New species of *Krombeinius* (Hymenoptera: Chalcidoidea: Perilampidae) from Indonesia, and the first description of first-instar larva for the genus

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Key words: Hymenoptera; Chalcidoidea; Perilampidae; *Krombeinius*; Indonesia.
Two new species of *Krombeinius* from Indonesia are described and illustrated, *K. kubah* from Java and *K. dictyon* from Sulawesi. In addition, *K. eumenidarum* Bouček and *K. megalaspis* (Cameron) are redescribed to allow comparison with the closely related species, *K. dictyon* and *K. kubah*, respectively. The first-instar larva of *K. kubah* is described from an aculeate wasp cocoon associated with the holotype and these planidia are compared with those known for Perilampidae and Eucharitidae. The new species are accommodated in the key to species and phylogenetic analysis of the genus presented in Darling (1988) and the biogeographic implications of the phylogeny are discussed.

Introduction

Since the publication of my review of the genus *Krombeinius* in 1988, two additional species from Indonesia have been found in the collection of the Nationaal Natuurhistorisch Museum in Leiden, the Netherlands (RMNH). One specimen is associated with a cocoon of an aculeate wasp and planidial larvae were found by clearing the cocoon and host remains in Nesbitt's solution. The only definite host association in the genus is primary parasitism of *Paraleptomenes mephitis* [Vespidae, Eumeninae] (see Darling, 1988; Krombein 1978). These planidia are the first immature stages recorded for the genus and only the second record for a genus of Perilampidae and therefore provide an opportunity to evaluate the cladogram of immature stages presented in Darling (1992).

With this, my third paper on this small genus, I abandon all hope that we actually know anything about the actual number of species in the genus; virtually every specimen represents a different species. To date, eight species have been described from less than 20 specimens (7 Oriental, 1 Afrotropical) – and five species are known only from the holotype. However, the diagnosis of the genus and certain features of the cladistic relationships presented in 1988 are robust to the addition of two additional species. The new species are described to better document the insect fauna of Indonesia, to have a name to associate with the planidial larvae, and to contribute cladistic and distributional data to the ongoing discussion of the biogeography of southeast Asia. And with the redescriptions provided herein for *K. eumenidarum* and *K. megalaspis*, consistent descriptions and measurements have been made for all species of the genus based on type material, which will facilitate future descriptive work should the need arise.

Abbreviations used in the text: F1-7, funicular segments; MSC, length of mesoscutum along midline; OOL, length of ocular-ocellar line; PN, length of pronotum along midline; POL, length of posterior ocellar line; SC, length of scutellum along midline; T2-8, metasomal tergites 2-8. Figures are referred to by the convention: Fig., for figures in this paper and fig., for figures in previous publications. Sculpture types follow Eady (1968).

Krombeinius Bouček, 1978

Krombeinius Bouček, 1978: 302, figs. 1, 2 [original description, key]; Darling, 1983, figs. 1, 2, 3, 6-17 [diagnosis, description, phylogenetic relationships]; Darling, 1988, fig. 19 [diagnosis, description, key to species, phylogenetic relationships].

Type species.— *Krombeinius eumenidarum* Bouček, 1978 [original designation].

Diagnosis (habitus drawing, fig. 1 in Darling, 1983).— Large (3 to 6 mm) and robust perilampids, black in color without metallic reflections, differentiated from other perilampid genera by the following combination of characters (putative apomorphies in bold face): marginal vein of forewing longer than postmarginal vein (Figs. 17-22); **labrum with a central stalk**, lacking aboral digits (Darling, 1988, fig. 4); **third metasomal tergite massive, much larger than second** (Darling, 1983, fig. 1); and malar sulcus obliterated by oblique costae (Figs. 1, 7, 12). For complete description, see Darling (1988).

Species accounts

Krombeinius eumenidarum Bouček, 1978
(Fig. 17)

Krombeinius eumenidarum Bouček 1978: 302, fig. 1; Darling, 1983, figs. 2, 3, 6-9 [♂ genitalia, labrum, phylogenetic relationships]; Darling, 1988, figs. 17, 19 [♂ scape, phylogenetic relationships].

Material.— Holotype, ♂ (USNM, #76270), Paratype, ♀♀ (BMNH, USNM: #76270): Sri Lanka, Trincomalee District, Trincomalee (see Bouček, 1978 for detailed label data); ♂ (USNM): India, Kerala, Pechiparai (D. Chris Darling Slide Nos. 160-162; mouthparts, genitalia). Note: the type material was prematurely killed in alcohol, with the wings unexpanded. Wing venation and the structure of the labrum and propodeum are based only on male specimens, but is likely consistent with females.

Distribution.— Sri Lanka, India.

Host.— This species is a primary parasitoid of *Paraleptomenes mephitis* (Cameron) [Vespidae: Eumeninae] (see Krombein, 1978).

Diagnosis.— Only *K. eumenidarum*, *K. saunion* Darling, and *K. dictyon* spec. nov. have the inner orbits developed as prominent scrobal walls with distinct raised sculpture (Fig. 1; Darling, 1983, figs. 8, 9, 16, 17) and the lateral pronotum with a distinct callus (Fig. 4; Darling, 1983, fig. 1). Longitudinal costae on the inner orbits are found only in the first two species and *K. eumenidarum* can be distinguished from *K. saunion* by the shape of the scutellum, truncate (Darling 1983, fig. 7) versus produced as an elongate spine (Darling 1983, fig. 15). See Darling (1988) for a key that will distinguish *K. eumenidarum* for its sympatric congener, *K. srilanka* Darling, 1988.

Redescription.— This description is a composite for males and females and sexual differences are noted where relevant; measurements for the holotype are provided in square brackets [ ].

Length about 4 mm. Black, except: tegula and mandible reddish-brown, legs dark brown with apices of tibiae and tarsi yellow; wings hyaline, veins darkened; antenna black; but see "Variation" section.

Head (Darling, 1983, figs. 6, 8, 9): wider than pronotum, in dorsal view transverse, width:length = 1.7-1.8 [1.67]; in frontal view transverse, width:height = 1.2 [1.18]; maximum width of scrobe 0.4-0.5 [0.47] head width; frontal carina extended below lower ocular line and almost reaching clypeus, in frontal view recurved with 3 inflection points between median ocellus and supraclypeus; length of malar space 0.3 [0.27] eye height; OOL 0.9-1.0 POL [0.96]; median ocellus not situated on frontal projection; inner orbits developed as raised scrobal walls, distinctly costate from OOL to lower ocular line; outer orbits with costae convergent on clypeus; scrobal cavity deep and broad, delimited by frontal carina; clypeus transverse, width:height = 1.6-1.7 [1.7], almost completely covered with long setae, glabrous only along supraclypeus; clypeus not delimited laterad by distinct suture and with weak raised median callus, upper margin not indicated by distinct suture, lower margin emarginate; tentorial pits indistinct; supraclypeus glabrous, height 0.6 clypeus height, strongly convex along midline, laterad with shallow channels for reception of antenna; antennal torulus above lower ocular line; ocular-ocellar region and ocellar triangle smooth and shining, without costae radiating from ocelli; vertex with weak costae at posterior margin. Labrum (Darling, 1983, fig. 3): with 5 short digits and 4 sessile setae, strongly excised medially. Antenna: scape narrowly linear, length about 5 maximum width [4.7]; pedicel and funicular segments (F1-F7) subequal in length; pedicel about one-quarter scape length; annellus about one-quarter length of F1; F1-F7 transverse, wider than long; clava about one-third length of funicle.

