muizon, 1982) and the very elongated braincase. There are differences in brain structure (Savage, 1957) too. Taking all into account, I think that a direct phylogenetic relationship with the Lutrinae is improbable.

The oldest known lutrine is *Mionictis artenensis* Ginsburg, 1968, from the Orleanian (MN 4 and 5) of France. *Mionictis* shows a number of meline characters, which even led Ginsburg (1968) to classify the genus as Melinae. In Ginsburg et al. (1983) the genus was referred to the Lutrinae again. *Mionictis* has too many characters in common with *Paralutra* to separate it from that genus on subfamily level. The meline character of *Mionictis* is especially clear in the M^1. This tooth is not known for *M. artenensis*, but it has been described for *M. dubia* de Blainville, 1841, from Sansan (Lower Astaracian, MN 6; Ginsburg, 1968). The M^1 is very elongated lingually and there is a well-developed metaconule. Other meline characters are the short lower canine which has a strong basis, the low and much elongated M_1, the short and robust premolars and the P^4 talon, which extends anteriorly of the paracone.

In general, the Lutrinae are considered to be rather closely related to the Melinae, both groups showing a rather robust dentition, with large talons in the P^4 and M^1 and a broad M_1 talonid. The meline characters of the oldest lutrine make a meline origin of the Lutrinae very probable. The origin of the Lutrinae probably was a group of Melinae which became adapted to a semiaquatic life and which eventually gave rise to the genus *Mionictis*.

De Muizon (1982) suggested a closer phylogenetic relationship with the Mephitinae and the Mustelinae than with the Melinae, but this is based on one character only: the condition of the crest joining the mastoid and the paroccipital processes.

Miocene Lutrini

In Fig. 22, the phylogenetic relationships between the different genera are given. As we saw, *Mionictis* is the oldest known lutrine. Its rather slender dentition and the morphology of M_1, which is slender, has high and sharp cuspids, an elongated hypoconid and of which the external cingulum is not broadened, make clear that this genus is most closely related to the Lutrini. In Europe, two *Mionictis* species are known: *M. artenensis* from the Orleanian (MN 4 and 5) and *M. dubia* (de Blainville, 1841) from the Astaracian of France (Ginsburg, 1968). The latter is larger and has a more elongated M_1 with a larger talonid. It probably evolved from *M. artenensis*. *Mionictis* is also known from North America by three species: *M. elegans* and *M. incertus* Matthew, 1924 from the lower Snakes Beds, Nebraska and *M. letifer* Cook & MacDonald, 1962 from the Middle Sheep Creek Beds, Nebraska, so it had a large geographical distribution. Since the American species are also Lower Miocene, it is impossible to say in which area the origin of the genus was located.

The tendency towards an elongation of the M_1 is most explicitely seen in *Siamogale thailandica* (Ginsburg, Ingavat & Tassy, 1983), a species from the late Middle Miocene or the early Late Miocene of Thailand. In this species, the lower carnassial is low, the talonid very much elongated and the metaconid elongated and slowly sloping down posteriorly. Ginsburg et al. (1983) noted similarities with *Mionictis*, especially with *M. artenensis*. It may be assumed that this genus was ancestral to *Siamogale*.

From several localities in Europe, *Paralutra jaegeri* (Fraas, 1862) is known (see e.g. Helbing, 1936; Viret, 1951; Ginsburg, 1968; Heizmann, 1973). All localities can be correlated to the Astaracian (MN zones 7 and 8). A mandible of this species has also been reported from La Romieu (Roman & Viret, 1934), a locality which can be referred to MN zone 4, but according to Ginsburg (1968) this specimen should in fact be referred to *Mionictis artenensis*. His arguments are convincing, and as far as can be judged from the description and illustrations in Roman & Viret (1934) the M_1 indeed resembles *M. artenensis* rather than *P. jaegeri*. The metaconid is elongated and not trenchant, sloping down to the entoconidal ridge, the talonid is long and not quadrangular and the email is plissated as in *M. artenensis* and *M. dubia*.

P. jaegeri resembles *Mionictis* in many respects. The M^1 has a similar morphol-

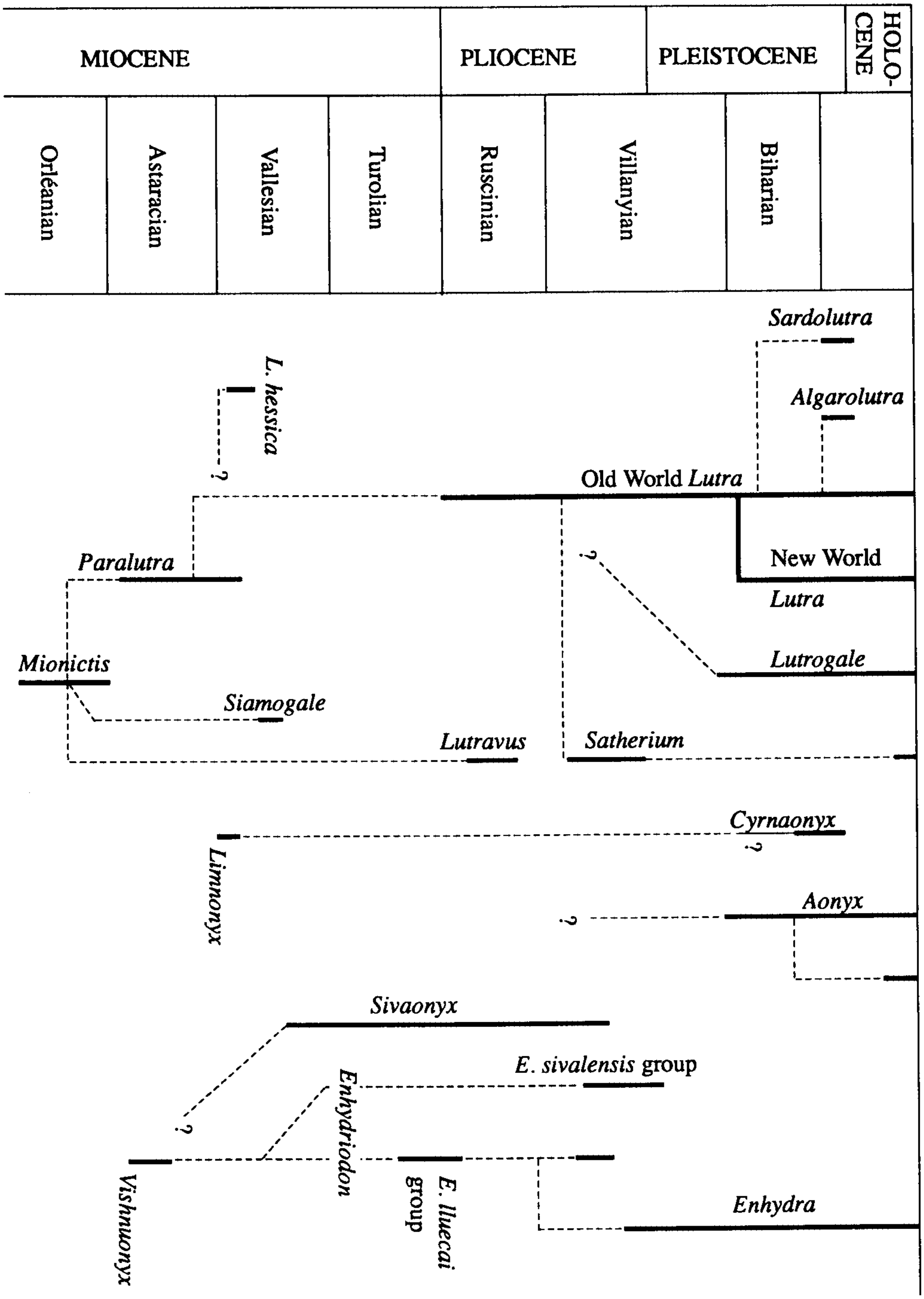

Fig. 22. Probable phylogenetic relationships and distribution in time of the Lutrinae. Fat lines indicate fossil evidence.

ogy, showing the same posterolingual expansion of the talon as in *Mionictis*, though the expansion is more developed in the latter. The M_1 resembles *Mionictis* also, but the talonid is small and quadrangular, the metaconid is trenchant, not elongated and very small. The similarities point to a phylogenetic relationship between the two genera. Since in *M. dubia* the lower carnassial is more elongated than in *M. artenensis*, there is a closer resemblance to the latter. *P. jaegeri* probably evolved from early *Mionictis*, possibly *M. artenensis*. In this phylogenetic line, the talonid became smaller and simpler and the M^1 talon less expanded. *P. jaegeri* had a geographical distribution covering at least the whole of Central Europe. *Paralutra* is clearly related to the genus *Lutra*. Malatesta (1977) pointed out that *Paralutra* cannot be ancestral to *Lutra*, since P^1 is absent in *Paralutra*. This is known through the holotype of *P. jaegeri* (Helbing, 1936). This does, however, not exclude the possibility that a closely related species of the same genus is ancestral to *Lutra*. It is even possible that the material referred to *P. jaegeri* in fact represents more than one species. Already Helbing (1936) noted differences between specimens from different sites. A revision of the *Paralutra* material would be needed. This is, however, beyond the scope of this study.

P. jaegeri also reached the Miocene island Gargano and, after becoming isolated, evolved to the rather aberrant endemic species *P. garganensis* Willemsen, 1983. In this species, the talon of P^4 was much larger than in *P. jaegeri*. The most striking difference, however, is the fact that the protocone in this tooth is present as a separate small cusp and not as a part of the anteroposterior ridge of the talon (Willemsen, 1983c). *P. jaegeri* clearly has the dentition of a fish-feeder, like *Lutra lutra*. *P. garganensis* was much more adapted to crushing, and thus to a shellfish-rich diet.

A third *Paralutra* species has been described by Kretzoi (1951) from Csákvár (Czechoslovakia): *P. transdanubica*. The description is very short and insufficient. Kretzoi had only a P^4 and an M^1. The only differences with *P. jaegeri* (*P. steinheimensis* in his publication) he mentioned, are: '... the deuteroconus of P^4 is more expanded in the Csákvár form. On the M^1 the inner cingulum is more developed, the outer cusps more labially situated.' It is questionable whether these differences justify the establishing of a new species.

