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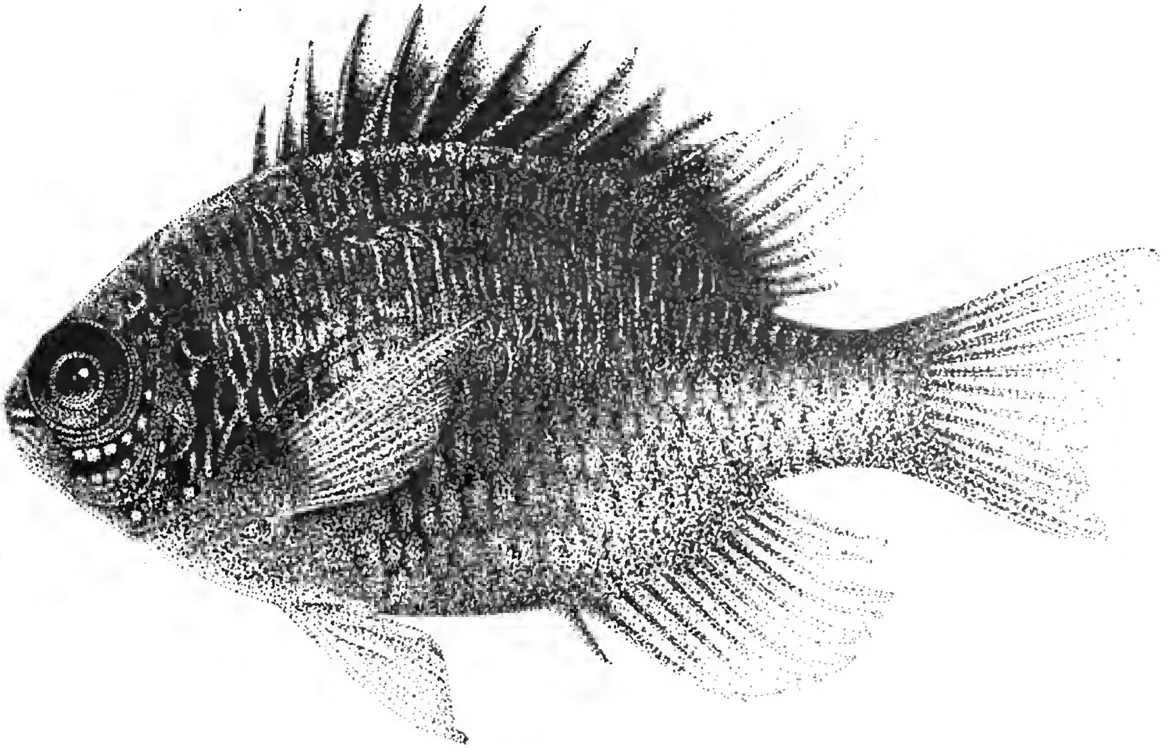

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Cover: A new species of damselfish from Irian Jaya (*Chrysiptera pricei*). Illustration by Jill Ruse.

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Hipposideros diadema (Chiroptera Hipposideridae) in the Lesser Sunda Islands, Indonesia: taxonomy and geographic morphological variation.

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Abstract

A morphological study, using multivariate statistical analyses, was carried out on 157 specimens of *Hipposideros diadema* from the Lesser Sunda Is, Borneo, Java, Thailand, Peninsula Malaysia, Philippines, New Guinea, Solomon Is, Bismark Is, and Australia.

This study indicates that two forms of *H. diadema* occur in the Lesser Sunda Is: *H. d. nobilis* (Horsfield, 1823) — Borneo, Java, Bali, Nusa Penida, Lombok; and *H. d. diadema* (Geoffroy, 1813) — Sumbawa, Moyo, Sumba, Flores, Roti, Savu and Timor.

Hipposideros diadema is sexually dimorphic for skull, dentary and dental characters; for many measurements males average slightly larger than females. Female *H. d. diadema* show a cline in overall skull size with a trend to increase from west to east along the Lesser Sunda island chain.

Hipposideros diadema subspecies morphologically similar to the Lesser Sunda subspecies were reviewed taxonomically, redescribed and diagnosed against each other. These were *H. d. masoni* (Dobson, 1872) — Thailand, Malay Peninsula; *H. d. griseus* (Meyen, 1833) — New Guinea, Philippines; *H. d. reginae* Troughton, 1937 — Queensland, Australia; and *H. d. oceanitis* — Solomon and Bismarck Is.

There are three phenetic groupings in the *H. diadema* subspecies considered, based on external and skull measurements combined. *Hipposideros d. diadema, H. d. reginae* and *H. d. masoni* form one group; *H. d. griseus* and *H. d. oceanitis* a second group; and *H. d. nobilis* clusters separately.

Introduction

Extensive surveys of the terrestrial vertebrate fauna of a number of islands in the Lesser Sunda chain have been carried out as a collaborative effort between the Western Australian Museum and Balitbang Zoologi, Indonesia. These surveys, which were begun in September 1987, still continue. They have resulted in the collection of specimens of *Hipposideros diadema* (E. Geoffroy, 1813) from Bali, Nusa Penida Lombok, Sumbawa, Moyo, Flores, Sumba, Roti, Savu and Timor islands — as well as Java.

Tate (1941) summarised information on the subspecies of *H. diadema* known at that time from across its distribution in the Indo-Australian region. Hill (1963) more comprehensively reviewed the taxonomy of *H. diadema* and recognised 16 subspecies. Since then additional subspecies have been described by Phillips (1967) from the Solomon Islands and McKean (1970) from the Northern Territory, Australia.

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Currently the following subspecies of *H. diadema* are generally recognised (Hill 1963; Phillips 1967; McKean 1970; Koopman 1982, 1984).

Hipposideros diadema diadema (Geoffroy, 1813) Timor I.; Lombok I.; Bali I.; Kangean I.; Sumbawa I.; Java.
H. d. masoni (Dobson, 1872) — Burma (Tenasserim); Indochina (Annam; Tonkin); Thailand; Malay Archipelago; Borneo; Sumatra and Nias I.
H. d. nicobarensis (Dobson, 1871) — Nicobar I.
H. d. enganus Andersen, 1907 — Engano I.
H. d. natunensis Chasen, 1940 — Bunguran I., N. Natuna Is.
H. d. griseus (Meyen, 1833) — Luzon, Philippine Is.
H. d. speculator Andersen, 1918 — Kalao Is, Flores Sea, south of Sulawesi.
H. d. ceramensis Laurie & Hill, 1954 — Seram, Buru Is.
H. d. euotis Andersen, 1905 — Batchian I.
H. d. pullatus Andersen, 1905 — Haveri, Papua New Guinea.
H. d. custos Andersen, 1918 — Ara, Kei Is.
H. d. mirandus Thomas, 1914 — Manus I, Admiralty Is.
H. d. trobrius Troughton, 1937 — Kiriwina I., Trobriand Is.
H. d. oceanitis Andersen, 1905 — Guadalcanal I., Fauro, Vella Lavella, Ysabel, Bougainville I. (Papua New Guinea).
H. d. demissus Andersen, 1909 — San Christoval I., E. Solomon Is.
H. d. malaitensis Phillips, 1967 — Malaita I., Solomon Is.
H. d. reginae Troughton, 1937 — Queensland, Australia.
H. d. inornatus McKean, 1970 — Northern Territory, Australia.

Hipposideros diadema diadema was considered by Andersen (1905) to occur on both Timor and Java. He noted that the holotype of the nominate subspecies was from Timor and that a skin from Timor closely agrees with Geoffroy's figure and description. However, Andersen (1905) noted that Javan specimens of *H. d. diadema* may average larger than those from Timor — and cautioned that Horsfield's (1823) name for the Javan and Balinese form (*nobilis*) may be valid. Goodwin (1979) also observed that the Javan and Balinese forms of *H. diadema* tended to have larger forearms than those from Timor. He stated that a "larger series of specimens from Java and Timor must be compared before it can be determined whether or not the populations on those islands were consubspecific". But, he concluded by agreeing with Hill (1963) that they were consubspecific and that the form '*nobilis*' should be synonymised with *H. d. diadema*.

Our extensive collections of *H. diadema* from the Lesser Sunda Islands showed considerable morphological variation and appeared to include several distinct forms. To identify these forms we compared them to closely related subspecies. These comparisons form the substance of this paper. Because these investigations have a bearing on some previous taxonomic judgments, this paper also rediagnoses the subspecies considered herein. All taxonomic judgements are the sole responsibility of the senior author.

Methods

Terminology used in the description of skull, dentary and dental (skull) characters and external characters follows Hill (1963) and Hill and Smith (1984). Pelage descriptions when following the colour terminology of Ridgway (1912) are capitalised.

Skull characters

Twenty four measurements of skull characters and eight of external characters (all in mm), and weight (in gms) were recorded from adults specimens (Figure 1, caption). Adults were diagnosed as those specimens with basioccipital and sphenoid bones completely fused and epiphyseal swellings absent from metacarpal joints. All measurements were recorded with dial calipers to two decimal places.

Specimens Examined

One hundred and fifty seven adult specimens of *Hipposideros diadema* were measured from: Thailand, Malay Peninsula, Borneo, Java, Lesser Sunda Is, Philippines, Solomon Is, Bismarck Is and Australia. They are listed in the "Specimens Examined" section.