Mesosoma (Bouček, 1978, fig. 1; Darling, 1983, fig. 7): pronotum massive, PN:MSC = 0.30 [0.27], lateral pronotum with a distinct callus, giving the suggestion of bumpy shoulders (as in *K. saunion*, Darling, 1983, fig. 1); pronotum bicarinulate, with complete double carina along mesoscutum, sculpture rugulose and irregularly pitted; midlobe of mesoscutum and scutellum regularly punctate-reticulate; sidelobes of mesoscutum smooth along notauli, laterally punctate-reticulate; scutellum truncate, SC:MSC = 1.3-1.4 [1.34], in lateral view smoothly tapered abruptly toward apex, underside smooth with shallow convergent grooves; propodeum about twice [1.85] as long as metanotum along midline, with deep crenulate groove along anterior margin and double row of foveae along midline, submedian areas imbricate with transverse costulae (as in Fig. 5), callus reticulate-rugose; metanotum with foveae along anterior and posterior margins, dorsellum glabrous, not expanded laterad as imbricate horizontal flange; prepectus 0.4 [0.36] width of adjacent pronotum, with about 12 irregular foveae, not restricted to central region, imbricate dorsad, sculpture not distinctly differentiated from lateral pronotal panel (as in Fig. 2); axilla punctate-reticulate above, costulate below; axillula small, upper margin regular and distinctly separated from scutellum, extended towards apex of scutellum as narrow triangular lobe, without distinct longitudinal costae. Forewing venation (Fig. 17): submarginal vein 2.6 marginal vein, postmarginal 0.7 marginal, stigmal 0.2 marginal, stigmal 0.3 postmarginal; stigmal vein thick, making almost a right angle (90 degrees) with marginal vein, stigma gradually expanded, with 4 sensilla.

Metasoma: T2 smoothly concave, coriarious in concavity, with setae and punctures laterad, laterotergite glabrous; border between T2 and T3 indicated by weak suture; T3 quadrate, length 0.8-0.9 [0.88] width along T2, smooth and shining, covered with short setae except along T2 and T4 border, almost completely covered with pinpunctures; ovipositor not examined; male genitalia (see Darling, 1983).

Variation.— In one male and one female paratype the flagellum is yellow in colour, contrasted with the dark scape and pedicel. These are regarded as the least developed of the specimens based on the degree of wing expansion and the light colour could be a teneral condition. The wild-caught male I examined from Kerala, India and a female from the Malabar coast of India discussed in Bouček, 1978 have uniformly dark brown antenna.

Krombeinius dictyon spec. nov.
(Figs. 1-5, 18)

Material.— Holotype, ♀ (RMNH), "Museum Leiden, J. v. d. Vecht, S. Celebes, Watang Lamura, 30.v.1940". The holotype is pinned and is in excellent condition.

Type locality: Indonesia, South Sulawesi Province (Sulawesi Selatan), Watanlamuru. The actual collecting locality (Watanlamuru) is west of the major city of Watampone at the following coordinates: 4° 36'S, 119° 58'E (C. van Achterberg, in litt.).

Etymology.— The specific epithet is a noun in apposition, from the Greek for "net" and is a reference to the reticulate pattern of sculpture on the inner orbits of the head.

Diagnosis.— This is the only species of the genus with reticulate sculpture on the inner orbits (Fig. 1). This species is closely related to both *K. eumenidarum* and *K. saunion*; in all three species the pronotum, in lateral view, has a distinct callus and the inner orbits are developed as massive scrobal walls. Following the key provided in Darling (1988), this species would run to couplet 2 where the configuration of the scutellum (acuminate, Fig. 3) would distinguish this species from both *K. eumenidarum* (truncate; fig. 7, Darling, 1983) and *K. saunion* (with prominent spine; fig. 15, Darling, 1983).

Description.— Female: length 5 mm. Black, except: mandible reddish-brown, apices of tibiae and tarsi yellow; wings hyaline, veins darkened.

Head (Fig. 1): wider than pronotum, in dorsal view transverse, width:length = 1.8; in frontal view transverse, width:height = 1.2; maximum width of scrobe 0.5 head width; frontal carina extended below lower ocular line to clypeus, in frontal view smoothly curved with a single inflection point between median ocellus and clypeus; length of malar space 0.3 eye height; OOL equal to POL; median ocellus not situated on frontal projection; inner orbits developed as raised scrobal walls, reticulate, with network of strong rugae from OOL to lower ocular line (Fig. 1); outer orbits with costae convergent on clypeus; scrobal cavity deep and broad, delimited by frontal carina; clypeus transverse, width:height = 1.4, almost completely covered with long setae, glabrous only along supraclypeus; clypeus not delimited laterad by distinct suture and with weak raised median callus, upper margin not indicated by distinct suture, lower margin emarginate; tentorial pits indistinct; supraclypeus glabrous, height 0.6 clypeus height, strongly convex along midline, laterad with distinct channels for reception of antenna; antennal torulus above lower ocular line; ocular-ocellar region reticulate laterad, without costae radiating from ocelli, shagreened inside ocellar triangle; vertex with weak costae at posterior margin. Labrum not examined. Antenna: scape narrowly linear, length about 7 maximum width; pedicel and funicular segments (F1-F7) subequal in length (7 versus 7, 8, 8, 8, 9, 9, 8); pedicel 0.24 scape length; annellus 0.38 length of F1; F1-F7 transverse, wider than long; clava 0.29 length of funicle.

Mesosoma (Figs. 2-5, 18): pronotum massive, PN:MSC = 0.35, lateral pronotum with a distinct callus, giving the suggestion of bumpy shoulders (Fig. 4); pronotum bicarinulate, with complete double carina along mesoscutum, sculpture irregularly pitted, collar produced cephalad; midlobe of mesoscutum and scutellum regularly punctate-reticulate; sidelobes of mesoscutum smooth along notauli, laterally reticulate; scutellum acuminate (Fig. 3), SC:MSC = 1.25, in lateral view tapering abruptly toward apex (Fig. 4), underside coriarious with shallow convergent grooves; propodeum about twice [1.7] as long as metanotum along midline, with deep crenulate groove along anterior margin and double row of foveae along midline, submedian areas delimited by deep foveae dorsad and laterad, imbricate with transverse costulae (Fig. 5), callus reticulate-rugose; metanotum with foveae along anterior and posterior margins, dorsellum glabrous (Fig. 5), expanded laterad as imbricate horizontal flange; prepectus 0.3 width of adjacent pronotum (Fig. 4), with about 12 irregular foveae, restricted to central region, margins smooth to imbricate, sculpture distinctly differentiated from lateral pronotal panel (Fig. 2); axilla punctate above, costulate below; axillula large, upper margin irregular and distinctly separated from scutellum, extended towards apex of scutellum as broad triangular lobe (Fig. 4), without distinct longitudinal costae. Forewing venation (Fig. 18): submarginal vein 2.6 marginal vein, postmarginal 0.6 marginal, stigmal 0.25 marginal, stigmal 0.40 postmarginal; stigmal vein thick, making almost a right angle (90 degrees) with marginal vein, stigma gradually expanded, with 4 sensilla.

Metasoma: T2 smoothly concave, coriarious in concavity, with setae and punctures laterad, laterotergite glabrous; border between T2 and T3 indicated by weak suture; T3 quadrate, length 0.95 width along T2, smooth and shining, covered with short setae and very fine pin-punctures except along T2 border, glabrous area wider along midline; ovipositor not examined.

Male.— Unknown.

Krombeinius megalaspis (Cameron, 1912)
(Figs. 6-10, 20)

Perilampus megalaspis Cameron 1912: 63; Bouček, 1978, fig. 2 [lectotype designation, n. comb.]; Darling, 1983, figs. 10-13 [phylogenetic relationships]; Darling ,1988, fig. 19 [phylogenetic relationships].

Material.— Lectotype and paralectotype, ♀♀ (BMNH): Malaysia, Sarawak, Kuching; ♀ (BMNH): Malaysia, Sarawak, Gunung Mulu National Park. See Bouček (1978) for detailed label data.

Distribution.— Northern part of the island of Borneo.

Diagnosis.— Only this species and *K. kubah* spec. nov. have a single large fovea on the prepectus (Figs. 9, 16); in all other species there are many smaller foveae (as in Fig. 2). Only in these two species is the median ocellus situated on a shelf-like frontal projection (Fig. 13); the frontal projection is rounded in *K. megalaspis* (Fig. 8), not acuminate or teardrop shape as in *K. kubah* (Fig. 14). In addition, the inner orbits are more weakly developed in *K. megalaspis* (Fig. 7, cf, Fig. 12).