From the Lower Vallesian three lutrines have been described: two *Limnonyx* species, forming the earliest record of the Aonyxini, which will be dealt with in the section on that tribe, and *Lutra hessica* Lydekker, 1890. Both *Lutra hessica* and *Limnonyx pontica* are known from Eppelsheim (Germany).

Lutra hessica is known by a mandible with M_1. According to Tobien (1955), it is absolutely not identical with *Limnonyx pontica*. Indeed, there are differences to be noted (Fig. 23). In *L. pontica* the metaconid is less trenchant and extends more backwards than in *L. hessica*. The external cingulum of the talonid is less developed in *L. hessica*, resembling the Lutrini rather than the Aonyxini. In the trigonid of *L. hessica*, there is no close basal contact at the lingual side between paraconid and metaconid, and in this it also differs from *Limnonyx*. In short, the tooth does not look very aonychoid. Pohle (1919) referred the species to *Aonyx*. Already Stromer (1931) expressed his doubts about this. Tobien (1955) pointed out, that Pohle (op. cit.) based himself on the illustration in Lydekker (1890), in which the tooth is much broader than in reality. According to Pohle (op. cit.), the tooth is 8.8 mm wide and 16 mm long. He took the

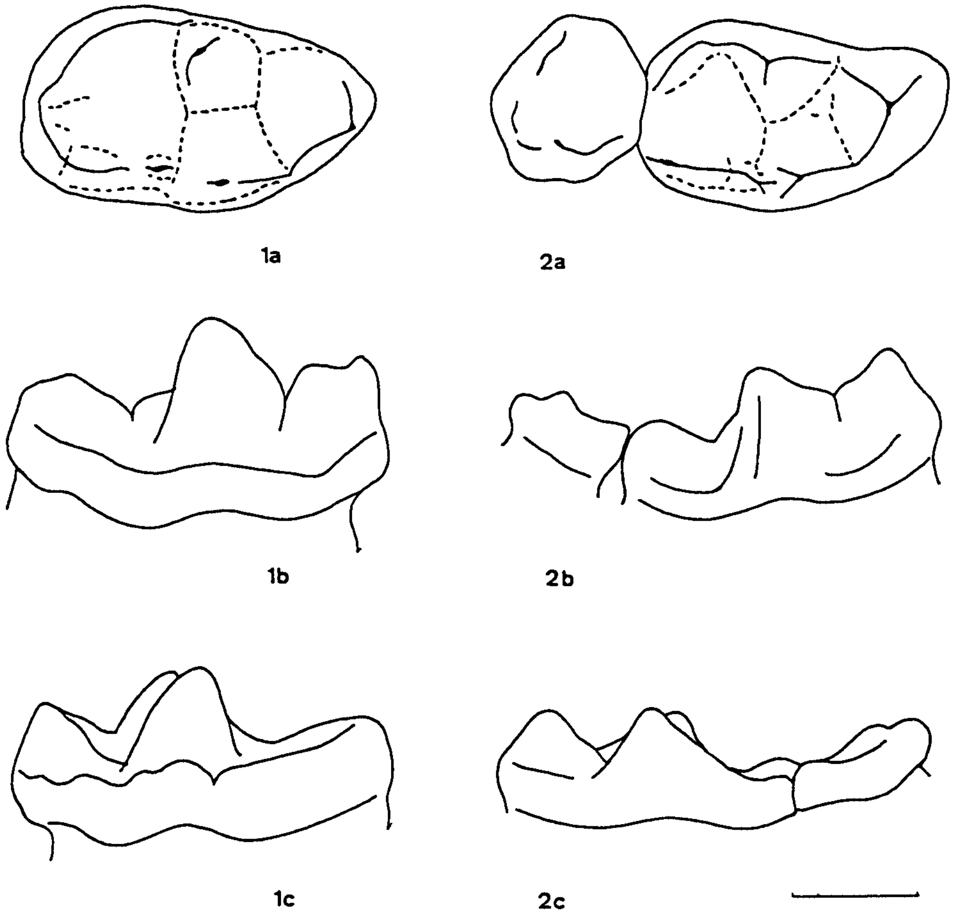

Fig. 23. Right M_1 of *Lutra hessica* from Eppelsheim (BM M 27486) and right M_1 and M_2 of *Limnonyx pontica* from Kishinev (UHGI P 1118), occlusal (a), buccal (b), and lingual view (c); scale = 5 mm.

width from Lydekker's figure (Pohle, 1919, p. 143). Tobien (1955) gave 7.2 and 16.0 mm respectively. He took his measurements on a cast which was at his disposal. Thus, Tobien argued that the M_1 of *L. hessica* is too narrow for *Aonyx*. According to his measurements, the width/length index is 45%, while in 16 *Aonyx* specimens it is 50-67.7%. Unfortunately, the measurements given by Tobien are even more beside the truth than those of Pohle. I took measurements on the original specimen, which is in the British Museum of Natural History (BM M 27486; measurements are given in Table 11). Its length and maximum width are 15.8 and 8.5 mm respectively, giving an index of 54%. Thus, the tooth falls within the range of *Aonyx*. The index does not differ very much from *Limnonyx pontica* (55% for the Kishinev specimen and 60% for the Eppelsheim specimen). The index falls also within the range of *Lutra*. In *L. lutra* the index is 44 to 54% (n = 95) and in other *Lutra* species it can be as high as 60%. It can be concluded, that the relative width of the M_1 cannot be used to determine the systematic position of the species in this case. Some other characters, however, point to a relationship with the Lutrini: the not very prominent outer cingulum of the talonid and the elongated hypoconid, which forms a sharp ridge. The material is too scarce to determine whether this species really is a *Lutra*. Apart from this specimen, the genus *Lutra* is not known earlier than the Pliocene.

Macdonald (1956) described some mandibular fragments from Western Nevada as *Lutra* sp., though with some doubt. According to him, the M_1 of this form is more like *L. lutra* than like *L. canadensis*, though it has a broader talonid and a more prominent hypoconid. As far as can be judged from the illustration (Macdonald, 1956, fig. 7) the talonid is shorter than in *Lutra* and the mandible is rather robust. The morphology of the carnassial is rather unlike *Lutra* in the restricted sense as it is used nowadays and a phylogenetical relationship with that genus must be considered highly unlikely.

Pliocene Lutrini

Lutrine remains from the Pliocene of Europe are rather rare. The genus *Lutra* is known from the Early Ruscinian (MN 14) by *L. affinis*. Though the status of the species is uncertain the original description makes it highly probable that this really is a *Lutra*. The genus probably evolved from a *Paralutra*-like form, though not from *P. jaegeri* as explained above. From the Late Ruscinian (MN 16A) *L. bravardi* is known. The material is too scarce to say anything about a possible phylogenetic relationship of this species with *L. hessica*. From Asia, *Lutra palaeindica* was described from the Siwalik Hills (Falconer, 1868; Lydekker, 1884; Pilgrim, 1932). The locality where the two specimens have been found is unknown, the stratigraphic position is not known either. Pilgrim (1932) only stated that it is 'Upper Siwalik, probably not older than the Pinjor Stage, but the level is uncertain.' If this is true, the age may be Late Pliocene or Early Pleistocene (see Pilbeam et al., 1977; Barry et al., 1982). The close resemblance with *L. sumatrana* was noted by many authors (e.g. Lydekker, 1884; Pohle, 1919; Pilgrim, 1932). Pohle (1919) also noted a great resemblance with *L. lutra barang* (described as a separate species, *L. intermedia*, by Pohle) and a close phylogenetic relationship with the *L. lutra*/*L. sumatrana* group is very probable.

Lutra lybica Stromer, 1914 was described from the Pliocene of Egypt (Wadi Natrun). The holotype and only specimen is a right mandible with P_2-M_1. As far as can be judged from the description of Stromer (1914), this species cannot be included in the genus *Lutra*. The structure of M_1 is quite aberrant. The talonid is relatively very short. Stromer (op. cit.) gave a talonid length of 4 mm (total length 11.6, width 6). The talonid is concave and a hypoconid is present as a small cuspid in the outer edge. In the illustration in Stromer (1914) it can be seen that the talonid has a triangular outline, the lingual and lingual edge converging in backward direction. The anterior part of the talonid is the widest point of the tooth, but the talonid is becoming narrower very rapidly behind this point. A talonid this short and with a triangular shape like in this species is not found in any *Lutra* species. Also, the mandibular ramus is more robust than in *Lutra*. Probably the best would be to describe a new genus for this species. The species does belong to the Lutrini, as is indicated by the small talonid. It is difficult to say anything about the phylogenetical relationships of '*Lutra*' *lybica*, especially since I did not see the actual specimen. It resembles *Paralutra jaegeri* in having a short M_1 talonid, but in the latter the talonid is not triangular but square and the widest point of the tooth lies at the posterior part of the trigonid. Malatesta (1977) also noted similarities with *Sardolutra*, but in *Sardolutra* also the M_1 talonid is larger and not as clearly triangularly shaped. The same is true for *Lutra simplicidens*, the ancestor of *Sardolutra* (see below). '*Lutra*' *lybica* may have evolved from some Lutrini, possibly from some *Lutra* form.

Howell & Petter (1979b) mentioned a P^4 and a M_1 from the Upper Pliocene Usno Formation of Omo, both damaged, which they referred to *Lutra*. This would suggest that *Lutra* reached Africa during the Pliocene.

From the New World, few Pliocene Lutrini are known. *Lutravus halli* Furlong, 1932 resembles *Paralutra* more than any other form according to van Zyll de Jong (1972). The characters, mentioned by him (e.g. short M_1 talonid, M^1 with posterolingual expansion) also remind one of *Mionictis*, which van Zyll de Jong (op. cit.) apparently did not consider to be lutrine. *Lutravus* may represent a lineage originating from the New World *Mionictis* and thus the Lutrini may have been present continuously since the Early Miocene.

Late Pliocene and Early Pleistocene large otters of the genus *Satherium* resemble extant *Pteronura* (van Zyll de Jong, 1972; Kurtén & Anderson, 1980). The genus is probably not phylogenetically related to the American river otters of the genus *Lutra*. As will be explained, the latter group probably originated from Early Pleistocene *L. licenti* from East Asia. Since *Satherium* resembles *Lutra* much more than the *Mionictis-Lutravus* group, it probably represents a Pliocene immigration from Asia. There are similarities between *Lutrogale* and *Pteronura*. Both have a flattened tail, a P^4 which has a large talon and a remarkably short facial part of the skull. The skull is rather high in both. Similarities in skull morphology are also evident from the analysis of van Zyll de Jong (1972). This might point to a common ancestor for *Pteronura* and *Lutrogale* in the Pliocene of Asia. There is, however, no evidence for this view in the fossil record.