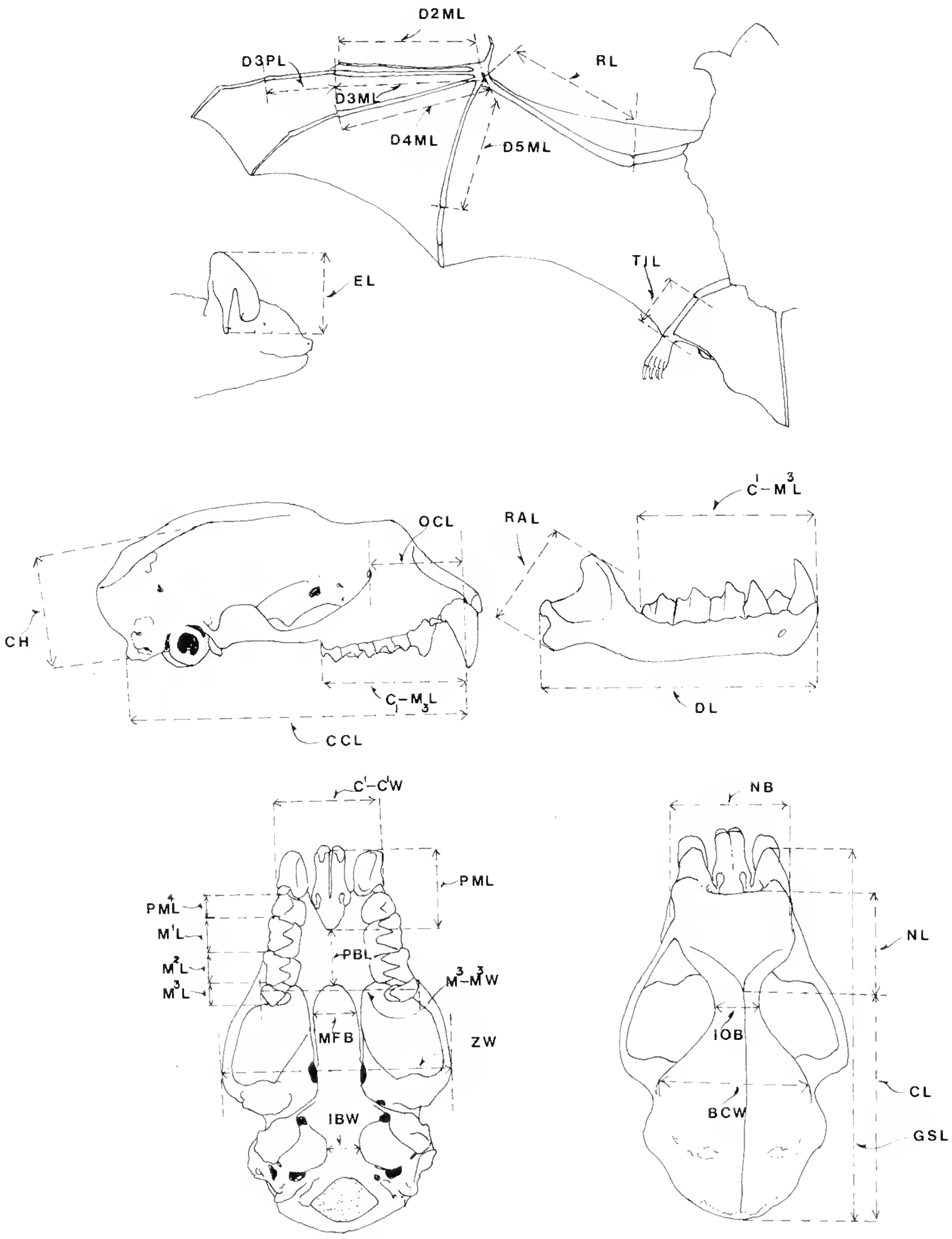
We examined specimens representative of the following taxa *sensu* Hill (1963): *H. d. masoni; H. d. griseus; H. d. pullatus; H. d. oceanitis; H. d. reginae; H. d. demissus* and *H. d. inornatus*. The distribution of these specimens is shown in Figure 1. Additionally we examined specimens of other principal species in the *H. diadema* group of Hill (1963) (*H. dinops; H. lankadiva* and *H. commersoni*). From our examination of these specimens and of the literature we consider the forms *demissus* and *inornatus*, are not closely related to the other subspecies of *H. diadema*. For this reason the small *demissus* and *inornatus* forms are not included in this paper.

To denote the institutional origins of specimens their catalogue numbers are prefixed by the following abbreviations:

WAM : Western Australian Museum, Perth
MZB : Museum Zoologicum Bogoriense (Balitbang Zoologi), Bogor
AM : Australian Museum, Sydney
JM : Queensland Museum, Brisbane
AMNH : American Museum of Natural History, New York
FMNH : Field Museum of Natural History, Chicago
S : Smithsonian Institute, Washington

Morphometric Analyses

Sexual dimorphism was analysed by MANOVA and ANOVA using a two factor analysis for measurements of skull and external characters separately for the factors: island groupings, and sex.


D2ML
D3PL
D3ML
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D5ML
RL
EL
TIL
C^1–M^3L
OCL
RAL
CH
C_1–M_3L
CCL
DL
C^1–C^1W
NB
PML
PM^4L
M^1L
M^2L
M^3L
PBL
M^3–M^3W
ZW
MFB
IBW
NL
IOB
CL
BCW
GSL

◀ **Figure 1** Skull and external measurements referred to in text and their recording points. GSL — greatest skull length, posterior lambdoidal crest to maxilla at C^1 dorsal base; CCL — condylocanine length, condyle to maxilla at C^1 dorsal base; CL — cranial length, posterior sagittal crest to supraorbital bifurcation point; NL — nasal length, posterior supraorbital crest point to rostral swelling anterior median edge; NB — nasal breadth, at posterodorsal contact of zygomatic with rostral swelling; CH — cranial height; IBW — distance between cochlea; PBL — palatal bridge length; MFB — mesopterygoid fossa breadth; OCL —orbit to canine length, orbit anteromost point to maxilla at C^1 dorsal base; IOB —minimum interorbital breadth; ZW — zygomatic width; BCW —braincase breadth, at point above zygomatic junction with braincase; DL — dentary length, condyle to dentary distal tip; RAL — tip ascending ramus to tip angular process length; C^1-C^1W —width outside upper canines at alveoli; M^3-M^3W — width outside upper third molar cusps; C^1-M^3L and C_1-M_3L — upper and lower maxillary toothrow length, at alveoli; PM^4L — second upper premaxillary cusp length; M^1L, M^2l and M^3L — first to third upper molar cusp length; PML — premaxilla length; RL — radius length; D2ML to D5ML — digit 2 to 5, metacarpal lengths; D3PL — digit 3, phalanx 1 length; TIL — tibia length; EL — ear length and WT — weight.

Principal component analysis (using varimax rotation) and canonical variate (discriminant) analysis were performed on external characters (with males and females combined) and for skull characters (males and females separately).

A euclidian distance matrix was subjected to a hierarchical cluster analysis using the unweighted pair group method using arithmetic averages (UPGMA).

Several skull and external characters were excluded from the above analyses. This was because many specimens lacked values for these characters and consequently had they been included the number of cases available would have been sharply reduced. The excluded characters were weight and ear length. These measurements could not be accurately recorded from specimens prepared as 'cabinet skins'. Additionally the length of the premaxillary was excluded. It was recorded for general description purposes only. It could not be measured as precisely as other skull characters because it varied considerably in its curvature.

Variation in size of skull (males and females separate) and external (males and females combined) characters was examined in *H. diadema diadema* from Lombok, Sumbawa, Flores, Sumba, Roti, Savu and Timor Is. Ear length was included as a variable in these analyses because all specimens of *H. d. diadema* examined were "alcoholic" specimens. The principal component Factor 1 score was taken to represent overall size of skull and external characters and related to both latitude and longitude using a stepwise multiple regression analysis. Additionally, greatest skull length, radius length, and weight, representing specific measurements of size, were compared in the same way with latitude and longitude. All statistical procedures were carried out on a NEC 286 computer using the SPSS/PCL+K programme.