Redescription.— Female: length 3.3-3.5 mm. Black, except: flagellum yellow, annellus and apex of clava brown; tegula and mandible reddish-brown, legs brown, inner surface of foretibia, apices of femora, tibiae, and tarsi yellow; wings hyaline, veins darkened.

Head (Figs. 6-8; see also Darling 1983, figs. 10, 12, 13): wider than pronotum, in dorsal view transverse, width:length = 1.8-2.0; in frontal view transverse, width: height = 1.1; maximum width of scrobe 0.51 head width; frontal carina extended below lower ocular line and almost reaching clypeus, in frontal view smoothly arched with a single inflection point between median ocellus and supraclypeus (Fig. 6); length of malar space 0.25 eye height; OOL equal to POL; median ocellus situated on frontal projection overhanging scrobal cavity, frontal projection oval with apex rounded (Fig. 8); inner orbits smooth and shining, developed as low scrobal walls (Fig. 7), with very weak rugulae parallel to frontal carina; outer orbits with costae convergent on clypeus; scrobal cavity deep and broad, delimited by frontal carina; clypeus quadrate, width:height = 1.1, almost completely setose, glabrous only along supraclypeus; clypeus delimited laterad by distinct suture and with raised median callus, upper margin indicated by distinct suture, lower margin weakly emarginate (Fig. 6); tentorial pits indistinct; supraclypeus glabrous, height 0.5-0.6 clypeus height, convex along midline, laterad with distinct channels for reception of antenna; antennal torulus above lower ocular line; ocular-ocellar region smooth and shining without costae radiating from ocelli; vertex with weak costae at posterior margin. Labrum not examined. Antenna: scape narrowly linear, length about 8.5 maximum width; pedicel and funicular segments (F1-F7) subequal in length (11 versus 12, 11, 10, 10, 10, 10, 9); pedicel 0.2 scape length; annellus 0.25 length of F1; F1-F7 transverse, wider than long; clava 0.32 length of funicle.

Mesosoma (Figs. 9, 10, 20; see also Darling, 1983, fig. 11): pronotum massive, PN:MSC = 0.35, lateral pronotum convex, without a callus or suggestion of bumpy shoulders; pronotum bicarinulate, with complete double carina along mesoscutum, sculpture imbricate except smooth along mesoscutum; mesoscutum and scutellum regularly punctate-reticulate; sidelobes of mesoscutum not differentiated or smooth along notauli; scutellum weakly bilobed (as in Fig. 15), SC:MSC = 1.25, in lateral view strongly convex, apex subvertical, underside smooth with shallow convergent grooves; propodeum short, only as long as metanotum along midline, with deep crenulate groove along anterior margin and raised median area, submedian areas very narrow, delimited by deep foveae dorsad and laterad (Fig. 10), callus reticulate-rugose; metanotum with deep arched foveae, dorsellum expanded laterad as costulate horizontal flange; prepectus 0.4 width of adjacent pronotum, with shallow rounded fovea (Fig. 9), devoid of surface sculpture except imbricate behind fovea, sculpture distinctly differentiated from punctate-reticulate lateral pronotal panel; axilla punctate-reticulate above, costulate below; axillula large and distinctly separated from scutellum and extended towards apex of scutellum as broad triangular lobe, with distinct longitudinal costae. Forewing venation (Fig. 20): submarginal vein 2 marginal vein, postmarginal 0.6 marginal, stigmal 0.2 marginal, stigmal 0.33 postmarginal; stigmal vein slender, making oblique angle with marginal vein, stigma abruptly expanded, with 4 sensilla.

Metasoma: T2 smoothly concave with sparse setae, without punctures, laterotergite glabrous; border between T2 and T3 indicated by weak suture; T3 transverse, length 0.7 width along T2, smooth and shining, in dorsal view with short setae and small punctures laterad and on midline along T2 border; ovipositor not examined.

Male.— Unknown.

Notes.— Fig. 11 in Darling (1983) is an inaccurate representation of the shape of the apex of the scutellum; the scutellum is weakly bilobed, indistinguishable from *K. kubah* (Fig. 15).

Krombeinius kubah spec. nov.
(Figs. 11-16, 21)

Material.— Holotype, ♀? (RMNH), "L. G. E. Kalshoven, Java, 40m, Semarang, Teak-forest 26.1.1931 S21[?]151a". The holotype is card mounted with venter and the left side of the head and both antennae embedded in mounting medium; the distal funicular segments are missing. There is uncertainty concerning the sex of the holotype because the genitalia and scape cannot be examined without remounting the specimen, which could result in additional damage. See "Notes" below.

Type Locality.— Indonesia, Central Java Province (Jawa Tengah), Semarang.

Etymology.— The specific epithet is a noun in apposition. "Kubah" is the Indonesian word for the dome of the mosque and these characteristic structures are prevalent throughout Java. The frontal projection that encloses the anterior ocellus (Figs. 13, 14) has the "double ogee curve" shape characteristic of these mosques.

Diagnosis.— This species can be recognized immediately by the characteristic structure of the median ocellus. This species is most similar to, and would be identified as *K. megalaspis* following the key provided in Darling (1988). These are the only two species of the genus with a single large fovea dorsad on the prepectus (Figs. 9, 16) and with the median ocellus situated on a distinct frontal projection. The frontal projection is acuminate in *K. kubah* (Fig. 14), not rounded as in *K. megalaspis* (Fig. 8). *Krombeinius kubah* and *K. megalaspis* can also be distinguished by the colour of the flagellum, brown versus bright yellow, and the shape of the inner orbits, recurved (Fig. 11) versus smoothly arched (Fig. 6).

Description.— Female: Length 3.6 mm. Black, except flagellum brown; tegula and mandible reddish-brown; legs dark brown, inner surface of foretibia, apices of femora, tibiae, and tarsi yellow; wings hyaline, veins darkened.

Head (Figs. 11-14): wider than pronotum, in dorsal view transverse, width:length = 1.78; in frontal view transverse, width:height = 1.14; maximum width of scrobe one-half head width; frontal carina extended below lower ocular line and almost reaching clypeus, recurved, with 3 inflection points between median ocellus and supraclypeus (Fig. 11); length of malar space 0.27 eye height; OOL much longer than POL, OOL/POL 1.23; median ocellus situated on frontal projection overhanging scrobal cavity, frontal projection acuminate, teardrop shaped (Figs. 13, 14); inner orbits smooth and shining, scrobal walls more prominent than in *K. megalaspis*, with 2-3 weak rugulae parallel to frontal carina (Fig. 12); outer orbits with costae convergent on clypeus; scrobal cavity deep and broad, delimited by frontal carina; clypeus quadrate, width:height = 1.16, polished, only anterior half setose; clypeus delimited laterad by incomplete suture and with raised median callus, upper margin indicated by distinct suture, lower margin weakly emarginate (Fig. 11); tentorial pits indistinct; supraclypeal area glabrous, height 0.6 clypeus height, convex along midline, laterad with distinct channels for reception of antenna; antennal torulus above lower ocular line; ocular-ocellar region smooth and shining without costae radiating from ocelli; vertex with weak costae at posterior margin. Labrum not examined. Antenna: scape narrowly linear, pedicel and funicular segments (F1-F5) subequal in length; annellus about one-quarter length of F1; F1-F5 transverse, wider than long.