Quaternary Lutrini

From the Early Pleistocene of Europe no Lutrini are known. The first record of this group is *Lutra simplicidens*, which is known from the Middle Pleistocene. This species cannot be compared directly to the Late Pliocene *L. bravardi*, since of the latter only the upper dentition is known, and this is completely unknown for *L. simplicidens*. The dentition of *L. bravardi* is rather robust and the contrary is true for *L. simplicidens*. The upper dentition of *L. trinacriae*, which is related to *L. simplicidens*, is not robust and does not resemble *L. bravardi*. So a direct phylogenetic relationship between *L. simplicidens* and *L. bravardi* is not probable. Within Europe, no species which can be considered ancestral to *L. simplicidens* is known. The species may very well have an Asiatic origin, as many other Lutrini. *L. simplicidens* had a large geographical distribution. It is known from Central European localities, from East Anglia and possibly from northern Italy also.

L. trinacriae, *L. euxena* and *Sardolutra* have many characters in common with

L. simplicidens (see descriptions). The resemblances strongly suggest that *L. simplicidens* was ancestral to those forms.

Certain trends towards a higher degree of adaptation to aquatic life, evident in *L. simplicidens*, are present more explicitely in *Sardolutra*. Resemblances are too many to be explained by parallel evolution. Also from a biogeographical point of view, *L. simplicidens* is the best candidate for an ancestry of the above-mentioned forms. Malatesta (1977) considered *Paralutra* to be ancestral to *Nesolutra* (which in his view included all three island species, *L. euxena* and *S. ichnusae*). In my opinion, the resemblances of all three species with *Paralutra* are much less striking than those with *L. simplicidens*. The large time gap between *Paralutra* and the island species, without any intermediate form, is also a problem. From this point of view too, a *L. simplicidens-L. trinacriae/L. euxena* and a *L. simplicidens-S. ichnusae* lineage are more probable. Both lineages probably originated independently from the common ancestor *L. simplicidens*, since a faunal exchange between Malta/Sicily and Sardinia is improbable. Faunal exchange in the Pleistocene between these two areas has never been demonstrated and the faunas have no common endemic elements. Of course, *Lutra* is a good swimmer, but there is no evidence that *L. trinacriae* had a marine way of life. Even coastal *Lutra*-populations do not travel that great distances at sea. Therefore an independent colonisation of Sardinia from the mainland is more plausible. *L. euxena* and *L. trinacriae*, probably of Middle Pleistocene age, may have been contemporaries of *L. simplicidens*. The most derived condition is found in the Late Weichselian or even Holocene *S. ichnusae*. It is not known, when its ancestor arrived on Sardinia. Most probably, in the Middle Pleistocene, since *L. simplicidens* did probably not survive into the Late Pleistocene. During the Middle Pleistocene, a faunal turnover took place on Sardinia and new immigrants from the mainland arrived (Sondaar et al., 1986). *L. simplicidens* may have reached the island in this time, when Sardinia/Corsica was not far from the mainland. The excellent swimming capabilities of *Lutra* do, however, not exclude a colonisation at a somewhat later time, when a larger sea barrier had to be crossed.

Thus, *L. simplicidens* is the basis of a radiation which took place on the islands in the central Meditterranean (Willemsen, in press). The Sicilian form probably resembles the common ancestor more than the Sardinian form. The longer isolation may explain the higher degree of endemism in the latter. The fact that other lutrines were present on Sardinia too (*Algarolutra, Megalenhydris*), caused a greater specialisation for marine life. We do not know when the ancestors of these other two arrived on Sardinia or even which their ancestors were.

Since the postcranial skeleton of *L. simplicidens* is far more specialised for aquatic life than that of *L. lutra*, *L. simplicidens* is most probably not ancestral to *L. lutra* (Thenius, 1965). *L. lutra* probably is of Asiatic origin. As we saw in the preceding section, Late Pliocene or Early Pleistocene *L. palaeindica* is probably phylogenetically related to the *L. sumatrana/L. lutra* group. The latter two resemble each other very much and probably are closely related within the genus. It is interesting to note, that in Southeast Asia a subspecies of *L. lutra* is found (*L. l. barang*) which is in many respects intermediate between the two species. Both may have evolved from *L. palaeindica*. *L. lutra* got its present wide geographical distribution only rather recently. It dispersed into Europe at the very end of the Pleistocene (Late Weichselian) or in the Early Holocene. As I pointed out in the chapter on Taxonomy, of this species no Pleistocene fossils are known from Europe. Not only did this species disperse westward rather recently, the same is probably true for its northeastward dispersal. From China, no fossil specimens are known (Teilhard de Chardin & Leroy, 1945).

The genus *Lutrogale* is known from the Pleistocene of Asia by two species: *L. palaeoleptonyx* (Dubois, 1908) and *L. robusta* (von Koenigswald, 1933), both from Java. Those species were referred to *Lutrogale* by Willemsen (1986). *L. palaeoleptonyx* belongs to the so-called Kedung Brubus fauna (Willemsen, 1986). The Kedung Brubus fauna is a mainland fauna (de Vos et al., 1982) and probably c. 0.8 Ma old (Leinders et al., 1985). It is very similar to the extant *L. perspicillata* and may be closely related to that species. The resemblance with *Amblonyx cinerea*, as was noted by Dubois (1907, 1908) is only very superficial and does not indicate a relationship (Willemsen, 1986).

L. robusta is a large species from Bumiaju (von Koenigswald, 1933). It belongs to either the Satir or the Ci Saat fauna (Sondaar, 1984; see Willemsen, 1986). Both faunas point to insular conditions to some degree (Sondaar, 1984; de Vos, 1985) and are c. 1.5 and 1.2 Ma old respectively (Leinders et al., 1985).

The genus *Lutrogale* may be derived from some *Lutra* form. The locomotory apparatus became somewhat less adapted than in *Lutra*, the skull became higher and narrower, the dentition became more robust and the position of the posterior heterostrophic vertebra changed (see Willemsen, 1980). As the fossil record of Asiatic *Lutra* is rather poor, it is impossible to be more specific about the origin of the genus.

L. cretensis probably originated from *L. perspicillata* (Willemsen, 1980). The presence of an alveole for the M^2 is problematical in this respect, since this tooth is not present in *L. perspicillata*. The alveole must be considered vestigial, as it is present on one side only and no lutrine with M^2 is known. *L. cretensis* is endemic on Crete. The trend towards a less aquatic adaptation, already present in *Lutrogale*, has gone much further in this species (Willemsen, 1980). The presence of *L. cretensis* suggests that *L. perspicillata* may have had a much larger geographic distribution during the Pleistocene, extending into West Turkey or Greece, from where it colonized Crete and gave rise to *L. cretensis*. No fossils of *L. perspicillata* are, however, known from Europe. The present existence of an isolated population of *L. perspicillata* in Iraq (Hayman, 1957) also points to a formerly wider distribution, extending more towards the west.

Another Late Pleistocene island species, *Algarolutra majori*, causes more phylogenetic problems. It is clearly a Lutrini, but it does not show great affinity with any other species. On geographical grounds, also in this case *L. simplicidens* would be the most probable ancestor, since no other Lutrini are known from the Pleistocene of Europe. Especially the M^1 is rather different from *Lutra*; we do not know its condition in *L. simplicidens*.

In Africa, *Lutra* sp. has been reported from several Early Pleistocene sites (Savage, 1978). Savage also mentioned *L. maculicollis* from the Late Pleistocene and he also reported *L. lutra* from one Late Pleistocene locality (Barbary). I do, however, not know how complete this specimen is. It would represent the only record of this species in Africa.

From the Early Pleistocene of China (Nihowan), *Lutra licenti* Teilhard de

Chardin & Piveteau, 1930 has been described. More material from another locality of about the same age was referred to this species by Teilhard de Chardin & Leroy (1945) and this material was described in detail by van Zyll de Jong (1972), who also made extensive comparisons with other species. Already Teilhard de Chardin & Piveteau (1930) noted similarities with *L. canadensis*. Van Zyll de Jong (1972) confirmed a close relationship with the American *Lutra* species and rightly considered *L. licenti* to be ancestral to the American *Lutra* group. The lineage probably migrated into the New World during the Early Pleistocene. The first record of *Lutra* in the New World is from the Middle Pleistocene, a form, originally described as *L. rhoadsi* Cope, 1899, but now considered to be conspecific with *L. canadensis* (Pohle, 1919; van Zyll de Jong, 1972). Several Middle and Upper Pleistocene records of *L. canadensis* are known (van Zyll de Jong, 1972). Van Zyll de Jong (op. cit.) concluded that *L. iowa* Goldman, 1941, from Iowa, is a valid species, related to the extant American river otters. Its age is unknown, but assumed to be Pleistocene. It has some characters in common with *L. provocax* and *L. longicaudis*. The latter two represent a more derived condition than *L. canadensis*. Both have a more robust dentition and in *L. provocax* the dentition is as robust as in *Aonyx*. Both species are restricted to South America. It is unknown when *Lutra* reached South America.

THE AONYXINI

Miocene and Pliocène Aonyxini

From the Lower Vallesian, two species of the genus *Limnonyx* have been described. From Can Ponsich (Spain, zone MN 9), *Limnonyx sinerizi* Crusafont Pairò, 1950 is known by a mandible with dentition. It was not very well figured by Crusafont (1950). Since no photographs were ever published, we present a photographic illustration in this paper (Pl. 5, fig. 5). *L. sinerizi* is a species with a very robust mandible and the M_1 has a very broad talonid with a large hypoconid. A less robust species, *Limnonyx pontica* (von Nordmann, 1858) has been described from Kishinev (Moldavia, USSR) and from Eppelsheim (Germany, zone MN 9; see Tobien, 1955). The species was originally described as *Lutra pontica* but Tobien (1955) referred it to the genus *Limnonyx*. Only mandibular fragments with lower dentition are known. The mandible is much less robust than in *L. sinerizi* but the M_1 shows strong morphological resemblances. The tooth is, however, relatively broader in *L. pontica* (Table 11). As far as can be judged from photographs of *L. sinerizi* at my disposal, the hypoconid is less trenchant on the lingual side and the lingual cingulum is more prominent than in *L. pontica*. Both *Limnonyx* species clearly show aonyxine characters and thus the genus is the oldest representative of the tribe.