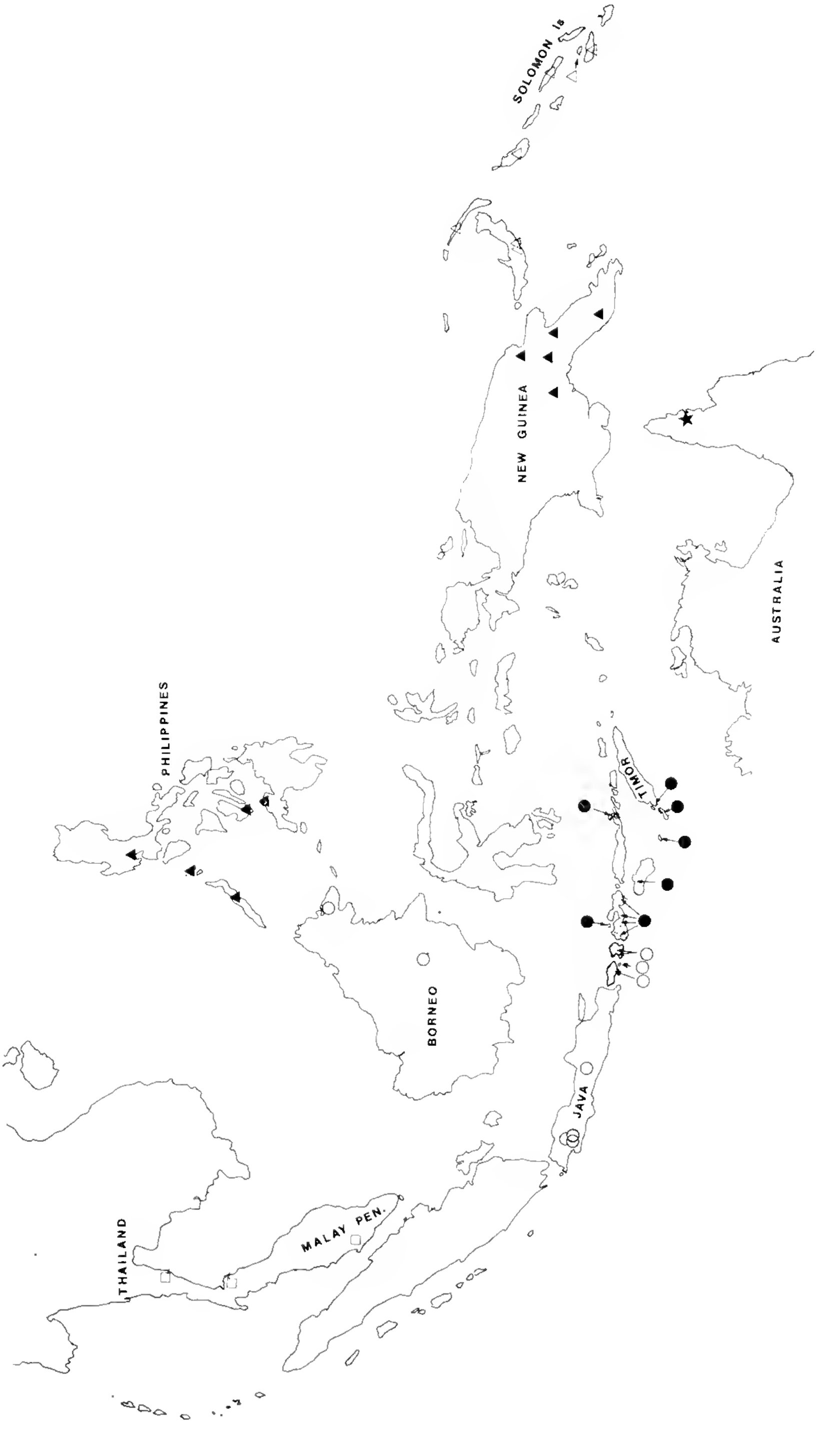


Figure 2 Location of specimens of *Hipposideros diadema* subspecies used in this study. *Hipposideros d. diadema* (●); *H. d. nobilis* (○), *H. d. griseus* (▲); *H. d. reginae* (★); *H. d. masoni* (□); and *H. d. oceanitis* (△).

Systematics

The specimens of *Hipposideros diadema* available to us from the Lesser Sunda Islands are resolved into two subspecies, *H. diadema diadema* (Geoffroy, 1813) from Sumbawa, Moyo, Flores, Sumba, Savu, Roti and Timor; *H. diadema nobilis* (Horsfield, 1823) from Borneo, Java, Bali, Nusa Penida and Lombok. We diagnose and describe these two subspecies against the following related subspecies, which we also redescribe: *H. d. griseus* (Meyen, 1833) from Philippines and Papua New Guinea; *H. d. oceanitis* Andersen, 1909 from the Solomon and adjacent islands (Ysabel, New Ireland, New Britain, Guadalcanal, Bougainville, Florida islands); *H. d. reginae* Troughton, 1937 from Queensland, Australia; and *H. d. masoni* (Dobson, 1872) from Peninsular Malaysia and Thailand.

Description of these forms is presented prior to the multivariate statistical analysis which in part assisted in their recognition.

Hipposideros diadema diadema (Geoffroy, 1813)

Table 1; Figures 3-9, 13-14

Rhinolophus diadema diadema Geoffroy [Saint-Hilaire] É. 1813 Sur un genre de chauve — souris, sous le nom de rhinolophes. Ann. Mus. Hist. Nat. Paris, 20: 263, pls 5,6.

Type: Paris Museum MHNP 918, skin with skull *in situ*, collected by Pèron and Lesueur.

Type locality: Timor.

Specimens examined: (see Appendix 1)

Diagnosis

Hipposideros d. diadema differs from *H. d. nobilis* in having its anterior noseleaf larger; tibia shorter relative to ear length (Figure 3); canines smaller and more slender and teeth generally smaller. For example: ♂♂ C^1-M^3 length 11.5 (10.9-12.2) *v.* 12.3 (11.3-13.1); M^2 length 2.7 (2.2-3.2) *v.* 3.0 (2.7-3.3) and ♀♀ C^1-M^3 11.2 (10.4-11.6) *v.* 11.9 (11.0-12.5); M^2 length 2.8 (2.3-3.1) *v.* 3.0 (2.7-3.2). Maxillary tooth rows generally closer together relative to greatest skull length (Figure 6a, b); cranium generally shorter relative to nasal length (Figure 7a, b); zygomatic width generally narrower relative to nasal length (Figure 8a, b).

It differs from *H. d. griseus* in averaging larger in all external and skull measurements (Table 1); nasal breadth absolutely larger: ♂♂ 9.5 (9.0-10.0) *v.* 8.5 (8.1-8.9) and ♀♀ 9.5 (9.1-9.9) *v.* 8.4 (7.9-9.0); nasals wider relative to their length (Figure 9a, b).

It differs from *H. d. reginae* by averaging larger in all external measurements (Table 1), e.g., radius length 85.9 (81.7-90.2) *v.* 81.2 (74.1-84.5); tibia length 34.4 (31.4-36.7) *v.* 29.8 (27.4-31.5); ear longer relative to radius length (Figure 4); tibia longer relative to metacarpal 3 length (Figure 5); molar rows generally narrower closer together relative to greatest skull length (Figure 6a, b).

It differs from *H. d. masoni* in that the tibia averages longer 34.4 (31.4-36.7) *v.* 31.4 (29.7-33.1); ear averages longer 32.1 (30.0-34.6) *v.* 27.0 (25.2-28.2); tibia longer relative

Figures (3-12) Univariate plots of external (males and females combined) and skull characters (**a**, male and **b**, female) adult *Hipposideros diadema*. Code for *H. diadema* subspecies as for Figure 2.

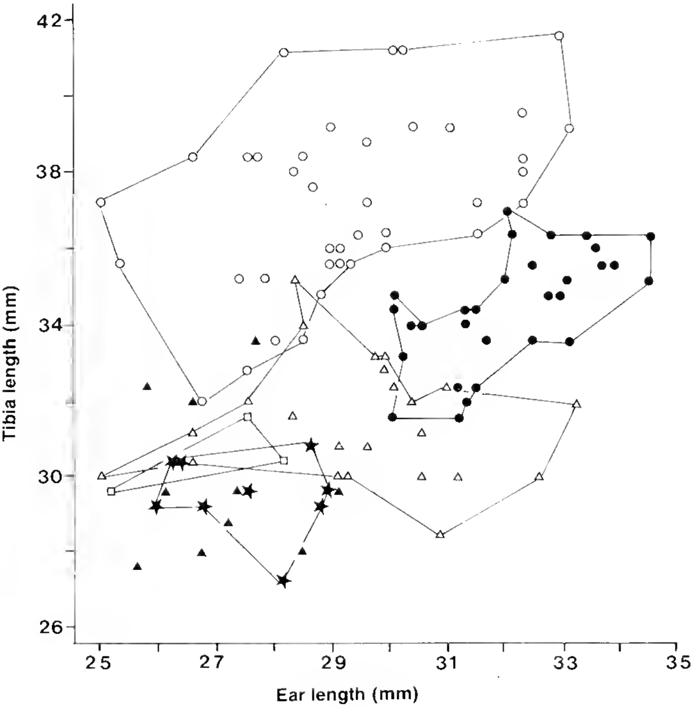


Figure 3 - tibia length v. ear length.

to metacarpal 3 length (Figure 5); ear longer relative to radius length (Figure 4); distance between molar rows further apart relative to cranial length (Figure 10 a, b). In ♀♀ only zygomatic width smaller relative to nasal length (Figure 8b).

It differs from *H. d. oceanitis* in that it averages larger in almost all external and skull measurements and weight (Table 1), e.g., radius length 85.9 (81.7-90.2) *v*. 76.5 (71.7-80.4), metacarpal 4 length 61.6 (57.8-64.8) *v*. 54.0 (48.7-56.9); greatest skull length ♂♂ 30.5 (29.1-31.5) *v*. 28.9 (26.4-29.9) and ♀♀ 30.0 (28.7-31.5) *v*. 29.1 (28.5-30.1); C^1-M^3 length, ♂♂ 11.5 (10.9-12.2) *v*. 10.7 (9.6-11.3) and ♀♀ 11.2 (10.4-11.6) *v*. 10.7 (10.0-11.2); three rather than two large supplementary leaflets on nose; radius longer relative to ear length (Figure 4); metacarpal 3 length longer relative to tibia length (Figure 5); nasals wider relative to their length (Figure 9a, b).

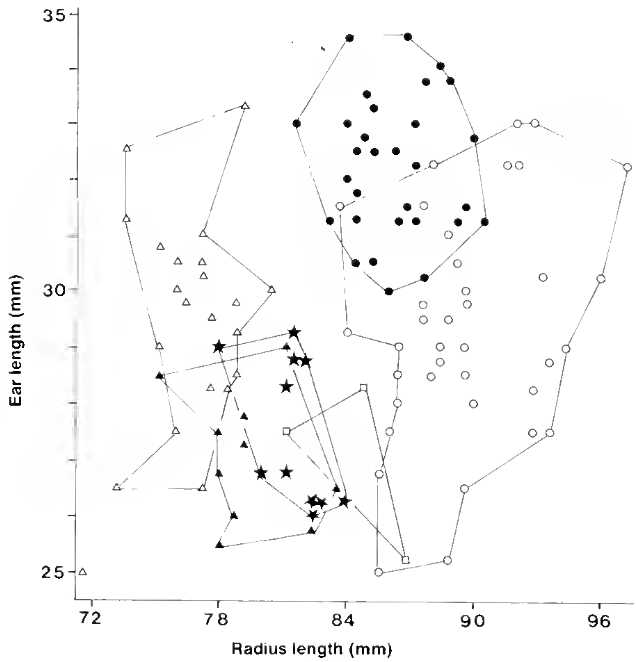


Figure 4 ear length v. radius length.