Mesosoma (Figs. 15, 16, 21): pronotum massive, PN:MSC = 0.35, lateral pronotum convex, without callus or suggestion of bumpy shoulders (Fig. 16); pronotum bicarinulate, with complete double carina along mesoscutum, sculpture imbricate except smooth along mesoscutum; mesoscutum and scutellum regularly punctate-reticulate; sidelobes of mesoscutum not differentiated or smooth along notauli; scutellum weakly bilobed (Fig. 15), SC:MSC = 1.42, in lateral view strongly convex, apex subvertical (Fig. 16), underside coriarious with shallow convergent grooves; propodeum short, only as long as metanotum along midline, similar to *K. megalaspis* (as in Fig. 10); metanotum with deep arched foveae, dorsellum expanded laterad as smooth horizontal flange; prepectus 0.3 width of adjacent pronotum, with fovea (Fig. 16), devoid of surface sculpture and distinctly differentiated from punctate-reticulate lateral pronotal panel; axilla punctate-reticulate above, costulate below; axillula large and distinctly separated from scutellum and extended towards apex of scutellum as narrow triangular lobe (Fig. 16), with distinct longitudinal costae. Forewing venation (Fig. 21): submarginal vein 2.2 marginal vein, postmarginal 0.5 marginal, stigmal 0.3 marginal, stigmal 0.46 postmarginal; stigmal vein slender, making oblique angle with marginal vein, stigma abruptly expanded, with 4 sensilla.

Metasoma: T2 smoothly concave with sparse setae, without punctures, laterotergite glabrous; border between T2 and T3 indicated by weak suture; T3 transverse, length 0.75 width along T2, smooth and shining, in dorsal view with short setae and small punctures laterad and on midline along T2 border; ovipositor not examined.

Male.— Unknown.

Notes.— The specimen is card mounted with the venter embedded in mounting medium; both antennae are broken (the distal funicular segments and clava are missing) and covered with mounting medium. For this reason it is impossible to determine the sex of the holotype. The genitalia are not visible and the scape, which is sexually dimorphic in the Perilampidae, cannot be examined for the presence of sensorial punctures (diagnostic for males). The large metasoma suggests that the sex is female. It is also impossible to get an unobstructed view of the propodeum because of the way the specimen was mounted, but what can be seen is consistent with the propodeum of *K. megalaspis* (Fig. 10).

Biology.— Two species of *Krombeinius* have been reared as primary parasitoids of *Paraleptomenes mephitis* (Cameron) [Vespidae: Eumeninae] (see Darling (1988) for details). Mounted below the holotype of *K. kubah* was a thin, white parchment-like cocoon. The cocoon was cleared and the host remains are tentatively identified as an aculeate wasp. More interestingly, four first-instar larvae were recovered from the cocoon. These are regarded at the first immature stages for the genus and the planidia are described below and compared with the planidia of *Perilampus* species and Eucharitidae.

First-Instar Larva (Figs. 23-26).— Four first-instar larvae (planidia) were found associated with the host remains in the cocoon associated with the holotype. Only Hoyer's slide mounts were prepared (D. Chris Darling Slide Nos. 1927-30, Royal Ontario Museum); scanning electron micrographs were not prepared and details of structure of the labrum, prelabium, and postlabium are therefore not available. Descriptions and terms follow Heraty & Darling (1984).

Description.— Length about 0.25 mm, maximum width about 0.07 mm; fusiform, circular in cross-section. Cranium and 13 body segments, I-XII sclerotized, brown in color, XIII translucent white.

Cranium heavily sclerotized, extended ventrad as broad triangular lobes (Figs. 25-26), posterior margin almost straight, not excised medially; antenna absent, not peg-like or papilliform, position probably indicated as large semi-transparent depressions (campaniform sensilla) posteriad; with 4 additional pairs of smaller campaniform sensilla, a group of 3 dorsad and 1 laterad (Fig. 25); 1 pair of large, stout pleurostomal setae (plst) situated on raised processes, and 2 pairs of more slender cranial setae (cs); pleurostoma (pls) heavily sclerotized, curved around bases of the mandibles, not divided medially, extended along midline as cup-shaped sclerite and tentorial bars (Fig. 25); mandibles (md) symmetrical, large and sharply curved, comma-shaped, bases broad and rounded.

Tergites I-XII heavily sclerotized, separated ventrad by membranous areas (i.e., tergites do not completely encircle body); tergites entire, without tergopleural line. Spiracle (sp) present dorsolaterad between tergite I and tergite II, not situated in membrane but completely surrounded by sclerites (Figs. 23, 24). Tergite I and II fused between spiracles, not capable of telescoping; tergites III - XII separate, not fused, capable of telescoping. Tergites I, II, V, VII, and IX with 2 pairs of setae, dorsal and lateral; tergites IV, VI, VIII with a single pair of lateral setae; tergite III with three pairs of setae, dorsal, lateral and ventral, the ventral pair not much smaller than the other setae; tergites X and XI without setae (Figs. 23, 24). Triangular tubercles (tb) present in rows on ventral anterior margin of tergites IV-VIII, serrations present in similar position on tergites IX-XII (Fig. 24). Caudal cerci long and flexible, arising from raised dorsal sockets on tergite XII.

Tergite I rounded ventrad, margin smooth without spines or serrations, tergites II-XII extended posteriad as long needle-like projections, tergite II without a dense row of ventral spines (cf. *Perilampus hyalinus*, Heraty & Darling, 1984, fig. 37). Dorsal setae longer than in *Perilampus hyalinus*, setae on VII and Xl much longer and stouter than lateral setae, and longer than length of respective tergites along midline; dorsal seta of tergite IX much greater than one-half length of caudal cerci (35:50). Caudal cerci about equal in length to length of the five terminal segments. Ventral membranous surface without strong setae or hook-like spines between posterior margin of cranium and anterior margin of tergite I (cf. *Perilampus hyalinus*, Heraty & Darling, 1984, fig. 37); II - V with small ventral spines, in rows between lateral margins of tergites patches along the midline (Fig. 24).

Discussion.— These planidia conform to the characterization of Perilampidae presented in Heraty & Darling (1984) and Darling (1992), which was based only on the genus *Perilampus*. There are, however, some important differences in the planidia of the *Perilampus* species and *Krombeinius kubah*, but the generality of these characters will need to be re-evaluated when more planidia have been described. Synapomorphic adult structures unite *Krombeinius* with the *Perilampus hyalinus* group (Darling, 1983) suggesting that the planidia of *Krombeinius* be compared with *P. hyalinus*. These planidia are very similar in habitus and detailed structure (however the mouthparts have not been studied in detail for *Krombeinius*). The most significant difference, which could be regarded as a synapomorphy of *Krombeinius*, is the dorsal fusion of tergites I and II with the result that the spiracle is completely surrounded by sclerotized tergites (Figs. 23, 24). In all species of *Perilampus* studied these tergites are not fused and the spiracle is situated on membrane (Heraty & Darling, 1984). Fusion of these tergites was regarded as a synapomorphy of Eucharitidae (Heraty & Darling, 1984; Darling, 1992) with a reversal to free tergites in the subfamily Oraseminae. More recently, and based on an analysis of characters of both the adults and immature stages (Heraty, 1994), fusion of these tergites is regarded as a synapomorphy of Eucharitinae. Free tergites are therefore present in the groundplan of the Eucharitidae and by extension in the ground plan of the Perilampidae – fusion of these tergites in *Krombeinius* would be synapomorphic and convergent with Eucharitinae. In all *Perilampus* species examined (Heraty & Darling, 1984) the pleurostoma is divided medially; in *K. kubah* the pleurostoma is apparently transverse and not divided. Also of interest is the presence of a row of tubercles on the ventral anterior margin of tergites IV-VIII (Fig. 24). These are more similar in structure to the rows of triangular tubercles in *Chrysolampus sisymbrii* (Ashmead) (Darling & Miller, 1991, fig. 3) than the patches of spines present in *P. hyalinus* (Heraty & Darling, 1984, fig. 37). Other characters that distinguish *K. kubah* and *P. hyalinus* are much longer dorsal setae and the absence of large recurved ventral spines between the cranium and tergite I; these characters are variable at the species level in *Perilampus* and may serve to distinguish species of *Krombeinius*.

Phylogeny and Biogeography

The phylogenetic relationships of the species of *Krombeinius* were not strongly supported by the previous cladistic analysis (Darling, 1988). A single most parsimonious cladogram (36 steps, CI = 0.667) was found but there were many trees only a single step longer and the strict consensus tree of these was almost completely unresolved. And one rather tenuous character was included (#10, angle of stigmal vein) which, when removed, resulted in 20 minimum length trees (35 steps). That analysis was not expected to be particularly robust to the addition of either additional taxa or additional characters.