From the Pliocene of Europe, no Aonyxini are known. From China, *Aonyx aonychoides* (Zdansky, 1924) has been described. It shows clear affinities with *Aonyx* and *Amblonyx* (Zdansky, 1924; Teilhard de Chardin & Leroy, 1945; Radinsky, 1968).

Quaternary Aonyxini

This group is represented in the European Pleistocene by *Cyrnaonyx antiqua*. This species was present in a large part of Europe in the Holsteinian/Saalian. The Saalfeld specimen suggests that the species was still present in the Late Pleistocene at least in eastern Germany. The Maasvlakte specimen would suggest that the species was present in Europe as early as the Bavelian, though this dating is tentative, as I explained in the section on this species.

Cyrnaonyx antiqua is characterized by the wide external cingulum of the M_1 talonid. This is wider than in most *Aonyx capensis* specimens and thus this character is more developed in this lineage than in any other Aonyxini lineage. A phylogenetic relationship with *Limnonyx* from the Vallesian of Europe has been suggested (Crusafont Pairò, 1950). *Limnonyx* species is the only other Aonyxini known from Europe (apart from the rather young *Megalenhydris*). Indeed, there are resemblances between the two genera and *L. pontica* resembles *Cyrnaonyx* even more than *L. sinerizi* with its very massive mandible (see Crusafont Pairò, 1950; Tobien, 1955). The structure of the talonid is similar. There is a large hypoconid and a well developed lingual cingulum, though the latter is not as large as in *Cyrnaonyx*. Like *Cyrnaonyx*, *Limnonyx pontica* has two mental foramina (the condition in *L. sinerizi* is not known), an otherwise unique feature among lutrines. A difference is the obliquely placed P_3 of *Limnonyx* and the rather massive mandibular ramus. The lineage leading to *Cyrnaonyx* could very well have originated from *Limnonyx*. The differences between the genera could have developed during the long time span between the known fossil record of both species. The lineage *Limnonyx-Cyrnaonyx* would then represent the European lineage of the Aonyxini. On the other hand, the possibility of another, non-European origin of *Cyrnaonyx* cannot be ruled out. That alternative is less probable because of the above mentioned resemblances.

From Africa, the genus *Aonyx* is known throughout the Pleistocene. A form resembling *A. capensis* is known from Olduvai (Petter, 1973) and *A. capensis* is reported from several younger localities (Savage, 1978). No Asiatic remains are known to me. The fossil record of the genus is too fragmentary to answer the question whether the genus originated in Africa or Asia. *A. capensis* probably represents the most derived form, with its extremely robust dentition and with the many small cuspids on the edge of the M_1 talonid. Those small cuspids are not found in other Aonyxini. The less extreme condition in the form from Olduvai, as reported by Petter (1973) suggests that *A. capensis* evolved during the Pleistocene in Africa. In Asia, *Amblonyx* evolved. The fossil record is unknown, but the great similarity with *Aonyx* points to a close relationship.

THE ENHYDRINI

Miocene and Pliocene Enhydrini

The Enhydrini formed a clearly distinct group already in the Miocene. The most widely spread genus, *Enhydriodon*, is characterized by a very robust dentition with low, conical and rather blunt cusps. In the P^4, the protocone and the hypocone are developed as clear cusps too. No cutting ridges are present in the dentition. From the dentition it can be inferred that *Enhydriodon* and related forms were specialized shellfish-eaters. The genus was originally described from the Siwaliks (*E. sivalensis* Falconer, 1868). In Fig. 24, the supposed phylogenetical relationships between the different Enhydrini are given.

The origin of the Enhydrini is not clear. Probably the oldest form is *Vishnuonyx chinjiensis* Pilgrim, 1932. Two specimens are known, a maxillary fragment with P^4 and a mandibular fragment with P_4 and part of M_1 and M_2, both from Chinji in the Siwaliks (Pilgrim, 1932). Pilgrim referred them to the 'Chinji Stage'. At that time, the Siwalik fossils were divided in a number of not very well defined faunal zones. Pilbeam et al. (1977) reassessed the stratigraphy of the region. According to them, the Chinji Formation, from which *Vishnuonyx* comes, can be dated at about 12 to 14 Ma. The fauna can be correlated with the Astaracian faunas of Europe. Wessels et al. (1982) assigned an Early Astaracian age (MN zone 6) to a rodent fauna from the Chinji Formation on the basis of the Muridae and the Myocricetodontinae in that fauna. *Vishnuonyx* is in many respects intermediate between *Enhydriodon* on one hand and the Lutrini and Aonyxini on the other hand. The talon of P^4 is not as large as in other Enhydrini, in fact, it has about the same relative size as in *Lutra*. The paracone, the highest cusp, is rather sharp and the metacone is low and elongated. Protocone and hypocone are much smaller. The protocone is not as conical as in *Enhydriodon*, but it is clearly a cusp and not merely the edge of the talon as in the Lutrini. Between the hypocone, the protocone and the paracone a small basin can be seen. Probably, *Vishnuonyx* is very near the origin of the Enhydrini. The outline of the tooth points to an origin from the Lutrini rather than from the Aonyxini. Also the fact that the oldest known Aonyxini (*Limnonyx*) are younger than this genus makes an aonyxin origin improbable. Probably, the Aonyxini and the Enhydrini originated independently from the Lutrini. An independent origin is supported by the cortical patterns of the brain, which suggest that *Enhydra* and *Aonyx* represent separate lineages (Radinsky, 1968). *Vishnuonyx* suggests an Asiatic origin for the Enhydrini.

Many different Enhydrini evolved on the Indian subcontinent. One of the lines led to *Sivaonyx bathygnathus* (Lydekker, 1884). This species is known by a number of mandibles with dentition. The holotype and all specimens known to Pilgrim (1932) were from Hasnot, except for one specimen from Kamlial. In the British Museum (Natural History) there is also one specimen from Tatrot (no. M 13397). According to Pilgrim (1932), they must be referred to the Dhok Pathan Stage. The 'stages', used by Pilgrim and many other early workers in the Siwaliks, are in fact not very well defined faunal zones. Later, those units were defined as formations (Pilbeam et al., 1977). According to Pilbeam et al. (1977), the Dhok Pathan Formation is of Late Vallesian to Middle Turolian age. Most localities in the Hasnot region lie in the Dhok Pathan Formation or in the Upper Siwaliks. The Tatrot Beds, from which BM M 15397 probably comes (Pilgrim developed his Tatrot faunal zone on the basis of these beds) are between 2.5 and 3.4 million years old (Barry et al., 1982) and thus of Late Pliocene age. Concludingly, we have evidence for the presence of *Sivaonyx* from the Late Vallesian to the Late Ruscinian. Pilbeam et al. (1977) also quote *Sivaonyx bathygnathus* in their faunal list of the Nagri Formation. Barry et al. (1982), however, correctly questioned the broad Nagri concept used by Pilbeam et al. (op. cit.).

Within the species there is some variation in size and morphology. The lower carnassials show a resemblance to the specimens of *Enhydriodon lluecai* and *E.* cf.