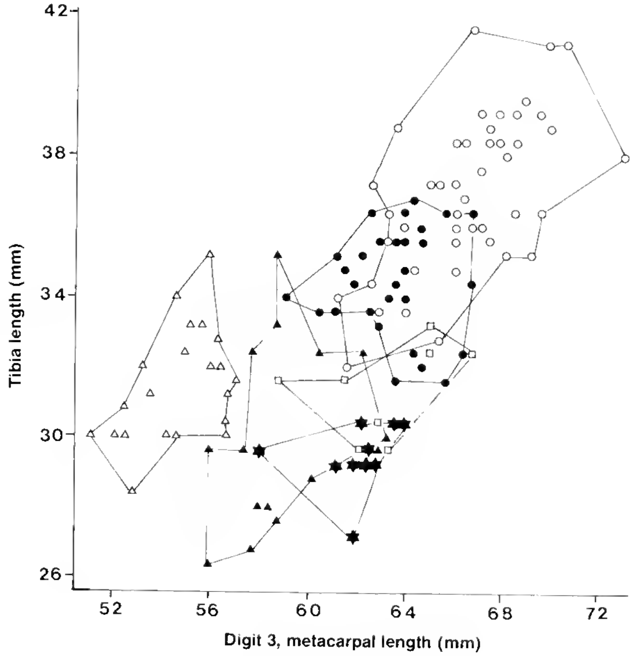


Figure 5 tibia length v. metacarpal length, digit 3.

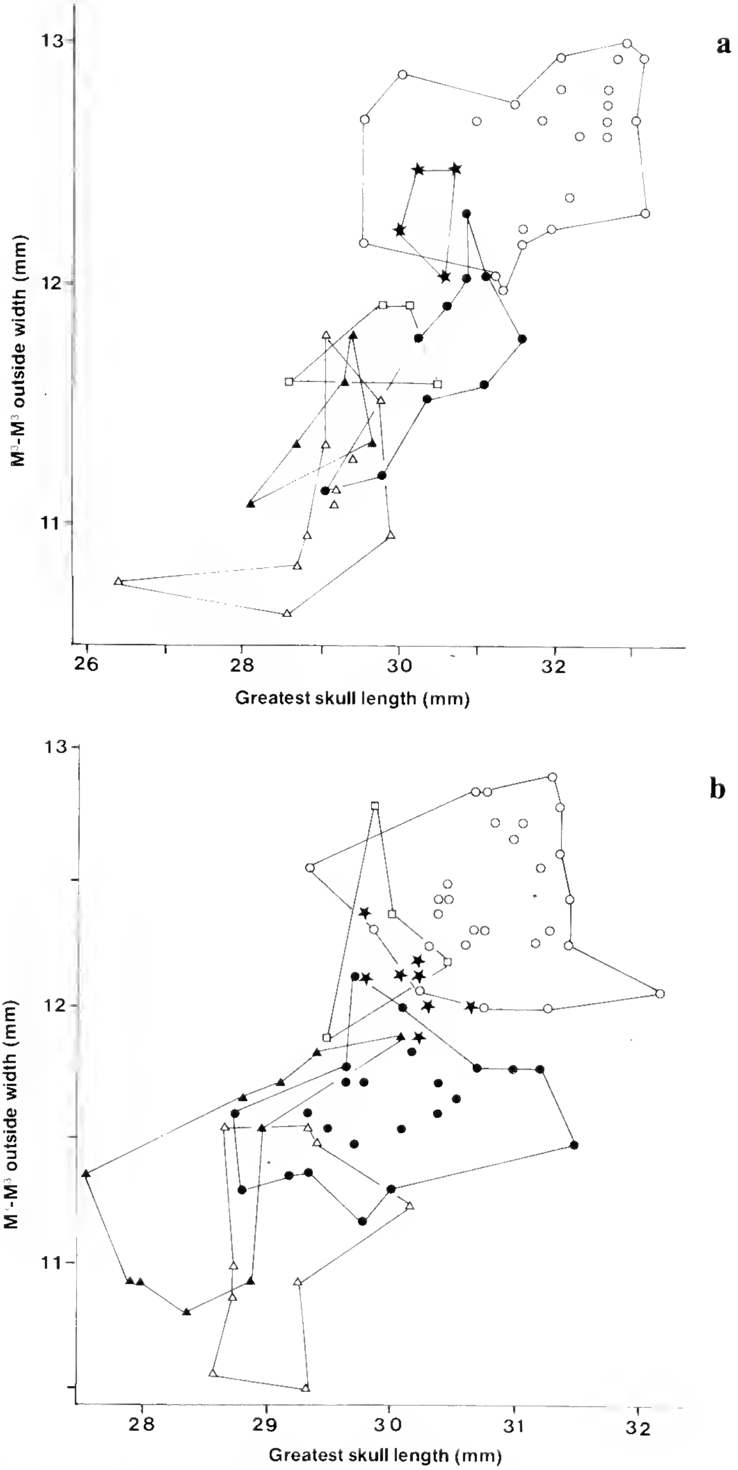
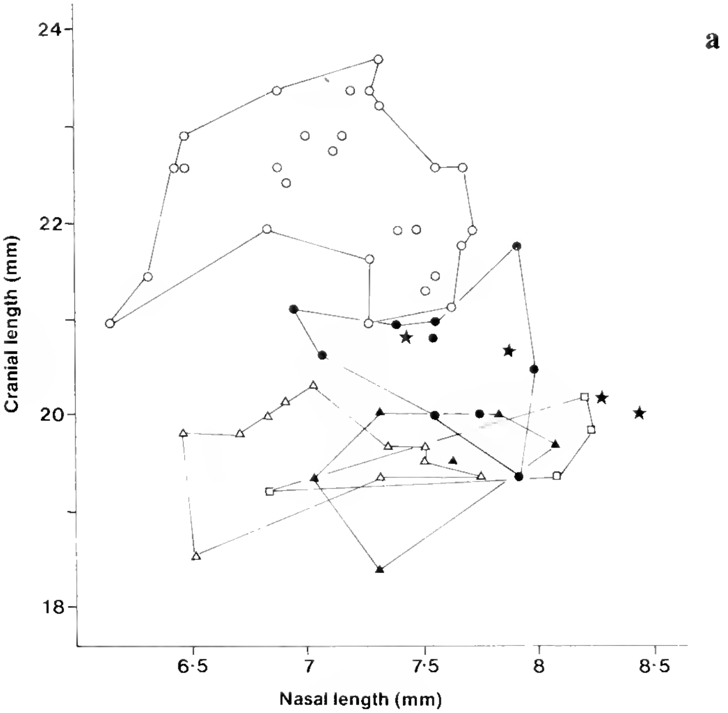


Figure 6a, b — Width outside upper third molars *v.* greatest skull length.



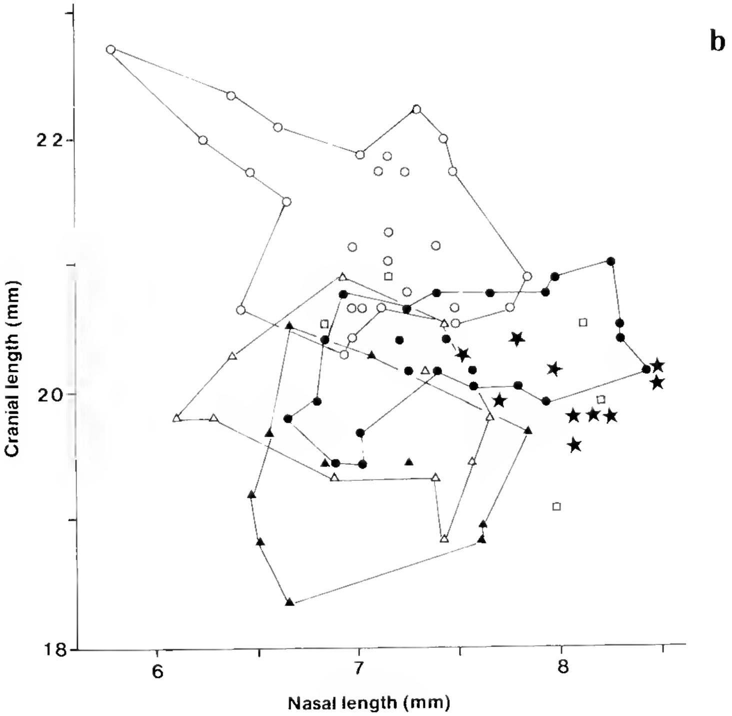
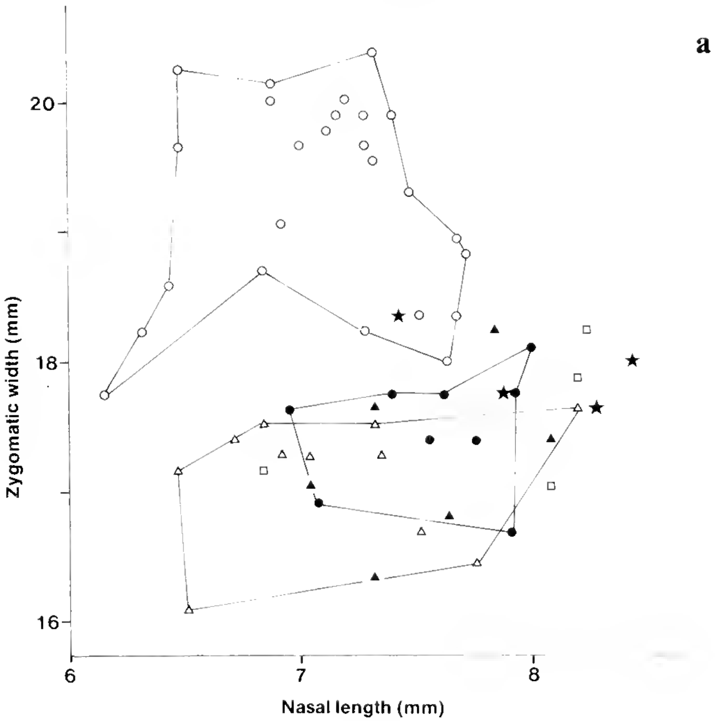


Figure 7a, b — cranial length *v.* nasal length.