The two new species described herein were coded for the 23 characters discussed in Darling (1988), with the following modifications – and one new character was added (character 24):

Character 10; angle of stigmal vein. In 1988 there was uncertainty expressed about the intermediate conformation of the stigmal vein of *K. taiwanensis* Darling (Darling, 1988, fig. 8) which was coded as state 1. It now seems that the stigmal vein of this species conforms better with the more oblique angle of *K. megalaspis*, *K. kubah*, and *K. lerouxi* Rasplus (state 0) than to the almost 90 degree angle found in the other species (state 1). In addition, the stigmal vein is more gracile in all species with an oblique stigmal vein (Figs. 20-22 cf. robust in Figs. 17-19) including *K. taiwanensis*. In both regards *K. taiwanensis* is more similar to the plesiomorphic configuration of the stigmal vein. Excluding this character does not alter the results of the parsimony analysis.

Character 16, 17; sculpture of third metasomal tergite. Two characters were coded to represent these sculpture patterns. Although much smaller than the punctures in *K. eumenidarum*, *K. dictyon*, and *K. taiwanensis* (states 1,0), distinct punctures are also present in *K. megalaspis* and *K. kubah* (states 1,0). The topology of the minimum length cladogram does not change if these two species are coded as having a distinct sculpture pattern (states 1,1).

Character 19; median area of propodeum. It is difficult to unequivocally score this character but it now seems more appropriate to consider the median area of the propodeum as foveate in *K. saunion* and *K. lerouxi* (state 1).

Character 24; dorsal margin of clypeus. A new character was added for the two configurations of the upper clypeal margin in *Krombeinius*. The plesiomorphic condition, also found in the *Perilampus hyalinus* group and in *Euperilampus*, is a distinct suture and a clear demarkation between the clypeus and supraclypeal area (state 0, Figs. 6,11). In *K. eumenidarum*, *dictyon*, *saunion*, and *taiwanensis* this suture is absent (state 1, Fig. 1).

The expanded and revised data matrix is presented in table 1. Parsimony analysis was conducted using PAUP version 3.1.1 (Swofford, 1993) and alternative character optimizations were investigated using MacClade version 3.0 (Maddison and Maddison, 1992). Multistate characters were run as unordered to prevent a priori decisions of character transformation from biasing the parsimony analysis. This analysis resulted in a single most parsimonious cladogram of 33 steps when uninformative characters are excluded (CI = 0.67, RI = 0.69). Figure 27 shows the pattern of relationships based on the 18 informative characters (4, 5, 8, 17, 21, 23 excluded) and the support for the internal nodes of the cladogram – autapomorphies are not shown. The two characters with equally parsimonious or ambiguous reconstructions (11, 24) were resolved using delayed transformations (DELTRAN) which favours convergences over reversals. Character support for each internal node is summarized as x/y, where x is the total number of character changes on the internode and y is the number of unique and unreversed synapomorphies. As in the previous analysis, only a few of the nodes on the cladogram are strongly supported. In addition to the monophyly of the genus, only three nodes are supported by more than a single unique and unreversed character, viz. *saunion* + *dictyon*, *taiwanensis* + (*megalaspis* +

Table 1. Character states for 24 characters and 8 taxa included in the cladistic analysis. *Perilampus hyalinus* and *Euperilampus scutellatus* served as outgroup taxa for polarity decisions within *Krombeinius* (0 = ancestral state; 1, 2, 3 = derived states; ? = missing data). See text and Darling 1988 for discussion of character polarity and transformation series.

	Characters																							
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Perilampus hyalinus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euperilampus scutellatus	0	3	0	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	1	0	1	0
Krombeinius megalaspis	1	2	0	?	?	?	1	0	1	0	0	1	1	1	0	1	0	0	0	0	0	1	0	0
Krombeinius kubah	1	2	0	?	?	?	1	0	1	0	0	1	1	1	0	1	0	0	0	0	0	1	0	0
Krombeinius eumenidarum	0	2	0	1	0	1	1	0	0	1	2	0	0	0	0	1	0	0	1	0	0	1	0	1
Krombeinius dictyon	2	2	0	?	?	?	1	0	0	1	2	0	0	0	0	1	0	1	1	1	0	1	0	1
Krombeinius saunion	0	2	0	?	?	?	1	0	0	1	2	0	0	0	0	0	0	1	1	1	0	1	0	1
Krombeinius taiwanensis	1	1	1	1	0	1	1	0	1	0	1	0	0	0	1	1	0	0	0	0	0	1	0	1
Krombeinius lerouxi	1	2	0	?	?	?	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0
Krombeinius srilanka	1	1	0	?	?	?	1	0	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0	0

kubah), and *megalaspis* + *kubah*. There are 12 trees only one step longer than Figure 27 and the strict consensus tree of these supports only these three relationships; and only these are regarded as significantly robust to warrant discussion of their biogeographic implications. Fig. 28 is the area cladogram for the outgroup taxa and the species of *Krombeinius* – only robust nodes, i.e. those supported by at least two unique and unreversed characters, are resolved.

A comparison of the previous (Darling, 1988) and present cladograms was made by excluding the new species (*K. dictyon*, *K. kubah*) and constraining the topology. The present cladogram (38 steps, CI = 0.71, 2 species excluded) is only two steps shorter (40 steps, CI = 0.68) and the cladograms differ only in the switching of positions of *K. megalaspis* and *K. srilanka*. The relationship of *K. eumenidarum* and *K. saunion* and the intermediate position of the African species (*K. lerouxi*) are consistent in both analyses. The intermediate position of *K. lerouxi* is unexpected and cladograms of only one step longer result if this species is constrained to be the sister group of all of the other species, i.e., the Oriental species. And arranging the species in a consistent geographic pattern results in cladograms only 13% longer, 38 steps (cf. 33) if the relationships are constrained as (Africa *[lerouxi*], (Western Oriental; India, Sri Lanka [*eumenidarum, srilanka*)] + Eastern Oriental; Indonesia, Philippines, Taiwan [*kubah, megalaspis, dictyon, saunion, taiwanensis*]) . These results support a conservative approach to biogeography that involves only the better supported nodes.

There has been renewed interest in the biogeography of Indo-Pacific region in the last decade. The motivation has come from cladistic approachs to historical biogeography (Schuh & Stonedahl, 1986), from a more explicit understanding of the plate tectonics of the region (see Whitmore, 1987), and from the need to establish conservation priorities (e.g., Vane-Wright and Peggie, 1994). Given the importance of both dispersal and vicariance in the development of island biotas – and the differences in the relative importance of these factors in different groups of organisms (e.g., de Jong, 1990) – it is not unexpected that there are many conflicting biogeographic patterns. The consensus seems to be that the best approach is to extend the analysis to other groups of organisms and to compare how areas of endemism are related across taxa (Holloway, 1990). It is in this spirit that the area cladogram for species of *Krombeinius* is discussed. It should, however, be noted that degree of endemism of these species is unknown; most species have been only collected from single localities.

There is, however, a remarkable similarity of the area cladogram (Fig. 28) with the cladistic analysis of the biogeography of the milkweed butterfly genus *Idea* (Kitching *et al.*, 1987). In both analyses there is a clade west of the Makassar Strait with connections to India and/or Sri Lanka. In *Krombeinius* this clade is distributed in Taiwan, Borneo, and Java; the sister group relationship between the later two species is consistent with the Sundaland (Sundaic) relationships found in many taxa (e.g., Lepidoptera, Holloway, 1987). And as in *Idea*, there is also a clade east of the Makassar Strait that supports a Sulawesi - southern Philippines link. In *Krombeinius*, the sister group relationship of *dictyon* + *saunion* mirrors area sister group relationship of *Idea electra* + *blanchardii*. An important role of the Philippines in the development of the fauna of Sulawesi has also been suggested by Duffels, 1990 (for certain groups of cicadas) and Vane-Wright, 1990 (for butterflies). *Krombeinius* has not been recorded from east of Sulawesi but the concordance of the biogeographic pattern with *Idea* predicts that species from the Australasian region will belong to the eastern clade.