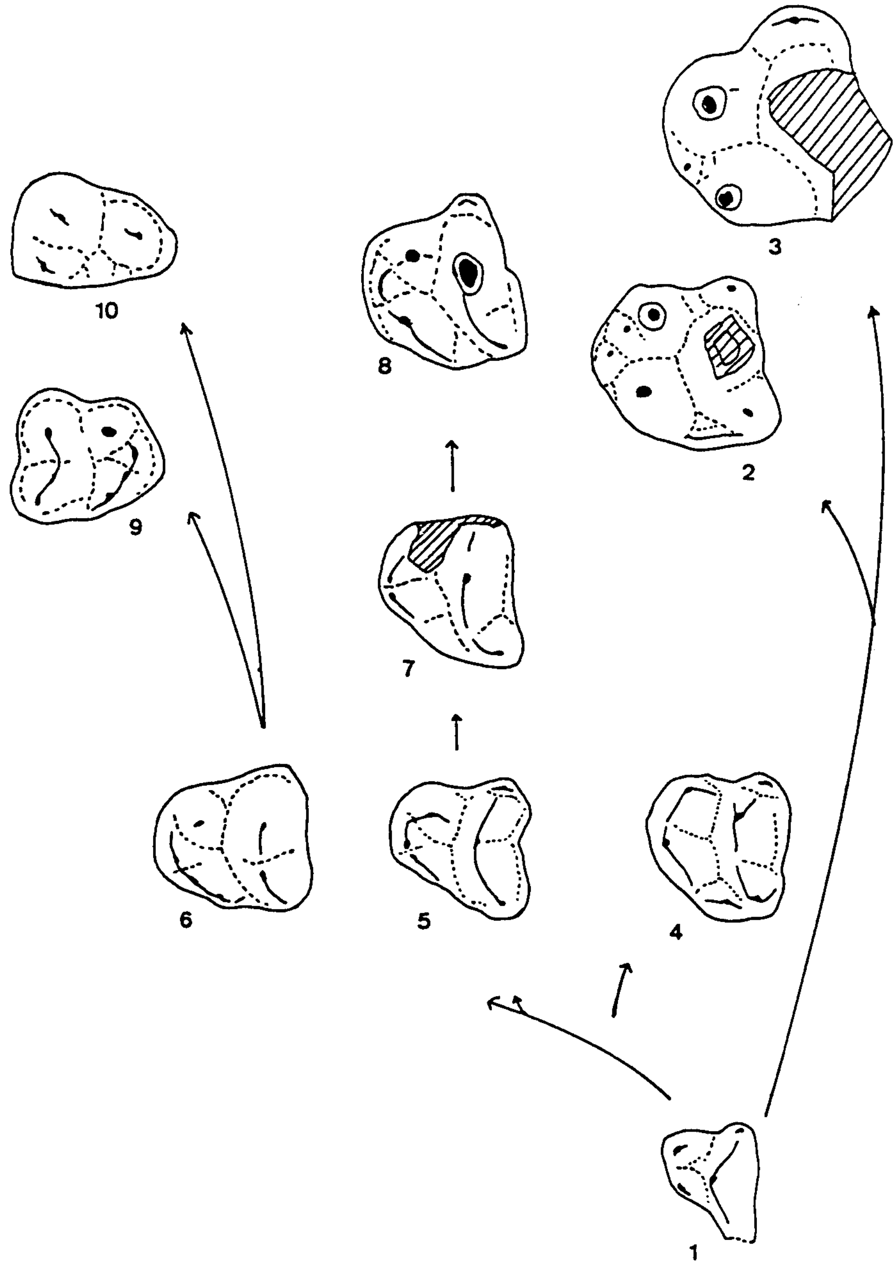

Fig. 24. Proposed phylogenetical relationships within the Enhydrini. Drawings of P^4, all to the same scale, are given; 1 = *Vishnuonyx chinjiensis*, GSI D 239; 2 = *Enhydriodon falconeri*, BM M 4847; 3 = *Enhydriodon sivalensis*, BM 37155; 4 = '*Sivaonyx bathygnathus*', GSI D 157; 5 = *Enhydriodon lluecai*, redrawn after Crusafont & Golpe (1962); 6 = *Enhydriodon* cf. *lluecai*, redrawn after Repenning (1976); 7 = *Enhydriodon* (*Paludolutra*) *maremmana*, redrawn after Hürzeler (1987); 8 = *Enhydriodon* (*Paludolutra*) *campanii*, redrawn after Hürzeler (1987); 9 = *Enhydriodon* n. sp. from California, redrawn after Repenning (1976); 10 = *Enhydra lutris*.

lluecai as illustrated by Repenning (1976). Pilgrim (1932) referred one P^4 to this species. It was not found in association with a mandible and only referred to this species on the basis of its size. According to Pilgrim (op. cit.), this tooth shows more primitive characters than *Enhydriodon.* Among other things, the outline of the tooth is more triangular than in *Enhydriodon* and the cusps are sharper and more elongate. The tooth shows resemblances to *E. lluecai* as far as can be judged from Pilgrim (1932). This led Crusafont Pairò & Golpe (1962) to their recognition of *Sivaonyx* in the Upper Miocene of Teruel. They described a new species, *S. lehmani.* With Repenning (1976), I think that the upper carnassial of Crusafont Pairò & Golpe (op. cit,) and the material described as *E. lluecai* must belong to one species. At the moment it is clear that *Sivaonyx bathygnathus* represents a Late Miocene and Pliocene lineage in South Asia. The morphology of the M_1 suggests some relationship with *E. lluecai.* To which extent those species may be separated generically remains to be seen. The taxonomical relationships of *Enhydriodon* and *Sivaonyx* species will the subject of a future study.

Enhydriodon is the most widely spread genus within this tribe in the Miocene and Pliocene. Two lineages can be distinguished within the genus. The first is the lineage to which the already mentioned *E. lluecai* belongs. *Enhydriodon lluecai* de Villalta Comella & Crusafont Pairò, 1945 is known from a number of Turolian localities near Teruel in Spain (de Villalta Comella & Crusafont Pairò, 1945; Crusafont Pairò & de Villalta, 1951, Crusafont Pairò & Golpe, 1962). A form, resembling this species (*E.* cf. *lluecai*) has been described from the Turolian of Lukeino, Kenya (Pickford, 1975). This is the oldest record of the Lutrinae in Africa.

From the New World, *Enhydriodon* cf. *E. lluecai* (Repenning, 1976) has been described. A mandible with M_1 and an isolated P^4 are known from the middle and upper Etchegoin Formation in the Kettleman Hills, California. According to Repenning, the deposits are probably of latest Miocene age, but they may also be Early Pliocene. The form is very much like *E. lluecai,* though there are minor differences as pointed out by Repenning (1976). The North-American form is probably closely related to *E. lluecai.* Another form of this genus, referred to as *Enhydriodon* n. sp. by Repenning (1977), is from the Upper Pliocene San Joaquin Formation, also in the Kettleman Hills, California. In this form, the P^4 (the only known tooth) is broader, the metacone blade more reduced and two extra cusps have appeared. The above-mentioned P^4 from the Siwaliks, referred to *Sivaonyx* by Pilgrim (1932), may represent an Asiatic form of this lineage.

E. campanii Meneghini, 1863 was described from Monte Bamboli (Grosseto) by Meneghini (1863). The fauna from Monte Bamboli may be correlated with the V2 level of Baccinello, also in Grosseto. This correlation is supported by the presence of *Emaiochoerus etruscus* (= *Sus choeroides*) and of *Anthracomys majori* in both faunas (Hürzeler & Engesser, 1976; Hürzeler, 1982). Hürzeler & Engesser (1976) placed V2 from Baccinello in MN zone 13, Hürzeler (1987) referred it to MN zone 12. Thus, the age of both faunas is Middle or Late Turolian.

Hürzeler (1987) gave a review of the lutrine material from Grosseto. He was the first author since a long time who studied the type of *E. campanii.* The specimens location was unknown but Hürzeler retraced it. The originally badly prepared specimen was prepared anew at the Natural History Museum in Basel. Hürzeler (op. cit.) placed this species in a new genus, *Paludolutra.* Further, he described two new species from Grosseto: *Paludolutra maremmana* Hürzeler, 1987 and *Tyrrhenolutra helbingi* Hürzeler, 1987. *P. maremmana* is from an older bed at Monte Bamboli than *P. campanii*. Still older is *T. helbingi*, which is from level V1 at Baccinello. This level is referred to MN zone 11 or 12 by Hürzeler & Engesser (1976) and by Hürzeler (1987) and thus of Early or Middle Turolian age. The V1 and V2 faunas are insular faunas (Hürzeler & Engesser, op. cit.). The presence of a similar fauna at Monte Bamboli suggests that both geographically close localities formed one single island.

Furthermore Hürzeler (1987) considered *Paludolutra maremmana* to be ancestral to *P. campanii*. He further suggested that *Tyrrhenolutra helbingi* is ancestral to *P. maremmana*. Hürzeler found a close relationship with *E. lluecai* improbable. As far as can be judged from the publications (Crusafont Pairò & Golpe, 1962; Repenning, 1976; Hürzeler, 1987), there is, however, a striking resemblance between *E. lluecai* and *Paludolutra*, especially *P. maremmana*, in the morphology of P^4. Hürzeler (1987) seems to have been unaware of the existence of a P^4 of *E. lluecai*, to judge from his statement: 'Ob sich beim spanischen Fund tatsächlich um einen *Enhydriodon* handelt, kann allerdings erst entschieden werden, wenn auch die maxillare Bezahnung ... vorliegt.' (op. cit. p. 40). Or he does not agree with Repenning (1976) in referring this tooth to *E. lluecai*. However, it may be, the P^4 described by Crusafont Pairò & Golpe (1962) resembles that of *P. maremmana* very much. I think the resemblance is so close that the two species cannot be separated generically. The diagnosis of *Paludolutra* given by Hürzeler (1987) clearly includes *E. lluecai*. The morphological resemblance is also too strong to be explained as parallelism and therefore I think a phylogenetical relationship is very probable. If one separates the genus *Paludolutra* from *Enhydriodon*, then *E. lluecai* has to be included in *Paludolutra* too. The same is probably true for the related forms from Lukeino and from California. Generic separation is supported by the differences mentioned by Hürzeler (1987) and by the presence of a paracone-metacone ridge, which is absent in the Siwalik species.

Resemblances of *E. lluecai* and *E. campanii* were already noted by Repenning (1976). Rather than being ancestral to the *E. lluecai* lineage, as suggested by him, *E. campanii* represents an insular form, which evolved isolated from the mainland form.

Thus, the lineage of *E. lluecai* spread to both Europe, North Africa and North America, most probably from the Indian subcontinent. If we consider *E. lluecai* ancestral to the *Paludolutra*-lineage from Tuscany, which is difficult to deny, *Tyrrhenolutra* has a somewhat isolated position. The dentition is much less robust than in the *Enhydriodon/Paludolutra* forms. It might represent an earlier branch of the *Enhydriodon* group. Another possibility would be a relationship with *Paralutra*.

From the Siwalik Hills, two *Enhydriodon* species are known: *E. sivalensis* Falconer, 1868 and *E. falconeri* Pilgrim, 1931 were described (see Falconer, 1868; Lydekker, 1884 and Pilgrim, 1932). Their exact localities and their stratigraphic position are not known. According to Pilgrim they are probably 'Upper Siwalik'. In that case they may still be dated anything between Late Miocene and Early Pleistocene. In those two species, the P^4 became clearly quadrangular, the hypocone became very large, nearly as important as the protocone, and there was a large parastyl. In the M_1, which is known of *E. sivalensis* (however, here again we have an isolated specimen, referred to this species by Pilgrim on the basis of its size), an accessory cuspid was present behind the protoconid. From the Pliocene of South Africa, *E. africanus* Stromer, 1931 was described. In this species, the accessory cuspid posterior to the protoconid, is also found. Stromer (1931) also described an M^1, which he unfortunately did not illustrate. According to his description, this tooth is rather similar to *E. sivalensis*, though Stromer (1931) also mentioned some differences. It is probable that *E. africanus* is phylogenetically related to the *E. falconeri*/*E. sivalensis* group. Howell & Petter (1979a) suggest as an alternative possibility, that *E. sivalensis* and *E. africanus* are the results of parallel evolution. Later, more *Enhydriodon* fossils were discovered in Africa at both Pliocene and Lower Pleistocene localities, partly representing one or even two new species (e.g. Howell & Petter, 1976, 1979a, 1979b; Patterson et al., 1970; Savage, 1978). The fossils from East Africa like Hadar and Omo represent a species which is larger than any other *Enhydriodon* and which according to Howell & Petter (1979a) evolved from *E. africanus*. This species was found in deposits from 3.5 to 2 My old.

From Pikermi, *E. latipes* Pilgrim, 1931 was described. Only foot bones are known. The large size led Pilgrim (1931) to referring them to *Enhydriodon* with some doubt. If this is right, the species might be identical with some other *Enhydriodon* species.