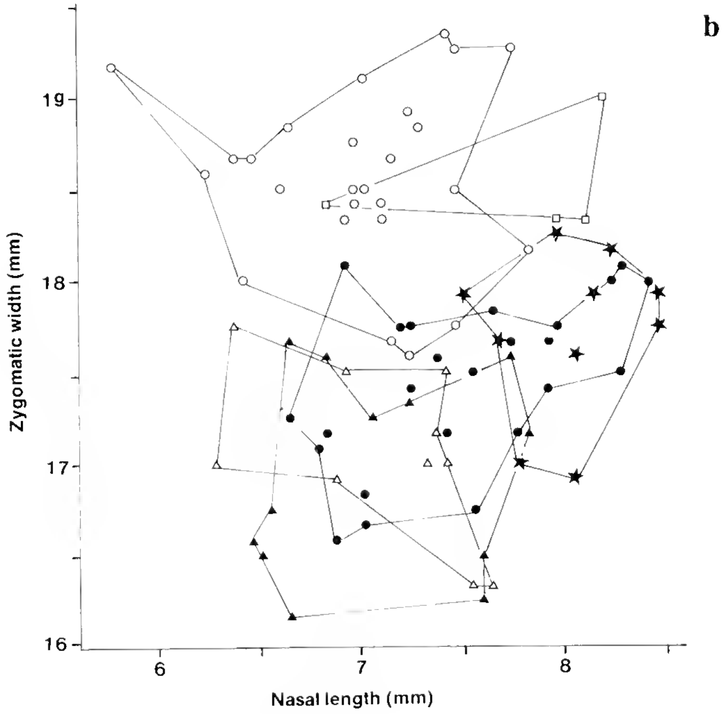
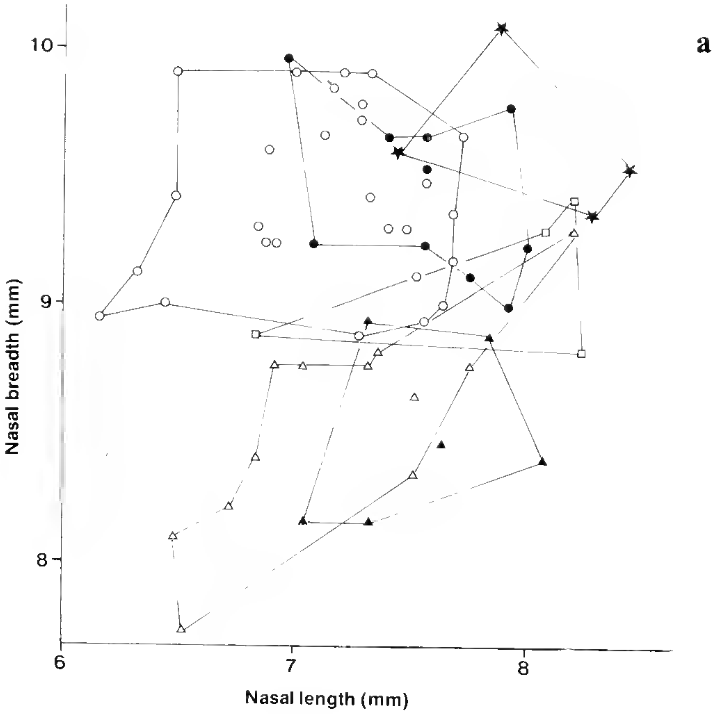


Figure 8a, b zygomatic width *v.* nasal length.



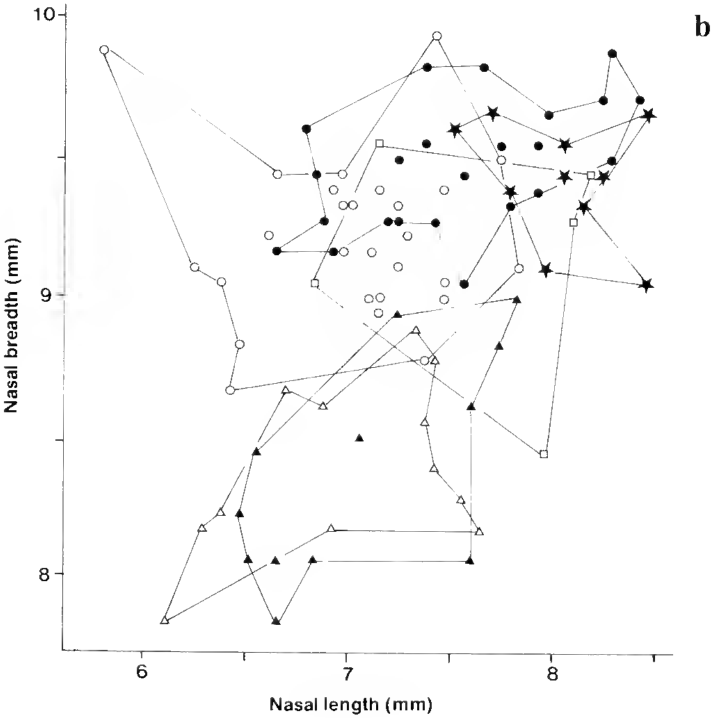


Figure 9a, b — nasal breadth *v*. nasal length.

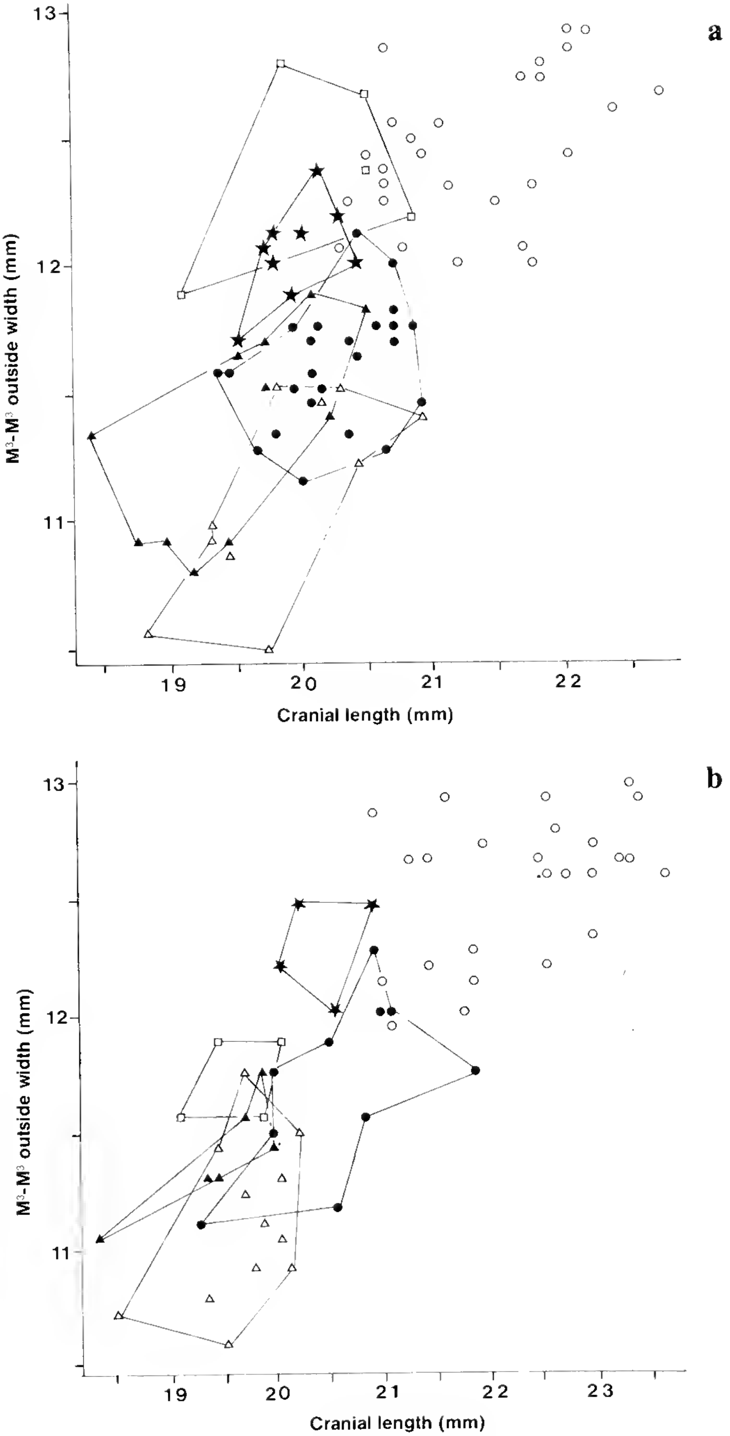


Figure 10a, b — width outside upper third molars *v.* cranial length.