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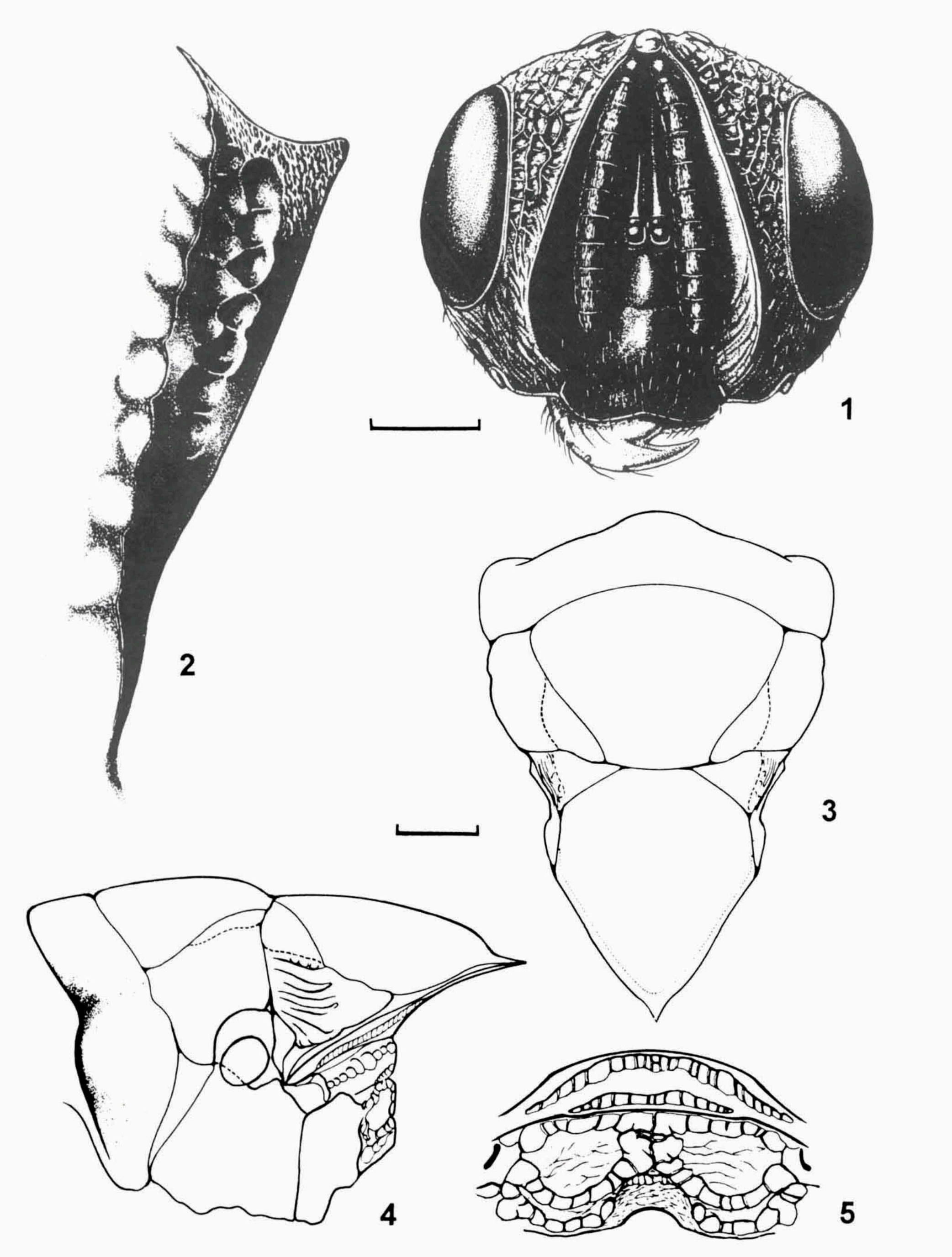
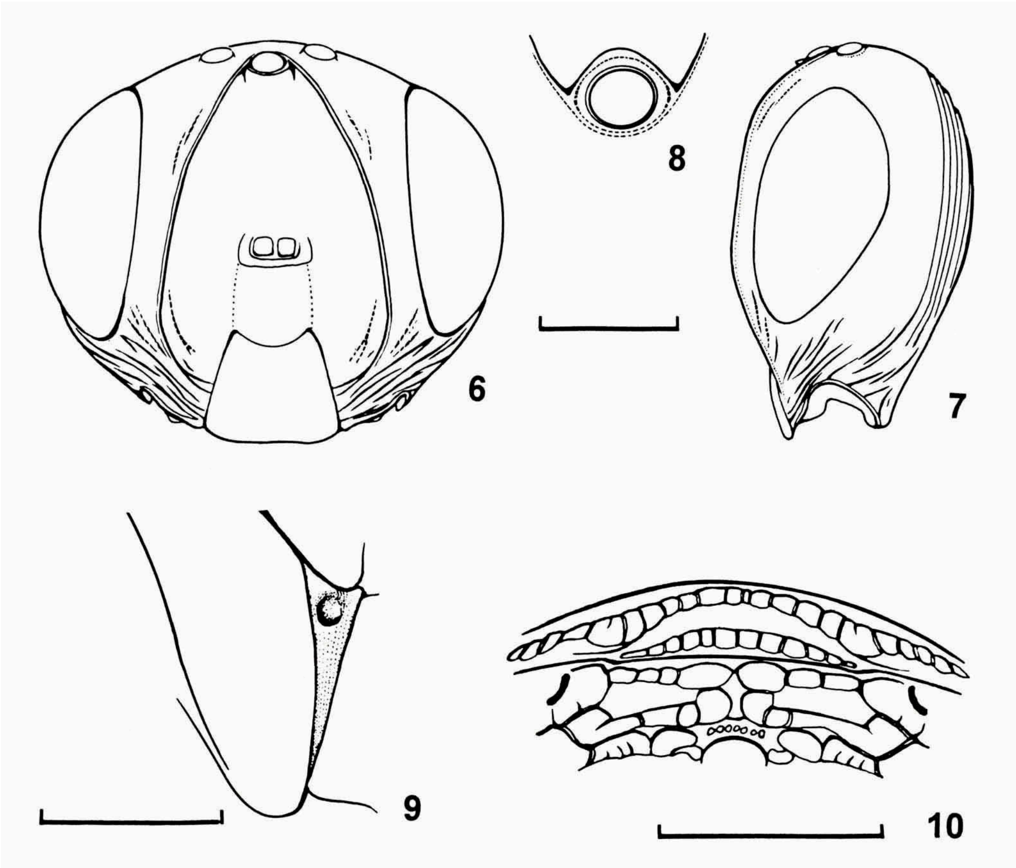
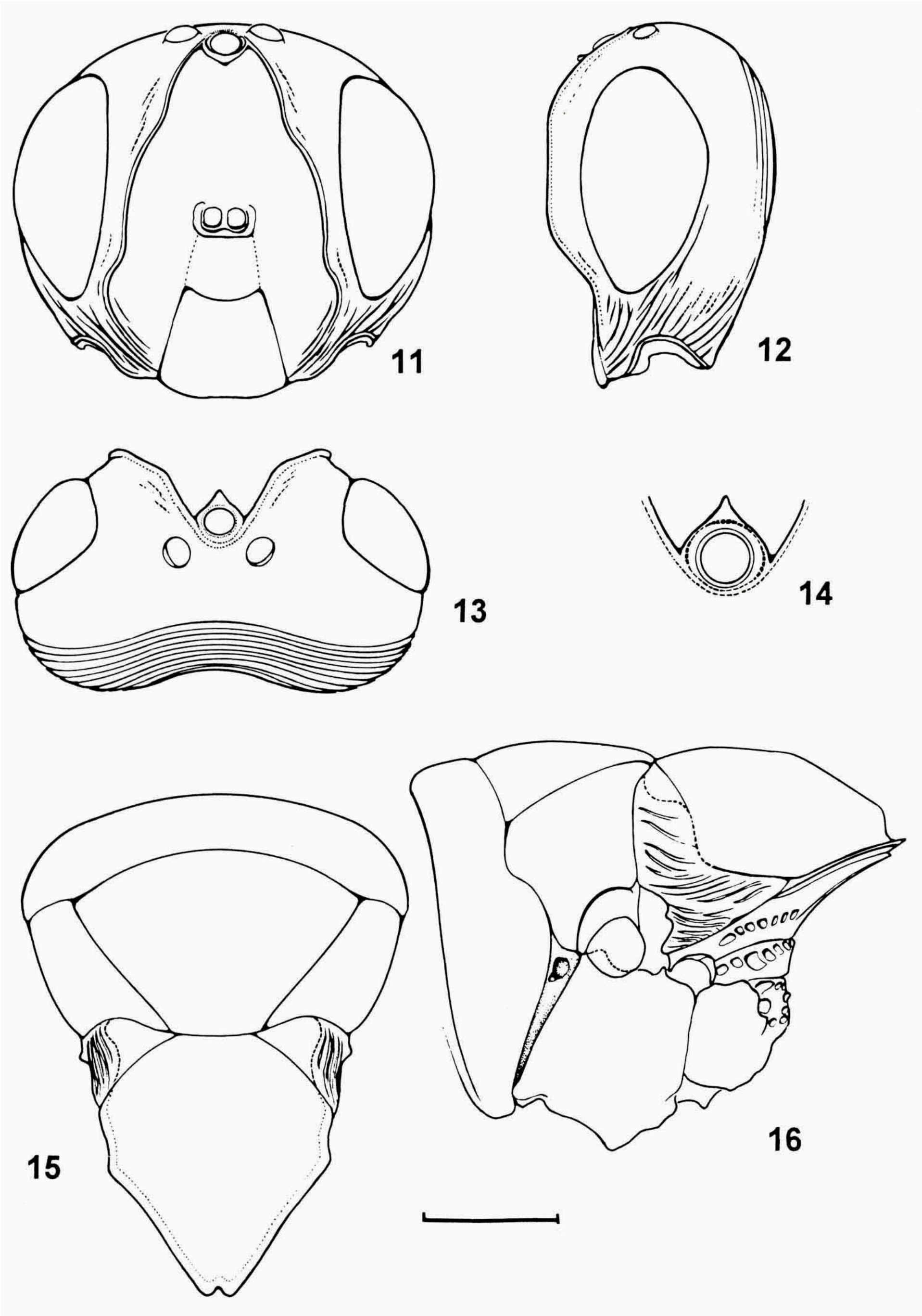