Quaternary Enhydrini

Apart from some Early Pleistocene *Enhydriodon* finds from Africa, *Enhydra* is the only genus representing this tribe during the Quaternary. In historical times, *E. lutris* was distributed along the eastern and western coasts of the northern part of the Pacific Ocean (Harris, 1968; Mason & Macdonald, 1986). *E. lutris* is quite well known from the Late Pleistocene of California (Mitchell, 1966).

During the Late Pleistocene, a slightly different species, *Enhydra macrodonta* Kilmer, 1972 was also present in California. It differs from *E. lutris* by the larger posterior cheek teeth, the longer tooth row and the less specialised postcranial skeleton (Repenning, 1976; Kurtén & Anderson, 1980).

From the Early Pleistocene, only a few specimens are known from Oregon and California (Mitchell, 1966; Repenning, 1976). Those records are the oldest records of the genus. At least some of those specimens resemble *E. macrodonta* in some respects and are tentatively referred to it (Kurtén & Anderson, 1980).

The ancestry of *E. lutris* has been much discussed. Pohle (1919) and several later authors considered *E. reevei* to be ancestral to *E. lutris*. As Mitchell (1966) pointed out, this is not possible because of the age of the oldest records of *Enhydra*. Those records do, even if they do not belong to the extant species, resemble *E. lutris* very much and clearly represent the lineage leading to *E. lutris*. The specimen from the Timms Point Silt Member at San Pedro (California) probably is c. 2 Ma old and thus older than *E. reevei* from Bramerton. Further, it is difficult to conceive that the species originated in the Eastern Atlantic, while the fossil record points to an exclusively Pacific distribution during the entire Pleistocene. Repenning (1976) suggested a much more plausible origin for *Enhydra* in the North American *Enhydriodon* lineage. He showed that there are homologies between the P^4 of *E. lutris* and that of *Enhydriodon*.

Within the *Enhydriodon* lineage there is a trend towards a more prominent hypocone. This trend has continued in the line leading to *Enhydra* and in *E. lutris* the hypocone is prominent, while the protocone has been totally suppressed. Repenning (1976) showed quite convincingly that the cusp, normally called 'protocone' in *E. lutris* in fact is the same cusp as the hypocone of *Enhydriodon.*

Repenning (1976) supposed that *E. reevei* originated independently from European *Enhydriodon* and is not related to *Enhydra.* After comparing the casts of the holotype of *E. reevei* and the second specimen described in this paper with *E. lutris* I have come to the conclusion that the resemblance in morphology of the M_1 is so great, that a more direct relationship is more probable. Since *Enhydra lutris* was present in the Early Pleistocene, the genus *Enhydra* may have originated during the Pliocene at the eastern Pacific coast. *E. reevei* may represent an early offshoot of the genus, which migrated from the Pacific to the Atlantic basin sometime during the Late Pliocene or the earliest Pleistocene. As Mitchell (1966) pointed out, there was a possibility of migration between the two oceanic basins via a Central American seaway during the Pliocene and via the northern route intermittently during both Pliocene and Pleistocene. If we assume that the genus originated at the southern Pacific coast of North America, as seems to be indicated by the fossil material, a dispersal via a Central American seaway seems more probable. Though I think this scenario is the most probable, based on the fossil record known at this moment, I would like to stress that the view held by Repenning (1976) cannot be ruled out completely until more complete material of *E. reevei* becomes available.

OTTERS ON ISLANDS

A number of species, dealt with in this paper, are endemic island species from Mediterranean islands. It is known, that the faunas on the Pleistocene Mediterranean islands were so-called unbalanced faunas (Sondaar, 1977; Dermitzakis & Sondaar, 1979). Similar unbalanced faunas are known from islands in other regions too (Sondaar, 1977). Only certain groups of animals were able to reach such islands and, after arrival, developed into endemic forms, due to isolation and to specific selective forces, differing from those on the mainland. Often, endemic ruminants, dwarf elephants and dwarf hippopotamuses are found on such islands. Unbalanced island faunas are characterized by a lack of large carnivores. The composition of the faunas can be explained by the fact that only animals with rather good swimming abilities were able to reach the islands (in the case of small mammals like rodents natural rafts may have been a means for dispersal). Large carnivores are worse swimmers than both ruminants, elephants and hippos. The obvious exception are otters. And indeed, otters are found in many unbalanced island faunas. This has long gone unnoticed. Many island otters have been described only recently. This is due to the fact that otter fossils are rather rare. All insular otter species are known by one or two individuals only.

The following endemic island species have been described up to now from the Pleistocene of the Meditterranean:

Lutrogale cretensis	- Crete	*Sardolutra ichnusae*	- Sardinia
Lutra euxena	- Malta	*Algarolutra majori*	- Sardinia and Corsica
L. trinacriae	- Sicily	*Megalenhydris barbaricina*	- Sardinia

Also from former islands endemic Lutrinae are known: *Paralutra garganensis* from the Miocene island Gargano (Willemsen, 1983) and *Tyrrhenolutra helbingi, Paludolutra maremmana* and *P. campanii* (= *Enhydriodon campanii*) from the island fauna from the Miocene of Toscany (Hürzeler & Engesser, 1976; Hürzeler, 1987). *Lutrogale robusta* is known from a Pleistocene fauna from Java (Willemsen, 1986). It is from the Satir or from the Ci-Saat fauna. Both faunas indicate a certain degree of isolation (Sondaar, 1984).

Apparently, in all those cases the sea was a sufficient barrier to prevent frequent genetic interchange of the island population with the mainland population. In many mammal groups, present in Pleistocene (and other) island faunas, common evolutionary trends can be seen. For example, in ungulates we see a tendency towards size decrease, relative shortening of the legs and the development of low gear locomotion (Sondaar, 1977). This common tendency is caused by a common factor: the absence of predators and the limited food resources of an island (Sondaar, 1977; Willemsen, 1983a, b). The endemic island otters, however, do not show a common trend in their morphological adaptations (Willemsen, in press). Some island forms have a more robust dentition than their mainland ancestors (*Paralutra garganensis, Enhydriodon campanii, Algarolutra majori,* and to some extent *Lutrogale cretensis*), in other cases this is not so (*Lutra* spp. and *Sardolutra ichnusae*). In some cases the island form developed a more terrestrial adaptation (*L. cretensis*), in other cases it became more aquatic (*Sardolutra*). We have to keep in mind that the different species originated from quite different ancestral species. The ecology and functional morphology of the different ancestral otters differed probably more than the ecology of e.g. the elephants, ancestral to the island forms.

A special case is the island Sardinia, where as many as three lutrines may have lived at the same time. Here, we may see an adaptation to a different ecological niche for each species: one species became very large and probably preyed on large fish and shellfish (*Megalenhydris barbaricina*), another species was a much smaller, marine fish-feeder (*Sardolutra ichnusae*) and the third was not very large as well, and probably fed on fish and shellfish (*Algarolutra majori*). Unfortunately, the last species is too incompletely known to say much about the ecology. The very high degree of aquaticy of *S. ichnusae*, compared to *L. trinacriae*, though both had the same ancestor, may be due to a longer period of isolation and to the competition with the two other otter species. Competition may have caused the three species to specialize on different ecological niches (Willemsen, in press). During the last few years, new excavations and intensive research in the Late Pleistocene fauna of Sardinia are going on at Corbeddu Cave, triggered by the discovery of palaeolithic man at this site (Sondaar et al., 1984, 1986; Spoor & Sondaar, 1986). This research probably will provide much new information on the ecological circumstances in Late Pleistocene Sardinia and thus also give more insight in the factors, determining the evolution of the three otter species.

The taphonomy of the otter fossils found on the islands is rather peculiar. Lutrine fossils are rather rare, generally speaking, and most fossils from the European mainland are teeth or mandibles or isolated bones. Only in very few cases, different bones are known from the same site and not one complete skeleton is known. The same rarity is shown by the island species: of the six species, three are known by one individual only, the others probably by two individuals (in the case of *Lutra euxena* the number is fairly uncertain: eight bones may belong to one individual, one bone definitely represents a second). Remarkably, however, of the total of nine individuals four are represented by more or less complete skeletons (Table 22). These skeletons belong to *Lutrogale cretensis*, *Sardolutra ichnusae*, *Lutra trinacriae* and *Megalenhydris barbaricina*. All otter fossils, apart from the Maltese material which is from a fissure filling, were found in caves. All those skeletons were found articulated and the bones do not show signs of transportation, so it is clear that the animals died in the cave or were transported shortly after their death. In the case of *Megalenhydris*, which was found in an abyssal cave, it seems clear that the animal was trapped in the cave and died. The same probably is true for the *Sardolutra ichnusae* specimen, which was found lying on the sand and partly covered by sand in a rather unaccessible part of a cave (Malatesta, 1977). At present, the strange taphonomy of the island otters as compared to mainland otters cannot be explained.

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Manuscript received 30 May 1990, revised version received 9 January 1992.

Table 1. Measurements of the mandible and the lower dentition of *Lutra lutra*.

		RGM 146662	RGM 147002	Ke RM238	Ke RM2974	Ke RM3246	Ke RM4109	IPP We2/1	IPP G20d/B7	IPP I21c/B4	IPP F20b/B2	IPP L387/8
mandible												
	L				59.4							
	H				29.9							
	Hra	10.5	13.1	12.4	10.0		13.7					
	Wra	5.8	7.1	7.0	5.8		7.5					
L	P_2-M_2	33.0	(37.4)		(31.4)			36.3		35.7	35.8	
P_2	L	4.8	5.4	(4.2)		(4.9)	(4.1)	5.8		5.2	5.3	4.8
	W	2.9	3.3	(2.1)		(2.2)	(2.6)	3.4		3.1	3.0	2.6
P_3	L	5.3	6.3	(5.8)	(5.0)	(4.5)	6.3	6.3	6.3	5.0	6.0	4.9
	W	3.0	3.5	(3.1)	(2.2)	(3.0)	3.6	3.4	3.4	3.2	3.2	2.9
P_4	L	7.6	8.2	7.1	(6.6)	(7.4)	8.0	8.4	8.4	7.6	7.6	5.5
	W	3.8	4.6	3.8	(3.6)	(4.9)	4.6	4.5	4.6	3.9	3.9	3.5
M_1	L	12.4	13.4	13.3	12.5	(13.2)	13.6	13.2	c. 13	c. 12.6	13.0	11.9
	Ltri	7.6	7.4		7.2		7.8	7.9	7.9	7.3	7.6	7.0
	Ltal	4.8	6.0		4.7		5.7	5.2	c. 5	c. 5.3	5.4	4.9
	B					(4.6)						
	Wtri	5.7	6.5		5.8		5.6	6.3	5.9	5.7	5.8	5.3
	Wtal	5.7	6.6	6.7	6.1		6.7	6.3	6.1	c. 6.4	6.1	5.3
M_2	L	4.4		(3.5)	(3.2)	(2.8)	(2.8)	4.7		4.7	4.8	
	W	4.6		(2.7)	(3.3)	(2.9)	(3.6)	5.3			5.2	

Table 2. Measurements of the mandible and lower dentition of *Lutra simplicidens*.
PIV Hsh VIII/36 after Thenius, 1965; measurements of SMF PA/F 8718 were provided by Dr J.L. Franzen; those of KMBF I-711K were provided by Dr W.-D. Heinrich.