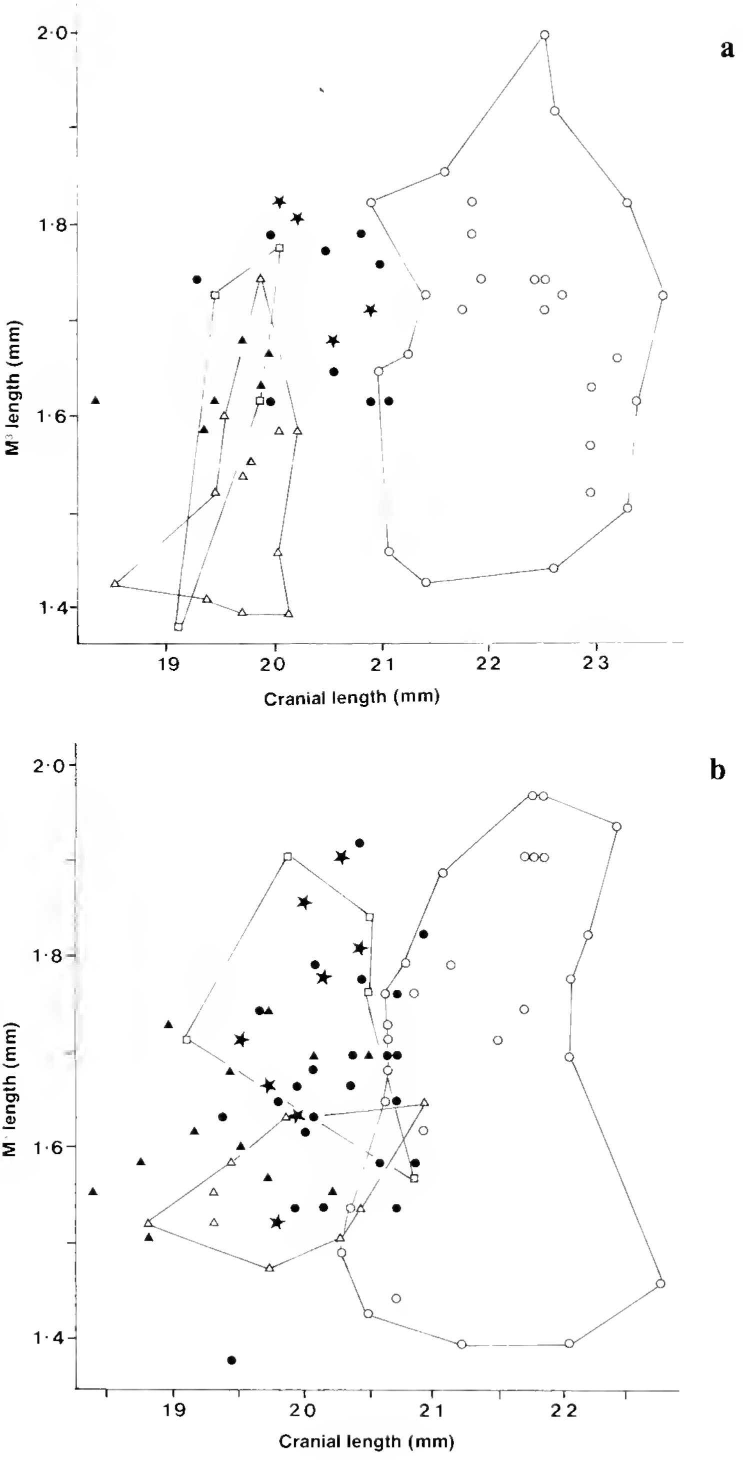


Figure 11a, b M³ length v. cranial length.

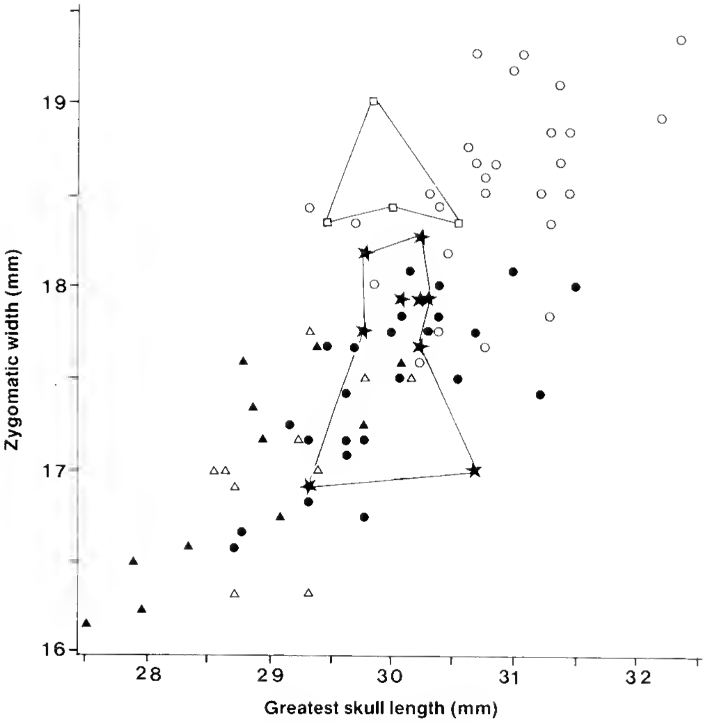


Figure 12b — zygomatic width *v*. greatest skull length.

Description

Externals (Table 1, Figures 3, 4, 5).

Moderately heavy (29.5-60.0) with moderately long forearm (81.7-90.2) and metacarpal 2-5 length; tibia moderately long (31.4-36.7); ear long (30.0-34.6) broad at base and sharply pointed with posterior margin behind the tip very gently concave; noseleaf well developed with three large supplementary leaflets (sometimes divided) always present; usually a fourth small leaflet present; anterior leaf large, greatest width up to 12, reaching anteriorly to distal point of lip, no anterior median emargination but usually this margin slightly scalloped and with a tiny median fleshy anterior projection; internarial septum very slightly thickened anteriorly but not inflated; narial lappets large, margins scalloped, when bent mesially will cover at least three-quarters of nostril opening; nostrils slightly pocketed; intermediate leaf expanded vertically to *c*. 6, prominent median keel terminating at apex to slight to obvious moderately sharp projection flanked laterally by two lower evenly curved projections, slightly narrower (*c*. 9 wide) than anterior leaf; posterior leaf slightly wider (*c*. 13) than anterior leaf, projects well above intermediate leaf, upper edge semicircular with faint gently arched median section sometimes apparent, supported by distinct median septum and two weak lateral septa.

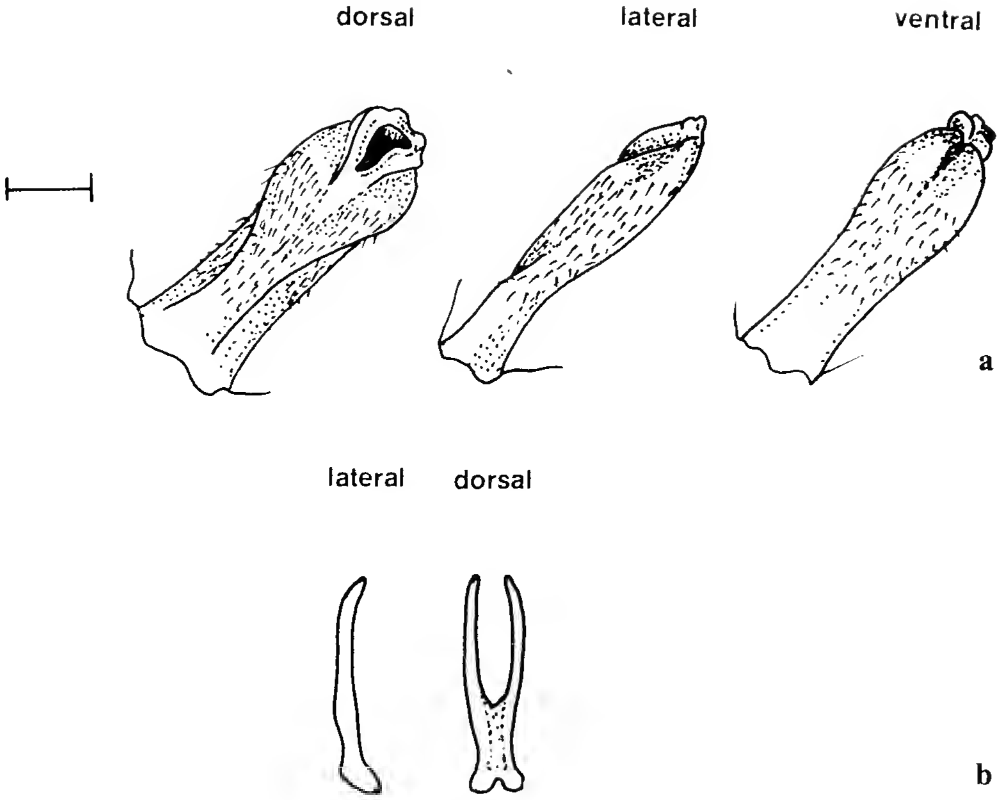


Figure 13 (**a**) Dorsal, lateral and ventral view of glans penis, with prepuce removed, of *H. d. diadema* from SW Timor (WAM M38086). (**b**) dorsal and lateral view of baculum of WAM M38086. Scale line 2 mm.

Pelage

Pelage with distinct colour pattern that is similar in specimens collected from throughout its range. Hair of face, rostrum, chin, throat, top of head, neck and shoulders, and occasionally as a mantle reaching to lumbar region a pale Vinaceous-Buff (light buff) to Wood Brown (pale brown); this colour from distal parts of hair, whereas basal half of hair a darker Buffy Brown to Olive Brown. Remainder of dorsum a contrastingly darker colour ranging from Snuff Brown (light-orange brown) to Clove Brown (dark brown); these hairs tricoloured with basal one-third same colour as distal parts; the middle part similar in colour to shoulder mantle. Pale wide Cartridge Buff to Pale Olive Buff stripe along each dorsal lateral margin in contact with plagiopatagium from femur almost to humerus. A tuft of hair coloured as for the lateral stripe present at both anterior and posterior base of humerus. Occasionally distinct spots or a marbled appearance occur on lower dorsum; these are also same colour as lateral stripe. On ventral surface paler hairs at base of humerus merge to form distinct lateral patches which occasionally spread almost to top of chest. Abdomen and majority of chest a darker colour ranging from Avellaneous (pale pink brown) to Brownish Olive. Usually paler fur of middle part of hair, which approximate colour of chin, emerges on abdomen to produce a marbled effect.

Penis and Baculum

Penis *c.* 9 long; prepuce covered with long hairs which exceed distal end by up to 3; prepuce opening distal; preputial sheath connects to glans base about 4.5 from distal end, glans dorsoventrally flattened (Figure 13a); urethral groove anterodorsal with low lateral lips which have two slight distal protuberances; small spines cover middle section of glans.

Baculum with shape of tuning fork; bifurcating distal arms connect a fragile base (*c.* 0.7 wide) which is about one third the total length (*c.* 2.6) (Figure 13b). These distal arms support lips of urethral groove.