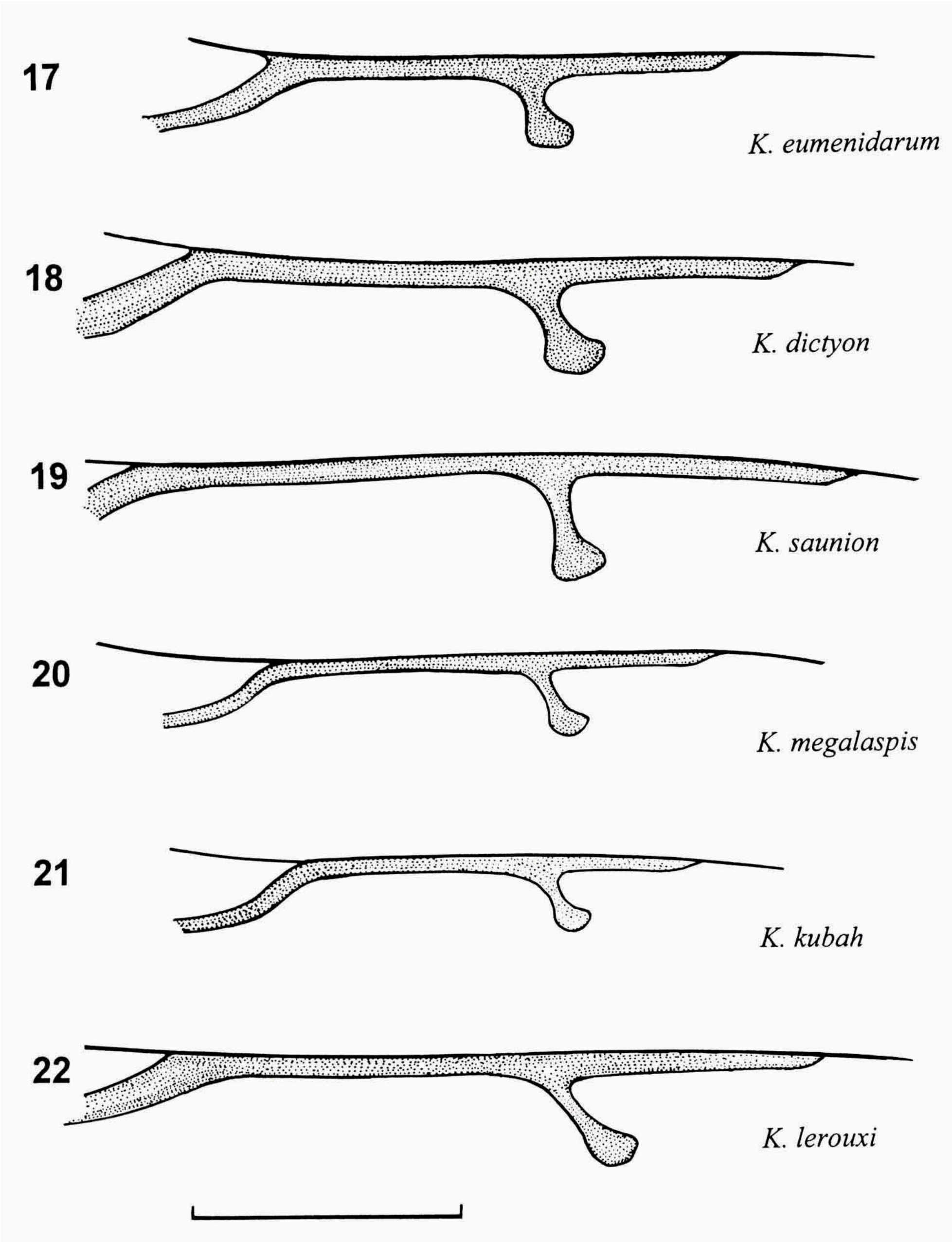
Figs. 1-5, *Krombeinius dictyon*, spec. nov. 1, Head, frontal aspect, scale line: 0.5 mm; 2, prepectus; 3, 4, mesosoma, dorsal and lateral aspects, dashed line indicates extent of smooth areas along notauli; scale line: 0.5 mm; 5, propodeum.