		PIV Hsh VIII/26 Hundsheim	BM 6089 E. Runton	CM CR4.984 W. Runton	SMF PA/F8718 Mosbach	KMBF I-711K Voigtstedt
mandible						
	Hra	13.1	13.7			
	Wra	6.8	7.3	6.2		
L	P_2-M_2	(33.9)	(32.3)			
P_2	L		(2.8)			
P_3	L		(5.9)			
P_4	L		(7.2)			
M_1	L	12.8	c. 12.0	12.7	12.95	12.5
	Ltri		6.8	7.1	8.00	7.5
	Ltal		c. 5.2	5.6	4.95	5.2
	Wtri		6.1	6.3	6.60	6.1
	Wtal		5.9	6.1	6.35	5.9
M_2	L			(3.4)		
	W			(3.7)		

Table 3. Measurements of the upper dentition of *Lutra* sp. from Hoxne and of *L. bravardi*. The measurements of *L. bravardi* were taken from the figure in Gervais (1859, pl. 27 fig.6). This author gives L P^1-M^1 in his text also and this agrees very well with the figure.

		BM Hoxne coll. 4936	*L. bravardi* holotype
L	P^1-M^1		34
P^4	Lb	12.3	12
	Ltal	7.4	8
	W	9.3	9
M^1	Lb		8
	Ll		9
	Wa		11
	Wp		9

Table 4. Measurements of the mandible and lower dentition of *Lutrogale cretensis* and of Recent *L. perspicillata*. Measurements of GIA 2/1974 after Symeonides & Sondaar (1975).

		Lutrogale cretensis				*L. perspicillata*	
		IvAU LiBa 1	GIA 2/1974	IvAU LiBa 2	IvAU LiBa 4	RMNH 4874	RMNH 15731
mandible							
	L	80.5	80.0				
	H	38.0	38.0				
	Hra	14.0	14.5				
	Wra	8.5					
L	P_2-M_2	41.0	42.2			38	40
P_3	L	6.3				6.4	6.8
	W	4.2				4.1	4.0
P_4	L	9.3	8.3			9.8	8.8
	W	5.0	5.1			4.8	4.9
M_1	L	(15.1)	16.5	15.7	15.6	15.2	15.4
	Ltri		9.0	9.2	9.3	8.7	8.5
	Ltal		7.0	6.5	6.7	6.1	6.2
	W		8.0				
	Wtri			7.8	7.8	7.0	6.6
	Wtal			7.9	7.8	6.9	7.1
M_2	L	(4.5)				5.5	5.0
	W	(4.5)				5.7	5.6

Table 5. Measurements of the skull and mandible of the holotypes of *Sardolutra ichnusae* and *Lutra trinacriae*.

	S. ichnusae UR coll.	*L. trinacriae* UP.PS1-PS25
skull		
Lb	92.0	105.3
Lcb	102.0	114
Ln	24.3	28.0
Lit	14.4	24.6
Lfac	42.7	43.4
Lcra	55.1	54.0
Lpal	45.0	52.0
Wc	24.6	30.7
Wio	23.4	28.4
Wppo	26.6	30.9
Wit	22.7	23.2
Wl	55.4	55.7
Wcra	55.0	54.8
Wmas	60.5	c. 64
Wjug	72.9	72.6
Wba	12.5	
Wbp	20.4	
Hsq	22.5	c. 28
mandible		
L	64.1	64
Hra	12.6	11.8

Table 6. Measurements of the dentition of *Lutra* spp., *Sardolutra ichnusae*, *Algarolutra majori* and *Megalenhydris barbaricina*. Measurements of *Algarolutra majori* from Corsica (UCBL coll.) after Helbing (1935).

		S. ichnusae UR coll. Sardinia	*L. trinacriae* UP PS1-PS25 Sicily	*N. euxena* BM 15450 Malta	*A. majori* UR 1944-1946 Sardinia	*A. majori* UCBL coll. Corsica,	*M. barbaricina* MCN coll. Sardinia
upper teeth							
L	$P^1(P^2)$-M^1	29.1	28.4				
C	L	6.2		5.8			
	W	6.4		5.4			
	H	c. 15		12.1			
P^1	L		2.0				
	W		c. 2.3				
P^2	L	6.7	c. 5.7				
	W	3.9					
P^3	L	6.8	7.2				7.9
	W	4.0	4.0				5.8
P^4	Lb	11.3	11.2			13.8	14.8
	Ltal	7.0	7.2		10.5	10.6	12.9
	W	8.1	8.6		10.0	12.0	13.5
M^1	Lb	7.5	8.0		7.4	9.2	12.0
	Ll	7.0	7.6		7.2	9.8	12.1
	Wa	10.5	10.0		11.8	13.6	15.2
	Wp	9.3	c. 8.3		9.9	11.4	12.7
lower teeth							
L	P_2-M_2	35.5	32				
C	L	6.3	6.4				8.8
	W	5.5	4.1				7.9
	H	c. 11	10.6				18
P_2	L	5.0					5.2
	W	3.1					4.2
P_3	L	6.0					8.2
	W	3.6					5.0
P_4	L	7.2	7.0				9.3
	W	4.5	3.8				6.0
M_1	L	12.9	13.1		14.2		17.7
	Ltri	7.2	7.9		6.8		10.2
	Ltal	5.1	5.2		7.4		7.7
	Wtri	6.3	6.3		6.5		9.2
	Wtal	6.3	6.3		6.5		9.1
M_2	L	5.6					
	W	4.5					

Table 7. Measurements of the skull of *Cyrnaonyx antiqua* and of Recent specimens of *Aonyx capensis*, *A. congica* and *Lutra lutra* for comparison.

	C. antiqua BM M 34370	*A. capensis* ZMA 316	*A. congica* ZMA 13533	*L. lutra* RMNH 20300
Lb		110.6	107.2	104.8
Ld	113.2	127.3	123.1	110.0
Lit	25	18.6	20.7	16
Lfac	62.0			54
Lcra	57.5			57
Wc	31	31.6	31.8	27.1
Wio	30.5	27.8	28.1	20.7
Wit	20.4	25.2	29.9	16.1

Table 8. Measurements of the upper dentition of *Cyrnaonyx antiqua* from Tornewton Cave and of the specimen from Verona which may be referred to this species. Measurements of the Verona specimen after Pasa (1947).

		BM M 34370	BM M 34373	BM M 34374	BM M 50707	Verona specimen
P^2	L	5.3				
P^4	Lb	11.2	11.3	11.6	11.0	11.8
	Ltal	9.9	9.2	10.1	9.0	
	W	9.5	9.4	10.0	9.4	10.0

Table 9. Measurements of the mandible and the lower dentition of *Cyrnaonyx antiqua*. Measurements of the Lunel-Viel specimen after de Serres et al. (1839); measurements of the Saalfeld and Weimar-Ehringsdorf specimens were provided by Dr W.-D. Heinrich.

		LPM LUV 68 Lunel-Viel	MNB MB Ma8069 Saalfeld	Weimar-E.	Ke RM 226 Maasvl.	BM M 34371 Torn. C.	BM M 34372 Torn. C.	BM M 50708 Torn. C.	BM M 50709 Torn. C.
mandible									
	L					73.8			
	H					33.8			
	Hra	16	14.2		15.2	14.7	13.6		
	Wra	9			7.9	7.7	7.0		
L	P_2-M_2					c. 37			
P_2	L					4.7			3.8
	W					3.8			2.5
P_3	L				6.2	6.0			
	W				4.0	3.8			
P_4	L				8.0	8.0			
	W				4.8	5.0			
M_1	L	14	14.0	14.0	14.8	13.5	13.2	14.1	
	Ltri		7.8	8.4	8.6	7.5	7.2	7.6	
	Ltal		6.8	7.4	6.2	6.0	6.0	6.5	
	Wtri		7.5	7.5	8.3	7.0	7.2	7.0	
	Wtal	8	8.4	c. 8.4	8.6	7.6	7.8	7.9	
M_2	L				(4.8)	(4.9)	6.4		
	W				(5.0)	(3.6)	6.3		

Table 10. Measurements of the M_1 of *Enhydra reevei* and of Recent *E. lutris*. Measurements on NCM 548 were not taken on the original specimen but on a cast in the British Museum (BM M 4118).

		E. reevei	*E. reevei*	*E. lutris*
		NCM 548	SM X.17989	RMNH
M_1	L	15.7	13.5	15.8
	Ltri	9.3	c. 7.9	8.1
	Ltal	6.4	c. 6.0	7.7
	Wtri	10.3	10.2	12.4
	Wtal	10.3		12.4

Table 11. Measurements of the mandible and the lower dentition of *Limnonyx sinerizi*, *Limnonyx pontica* and *Lutra hessica*. Measurements on UHGI P 1118 were provided by Dr B. Kurtén, and on *L. sinerizi* by J. van der Made; MD Din 26 after Tobien (1955).