Skull, dentary, dentition (Table 1, Figure 14a)

Moderate length skull (28.7-31.5) with well developed sagittal and lamboidal crests; supraorbital ridges extending forward from anterior point of sagittal crest usually poorly but occasionally moderately well developed, terminating anteriorly at posterolateral margin of rostrum occasionally as a low protuberance; posterior triangle of supraorbital ridge encloses shallow frontal depression; rostrum profile slightly rounded from dorsal aspect; rostral swelling with moderately inflated paired eminences on either side separated by shallow groove, anterior eminences approximately twice surface area of posterior ones, occasionally also low small lateral eminence obvious; zygomatic width moderate (16.6-18.7): mastoid large squarish in dorsal profile, minimum orbital distance moderate (3.3-3.9); premaxilla level with or slightly exceeding canine anterior edge; premaxilla ventral junction with maxilla U-V shaped; anterior palatal foramina slit-like, enclosed within premaxilla or occasionally anterior edge of maxilla closing posterior edge of foramina; mesopterygoid fossa moderately wide (3.3-4.2); sphenoid bridge partially, and occasionally completely, obscuring large sphenorbital foramen when viewed from ventral aspect; median pterygoid groove slight, vomer occasionally projects slightly posterior of postpalatal margin; pterygoids, moderately long, base wide; cochlea width exceeds distance between cochlea; I^1 bilobed, outer lobe reduced, inner lobe taller sharply sloping mesially; upper incisors occasionally in contact, C^1 moderate size, base moderately wide, internal cingulum moderate but does not form an anterior basal cusplet, occasionally a minute posterior basal cusplet; PM^2 moderately large, separates C^1 from PM^4, slightly extruded and nestles in posterior notch of C^1; PM^4 large, encircled by slight to moderate cingulum, usually with cusplet on mid-point of lingual cingulum; M^{1-2} with moderately developed protocone with its posterior edge in contact with metacone base, hypocone moderate, slight internal cingulum; toothrows close together (M^3-M^3W 11.1-12.3), M^3 posterior cusp obsolescent, approximately one-third only of prematacristid present; I_1 bilobed, outer lobe two-thirds crown area of inner lobe; I_2 trilobed, crown area twice that of I_1; C_1 moderately large, cingulum moderately well developed, forms miniscule posterobasal cusplet; PM_2 buccal area almost diamond shaped, two-thirds that of PM_4, PM_4 cusp posterointernal ridge with slight to moderate basal cusp, encircled by moderate cingulum as is M_1-$_3$; dentary robust, ventral edge below toothrow slightly arched beneath M_3 then horizontal to PM_2, usually moderately arched ventrally below C_1 (only very slightly in M35210-Savu) to form a keel before rising gently to base of incisors; ascending ramus broadly triangular, erect, angular process broadly rectangular and terminates lateral to condyloid process.

Hipposideros diadema nobilis (Horsfield, 1823)

Table 1; Figures 3-9, 11 and 14

Rhinolophus nobilis Horsfield, T. 1823, Zoological researches in Java and the neighbouring islands, London No. 6, Pl. vii.

Hipposideros diadema vicarius Andersen, K. 1905. On *Hipposideros diadema* and its closest allies. Ann. Mag. nat. Hist. (7) 16: 499, Sarawak.

Types: Two "co-types", skins, in British Museum, Natural History, BM 79.11.21.83.

Type locality: Java.

Specimens examined (see Appendix 1).

Diagnosis

Hipposideros d. nobilis differs from *H. d. diadema* in having its anterior noseleaf smaller; tibia longer relative to ear length (Figure 3), its canines larger and more robust and teeth generally larger. For example, ♂♂ C^1-M^3 length 12.3 (11.3-13.1) *v.* 11.5 (10.9-12.2); M^2 length 3.0 (2.7-3.3) *v.* 2.7 (2.2-3.2) and ♀♀ C^1-M^3 11.9 (11.0-12.5) *v.* 11.2 (10.4-11.6); M^2 length 3.0 (2.7-3.2) *v.* 2.8 (2.3-3.1); molar tooth rows generally further apart relative to greatest skull length (Figure 6a, b); cranium generally longer relative to nasal length (Figure 7 a, b); zygomatic width relative to nasal length generally larger (Figure 8a, b).

It differs from *H. d. griseus* in having its anterior noseleaf relatively smaller; external and skull measurements and weight averaging larger (in some cases without overlap); (Table 1) e.g., radius length 88.3 (76.9-97.0) *v.* 79.2 (71.6-85.6); tibia length 36.5 (30.1-41.8) *v.* 30.3 (26.5-35.1); ear length 29.3 (25.0-33.1) *v.* 27.1 (25.5-29.1); greatest skull length ♂♂ 31.9 (29.5-33.2) *v.* 29.1 (28.0-29.6) and ♀♀ 30.8 (29.3-32.3) *v.* 28.7 (27.5-30.1); C^1-M^3 ♂♂ 12.3 (11.3-13.1) *v.* 10.7 (10.3-11.0) and ♀♀ 11.9 (11.0-12.5) *v.* 10.8 (10.2-11.4); cranium longer relative to nasal length (Figure 7a, b), nasals wider relative to their length (Figure 9 a, b).

It differs from *H. d. reginae* in having its anterior noseleaf relatively smaller; averaging larger in all external measurements (Table 1) e.g., radius length 88.3 (76.9-97.0) *v.* 81.2 (74.1-84.5) and tibia length 36.5 (30.1-41.8) *v.* 29.8 (27.4-31.5); tibia longer relative to ear length (Figure 3); radius longer relative to ear length (Figure 4);

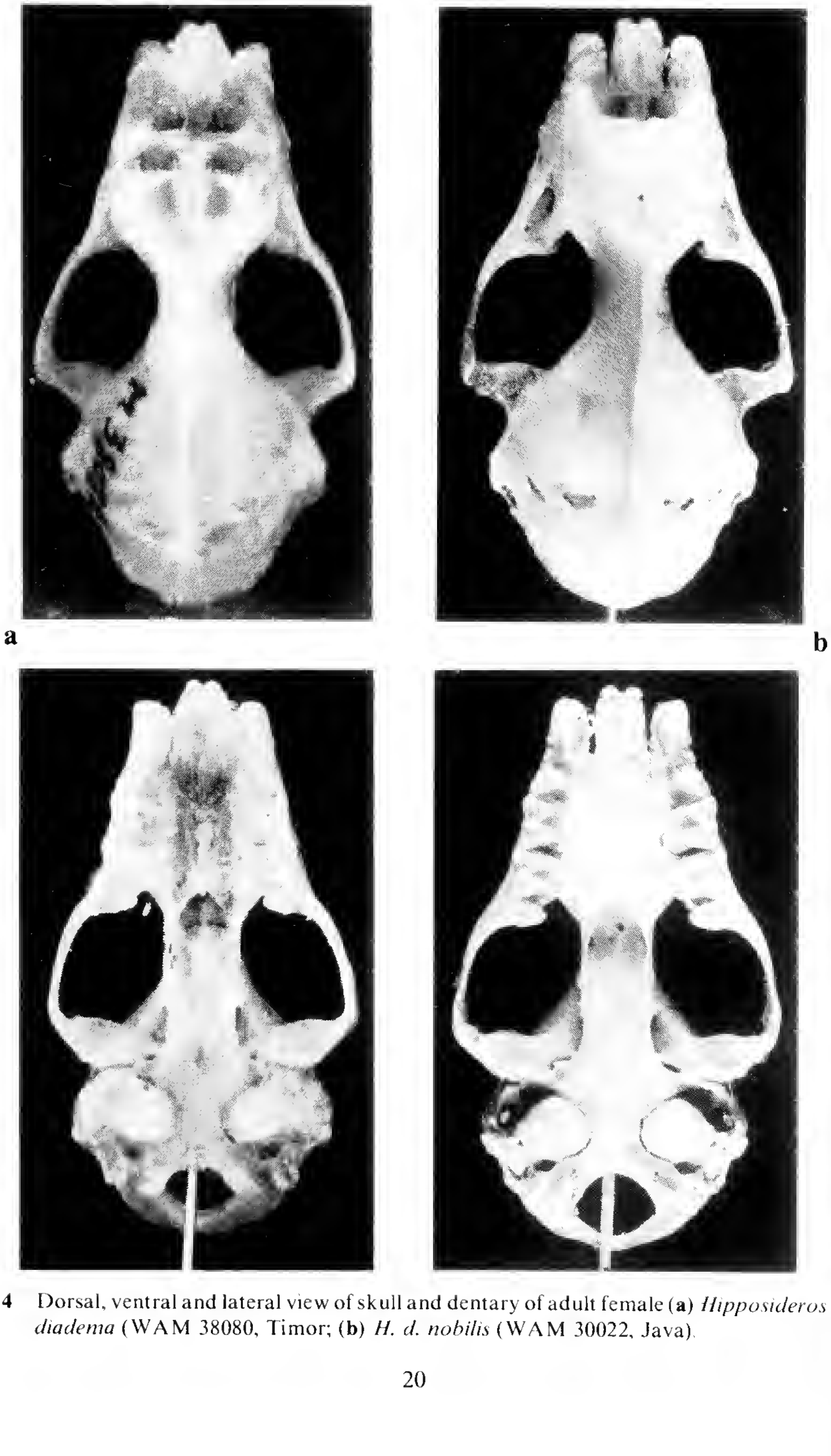


Figure 14 Dorsal, ventral and lateral view of skull and dentary of adult female (**a**) *Hipposideros diadema diadema* (WAM 38080, Timor; (**b**) *H. d. nobilis* (WAM 30022, Java).