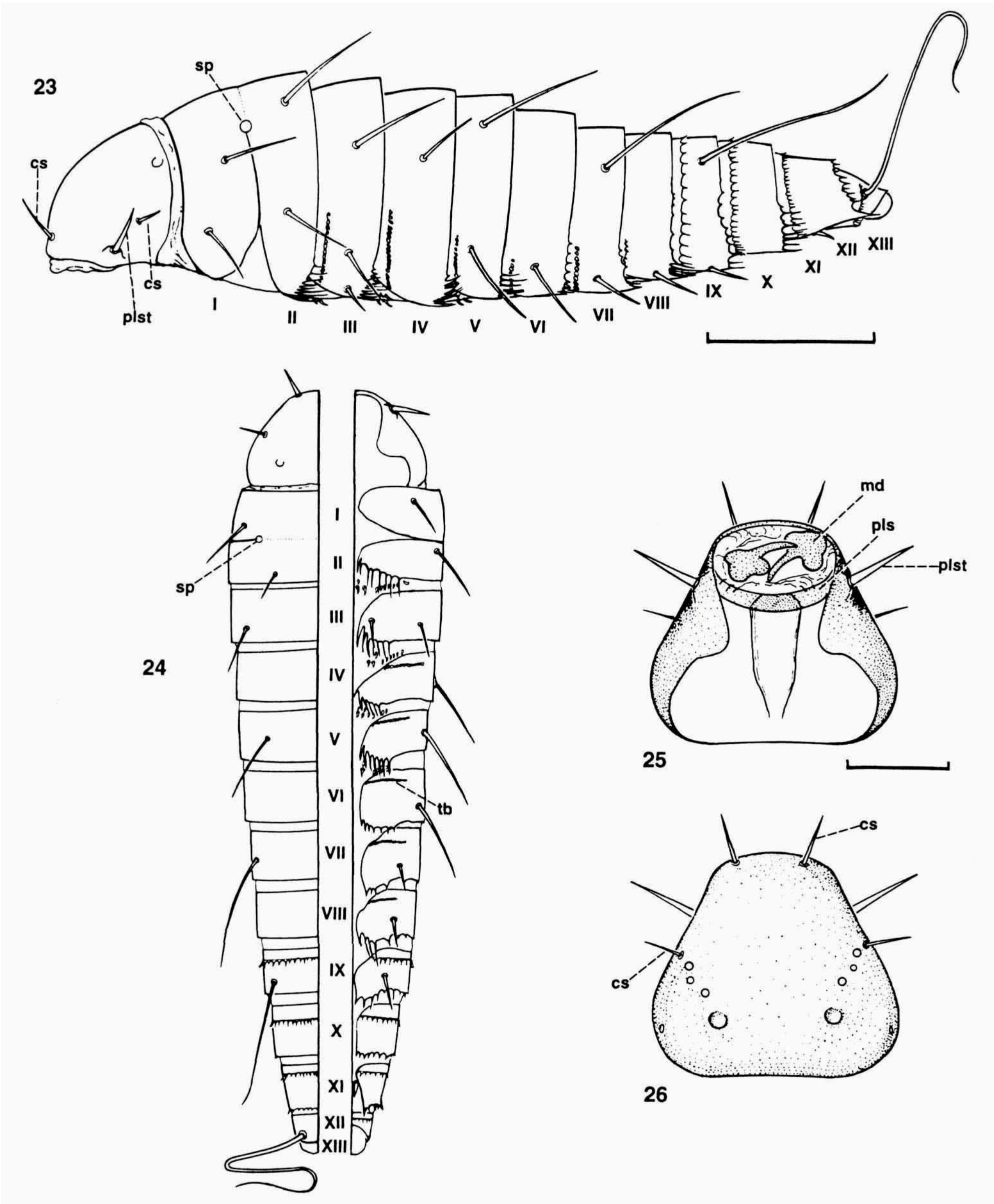
Figs. 6-10, *Krombeinius megalaspis*. 6, Head, frontal aspect; 7, head, lateral aspect; 8, median ocellus and shelf-like projection, dorsal aspect; 9, prepectus and lateral pronotal panel; 10, propodeum. Scale lines: 0.5 mm.



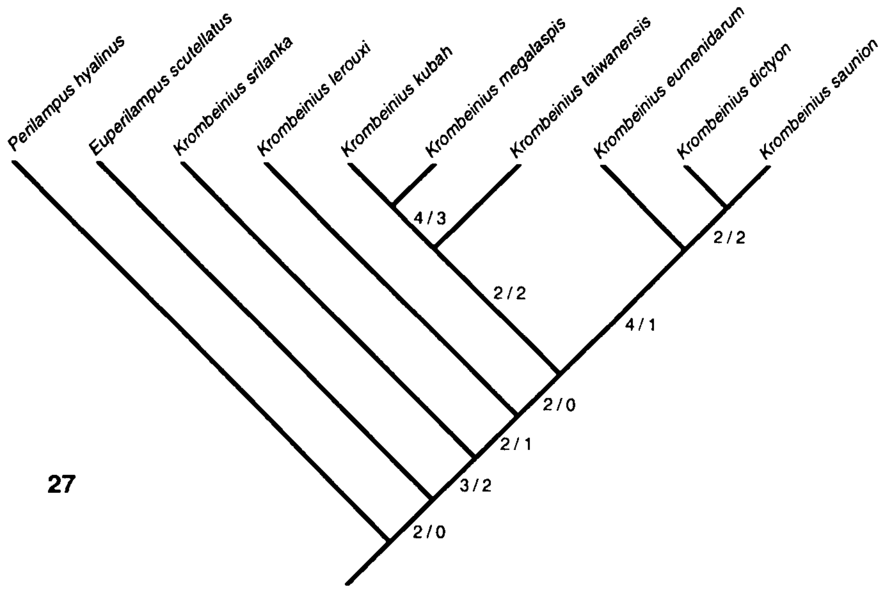
Figs. 11-16, *Krombeinius kubah*, spec. nov. 11, Head, frontal aspect; 12, head, lateral aspect; 13, head, dorsal aspect; 14, detail of median ocellus and shelf-like projection; 15, 16, mesosoma, dorsal and lateral aspects, dashed line indicates change in sculpture. Scale line: 0.5 mm.



Figs. 17-22, forewing venation and shape of stigmal vein. 17, *K. eumenidarum*; 18, *K. dictyon*; 19, *K. saunion*; 20, *K. megalaspis*; 21, *K. kubah*; 22, *K. lerouxi*. Scale line: 0.5 mm.



Figs. 23-26, first-instar larva of *Krombeinius kubah*. 23, Lateral habitus drawing, scale line: 0.05 mm; 24, schematic drawing of dorsal (left) and lateral (right) aspect showing the shape of tergites and distribution and length of setae; 25, dorsal view of cranium, scale line: 0.025 mm; 26, ventral view of cranium and mouthparts. cs = cranial setae; md = mandible; pls = pleurostoma; plst = pleurostomal seta; sp = spiracle; tb = tubercles.



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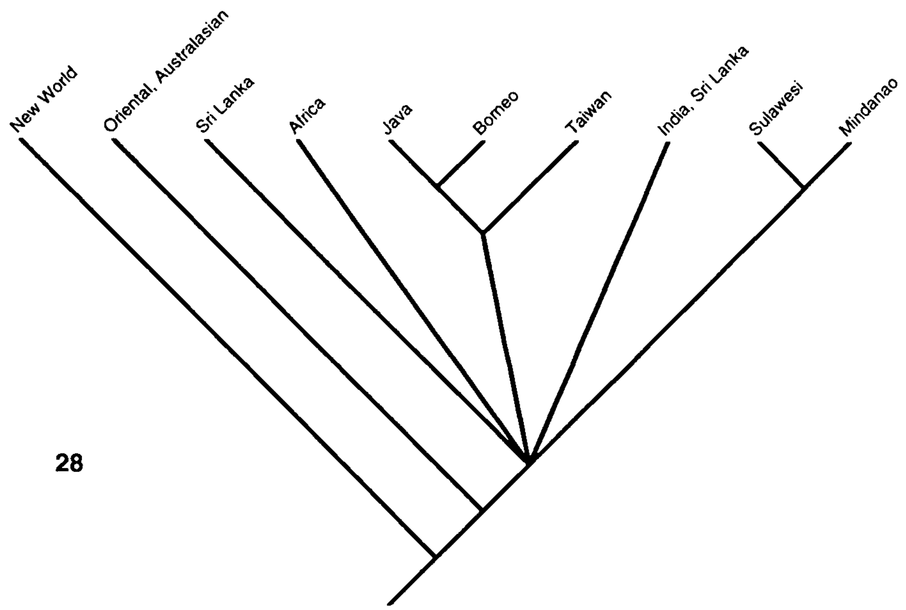

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Fig. 27, cladistic relationships of species of *Krombeinius*, see text for discussion. Fig. 28, area cladogram, only robust nodes resolved, see text for discussion. Note: the ordering of species and areas are consistent in these two figures.