		L. sinerizi MS IPS 2058 holotype Can Ponsich	*L. pontica* MD Din 26 Eppelsheim	*L. pontica* UHGI P 1118 (=2295) holotype Kishinev	*L. hessica* BM M 27486 holotype Eppelsheim
mandible					
	Hra	15.6		c. 15.4	15.0
	Wra	8.6		8.9	8.6
P_4	L	7.8	9.0		
	W	4.8	5.7		
M_1	L	11.7	14.6	13.5	15.8
	Ltri	6.0			9.0
	Ltal	5.7			6.8
	W		8.8	7.4	8.5
	Wtri	6.2		7.1	8.0
	Wtal	6.2		7.4	8.5
M_2	L			6.2	
	W			6.4	

Table 12. Measurements of the humerus of *Lutra* and *Sardolutra*. Measurements of *L. trinacriae* after Burgio & Fiore (1988); measurements on NHM 1956/296 were taken by Dr T. van Kolfschoten.

	L. lutra		*L. simplicidens*		*L. euxena*		*L. trin.*	*S. ichn.*
	Ke	Ke	BM	NHM	BM	BM	UP	UR
	RM 228	RM 229	17895	1956/296	M 15443	M 15444	PS1-PS25	coll
L		74.8					78.0	71.0
L troch. maj.-lat. epicondyle		73.2					78.0	69.4
L without prox. epiphysis					63			
Wmin diaphysis	8.3	6.3	6.4	8.0	5.5		7.8	6.5
W prox. epiphysis	21.3	18.0		19.7			22.7	19.1
ant-post L prox. epiphysis	20.4	17.4		21.0				20.4
W distal epiphysis		23.9			24.5	26.9	30	

Table 13. Measurements of the ulna of *Lutra* and *Sardolutra*. Measurements of IQW 1216/2850 after Thenius (1965).

	L. lutra	*L. simpl.*	*L. euxena*	*S. ichn.*
	Ke RM 231	IQW 1216/2850	BM 15448	UR coll.
L	72.1	68.1		70.0
L olecranon	11		11.7	13.0
L styloid process	4.5			5.0
W ant-post distally of lesser sigmoid notch	9.5			9.8
L interosseous membrane tub.	5.2			8
W interosseous membrane tub.	2			2.6
Distance lesser sigmoid notch to inteosseous membrane tub.	16.0			22.2

Table 14. Measurements of the radius of *Lutra* and *Sardolutra*. *L. simplicidens* after Thenius (1965) and N. trinacriae after Burgio & Fiore (1988).

	L. simplicidens			*L. euxena*	*L. trin.*	*S. ichn.*
	IQW Voi 2309	PIV Hsh no numb.	PIV Hsh VIII/14	BM 15445	UP PS1-PS25	UR coll.
L	48.7	49.0	52.0		57	50.3
L without dis. epiph.				45.9		
W prox. epiphysis	9.2	9.2	10.2	9.6		
T prox. epiphysis	6.3	6.3	7.5	6.5		
W dis. epiphysis	10.6	11.2	13.2		14	
T dis. epiphysis	8.3	8.4	9.2			

Table 15. Measurements of the innominate of *Lutra* and *Sardolutra*.

	L. lutra		*S. ichn.*
	Ke RM 233	Ke RM 3470	UR coll.
L			105.2
L ilium	42	c. 43	48.3
L ischiopubis			46.0
D acetabulum	13.7	13.4	17.8

Table 16. Measurements of the femur of *Lutra*, *Lutrogale* and *Sardolutra*. GIA 2/1974 after Willemsen (1980), *L. trinacriae* after Burgio & Fiore (1988).

	L. simpl.	*L. cretensis*		*L. trin.*	*S. ichn.*
	PIV Hsh no numb.	IvAU Li Ba3	GIA 2/1974	UP PS1-PS25	UR coll.
L	c. 70			79	71.0
L troch. maj.-lat. epicondyle		88.6	94.3	77.8	70.6
D head		13.5	14.8	12.8	11.7
W neck		10.6	12.4	10.1	9.7
Wmin diaphysis	8.2	8.8	11.8	c. 11	8.4
Tmin diaphysis	7.9	7.6	8.7		9.4
W trochlea at most distal point		10.0	11.0		9.7
Wmax med. condyle		9.7	10.7		7.9
Wmax lat. condyle		8.5	10.1		7.8

Table 17. Measurements of the tibia and fibula of *Lutra* and *Sardolutra*.

	L. lutra	*S. ichn.*
	Ke RM 235	UR coll.
tibia		
L	98.7	92.9
Wmin diaphysis	7.0	6.5
Tmin diaphysis	8.0	6.3
Wmax med. prox. condyle	7.6	9.2
Wmax lat. prox. condyle	10.0	11.0
fibula		
L		82.0

Table 18. Measurements of the metapodials of *Lutra euxena* and *Sardolutra ichnusae*.

	L. euxena		*S. ichn.*
	BM M 15447	BM M15449	UR coll.
2nd metacarpal			
L	19.9		19.5
Wmin diaphysis	4		
2nd metatarsal			
L		33.8	38
Wmin diaphysis		4	

Table 19. Ratio lo/li for the m. teres major for different carnivores; partly after Willemsen (1980).

Nesolutra ichnusae	UR coll.	2.0
Lutra lutra	RMNH 12915	3.1
Lutrogale perspicillata	SMF 44196	3.8
Lutrogale cretensis	GIA 2/1974	3.9
Amblonyx cinerea	IvAU unnumbered	4.0
Martes martes	Reumer coll. 7474	5.5

Table 20. The sacropelvic angle (in degrees)in different carnivores; after Savage (1957) and Willemsen (1980).

Pinnipedia	after Savage	< 30
Potamotherium valletoni	after Savage	25
Nesolutra ichnusae	UR coll.	30
Lutra lutra	RMNH 12915	35
	after Savage	35
Lutrogale cretensis	GIA 2/1974	40
Lutrogale perspicillata	SMF 44196	40
	ZMA 9556	40
Amblonyx cinerea	IvAU unnumbered	40
Terrestrial carnivores	after Savage	55

Table 21. Ratio of ilium length to ischiopubis length; after Willemsen (1980).

Phoca vitulina	RMNH 2349	0.31
Macrorhinus leoninus	RMNH 1595	0.39
Monachus albiventer	RMNH 25498	0.50
Trichechus rosmarus	RMNH	0.60
Eumetopias californianus	RMNH 1135	0.65
Potamotherium valletoni	after data from Savage	ca. 0.80
Lutra maculicollis	RMNH cat. ost. b	1.00
Enhydra lutris	RMNH cat. ost. a	1.07
Lutra lutra	RMNH	1.02-1.25 (mean 1.14, n=20)
Lutrogale perspicillata	SMF 44196	1.08
	ZMA 9556	1.14
Amblonyx cinerea	IvAU unnumbered	1.23
	RMNH cat. ost. a	1.25
Lutrogale cretensis	GIA 2/1974	1.34
Aonyx capensis	RMNH cat. ost. e	1.35
Martes martes	Reumer coll. 7404	1.42

Table 22. Island species: the minimum number of individuals, represented by the fossils, is given as well as the number of complete or partly complete skeletons; adapted from Willemsen (in press).

Species	min. nr. individ.	(part of) skeleton	type of site
Lutrogale cretensis	2	1	cave, Crete
Lutra euxena	2	0	fissure filling, Malta
Lutra trinacriae	1	1	cave, Sicily
Sardolutra ichnusae	1	1	cave, Sardinia
Algarolutra majori	2	0	caves, Sardinia and Corsica
Megalenhydris barbaricina	1	1	abyssal cave, Sardinia

Appendix

FOSSIL AND RECENT LUTRINAE

Tribus Lutrini Gray, 1865

Lutra lutra (L., 1758)
Lutra affinis Gervais, 1859
Lutra bravardi Pomel, 1843
Lutra bressana Depéret, 1893
Lutra canadensis Schreber, 1776
Lutra euxena (Bate, 1935)
Lutra felina Molina, 1782
Lutra iowa Goldman, 1941
Lutra licenti Teilhard & Piveteau, 1930
Lutra longicaudis Olfers, 1818
Lutra maculicollis Lichtenstein, 1835
Lutra palaeoleptonyx Falconer, 1868
Lutra provocax Thomas, 1908
Lutra simplicidens Thenius, 1965
Lutra sumatrana Gray, 1865
Lutra trinacriae (Burgio & Fiore, 1988)

Lutrogale perspicillata (Geoffroy, 1826)
Lutrogale cretensis (Symeonides & Sondaar, 1975)
Lutrogale paleoleptonyx (Dubois, 1908)
Lutrogale robusta (Von Koenigswald, 1933)

Sardolutra ichnusae (Malatesta, 1977)

Pteronura brasiliensis (Gmelin, 1788)

Satherium piscinarium (Leidy, 1873)

Algarolutra majori (Malatesta, 1978)

Paralutra jaegeri (Fraas, 1862)
Paralutra garganensis Willemsen, 1983
Paralutra transdanubica Kretzoi, 1951

Mionictis incertus Matthew, 1924
Mionictis artenensis Ginsburg, 1968
Mionictis dubia (de Blainville, 1841)
Mionictis elegans
Mionictis letifer Cook & MacDonald, 1942

Lutravus halli Furlong, 1932

Siamogale thailandica Ginsburg, Ingavat & Tassy, 1983

Lutra? *hessica* Lydekker, 1890
Lutra? *lybica* Stromer, 1914

Tribus Aonyxini Sokolov, 1973

Aonyx capensis (Schinz, 1827)
Aonyx congica Lönnberg, 1910
Aonyx aonychoides Zdansky, 1924

Amblonyx cinerea (Illiger, 1815)

Cyrnaonyx antiqua (de Blainville, 1841)

Limnonyx sinerizi Crusafont Pairò, 1950
Limnonyx pontica (Nordmann, 1858)

Megalenhydris barbaricina Willemsen & Malatesta, 1987

Tribus Enhydrini Gray, 1865

Enhydra lutris (L., 1758)
Enhydra reevei (Newton, 1910)

Enhydriodon sivalensis Falconer, 1868
Enhydriodon africanus Stromer, 1931
Enhydriodon falconeri Pilgrim, 1932

Paludolutra maremmana Hürzeler, 1987
Paludolutra campanii (Meneghini, 1862)
Paludolutra lluecai (de Villalta Comella & Crusafont Pairò, 1945)

Tyrrhenolutra helbingi Hürzeler, 1987

Sivaonyx bathygnathus Pilgrim, 1932

Vishnuonyx chinjiensis Pilgrim, 1932

Enhydriodon? latipes Pilgrim, 1931