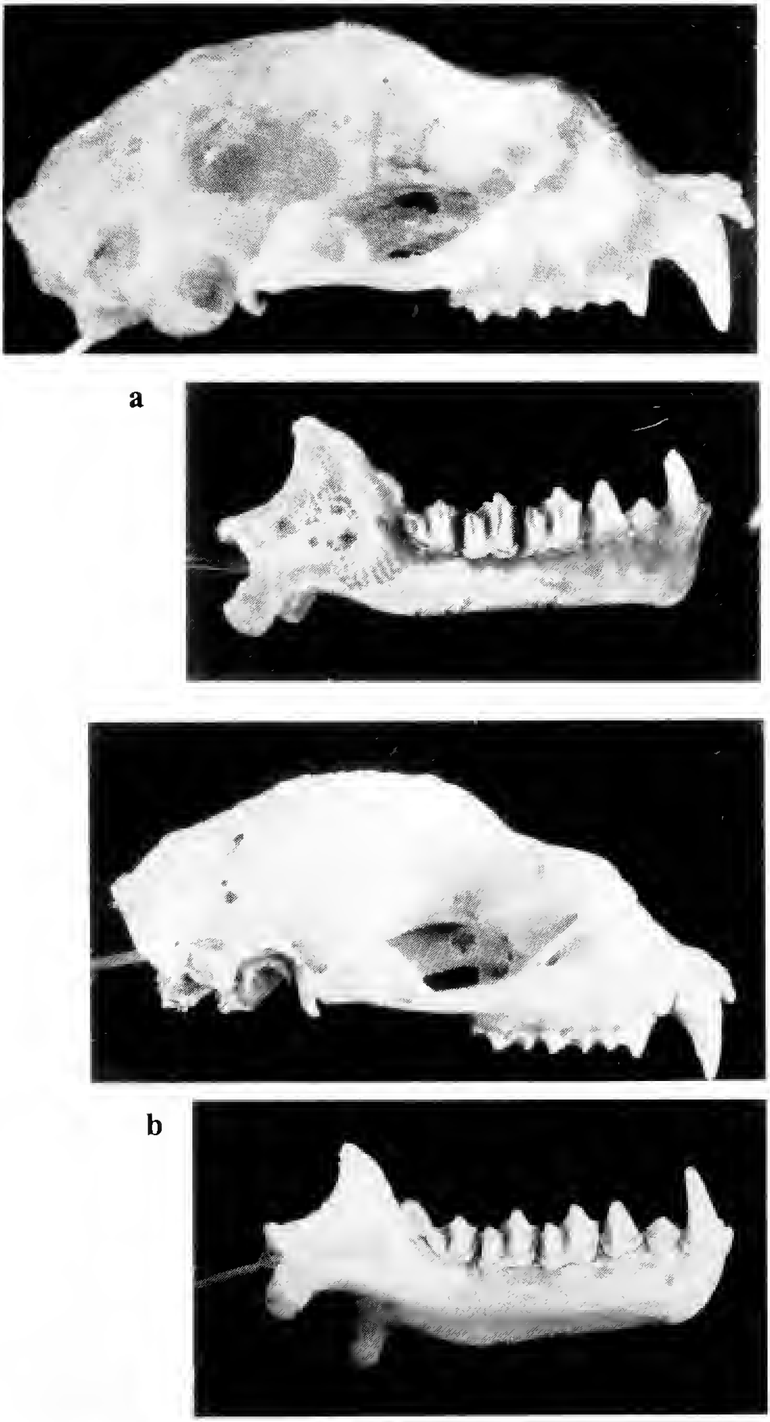
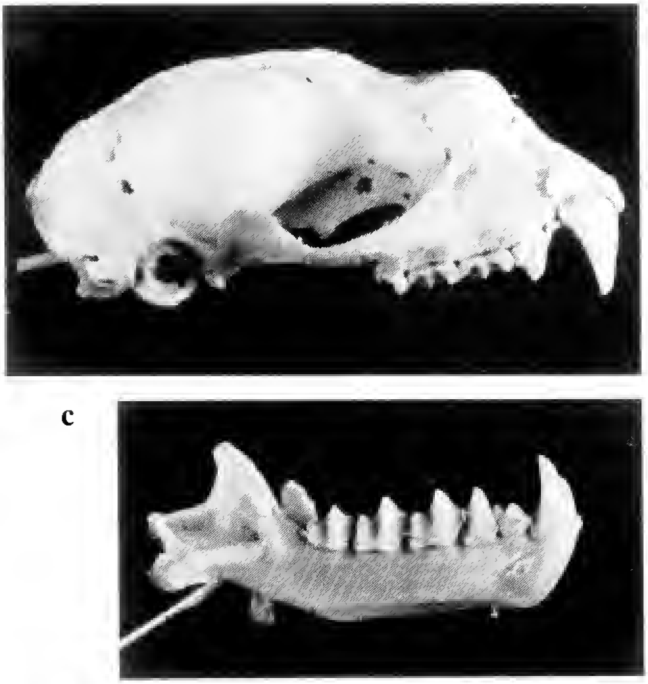
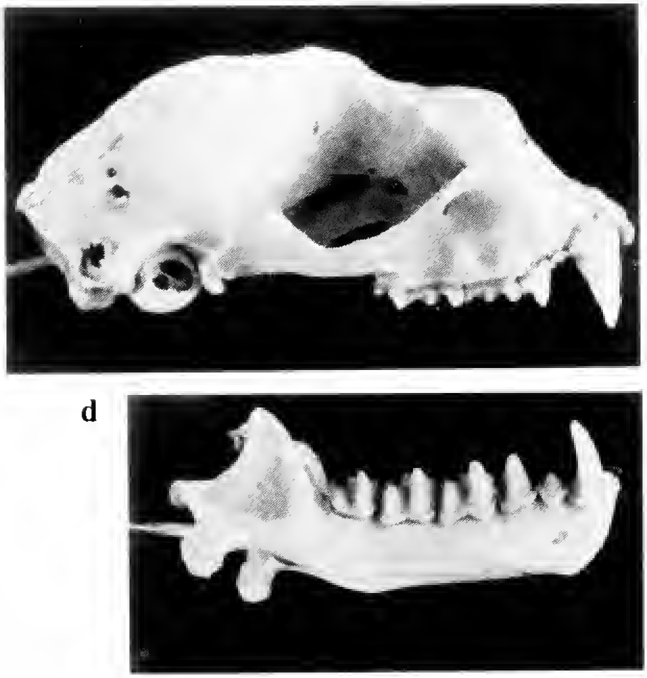

a
b

Figure 14 (cont.) Dorsal, ventral and lateral view of skull and dentary of adult female **(c)** *H. d. griseus* (WAM 27484, Papua New Guinea), **(d)** *H. d. reginae* (JM 2453, Queensland).

c



d



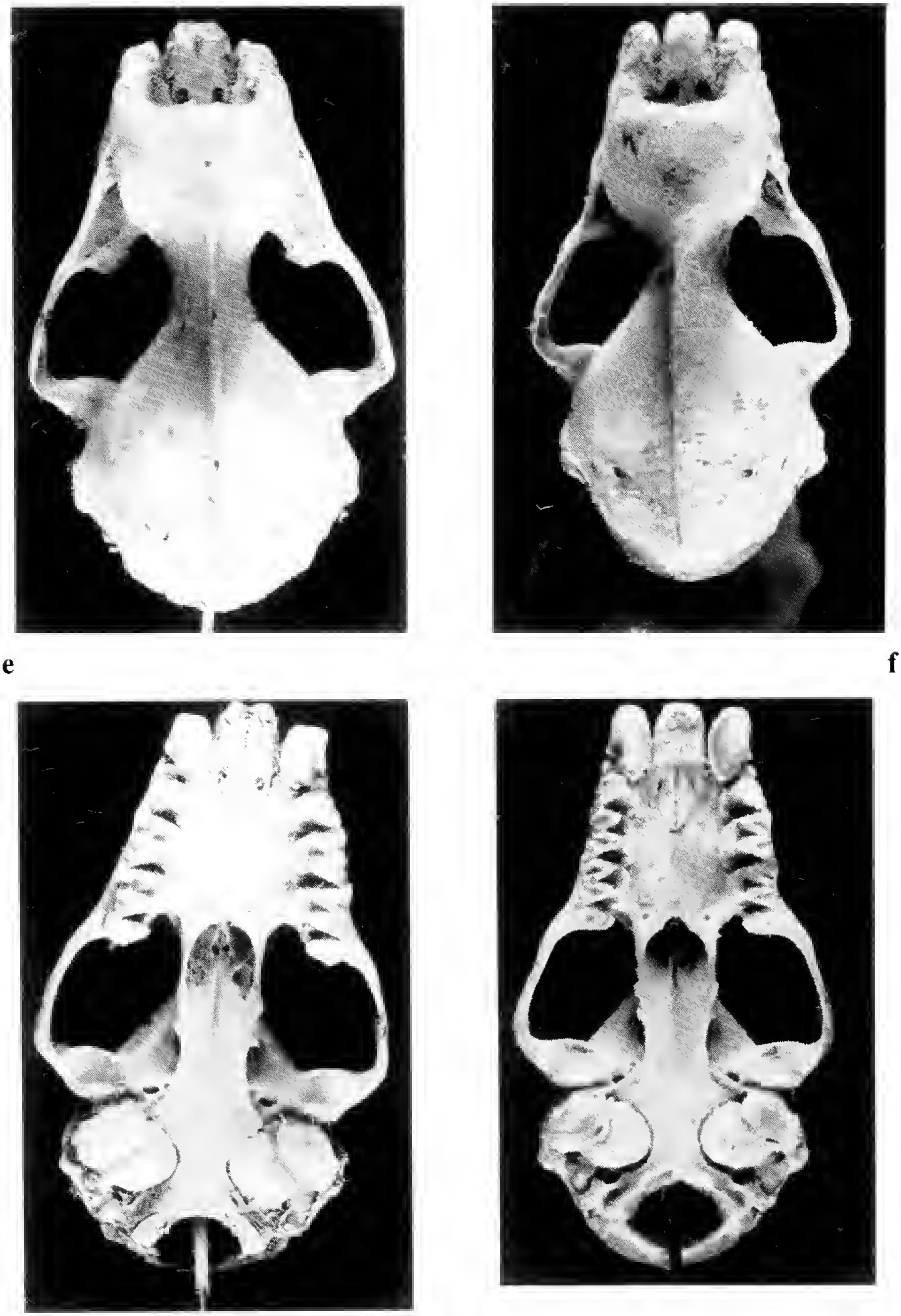
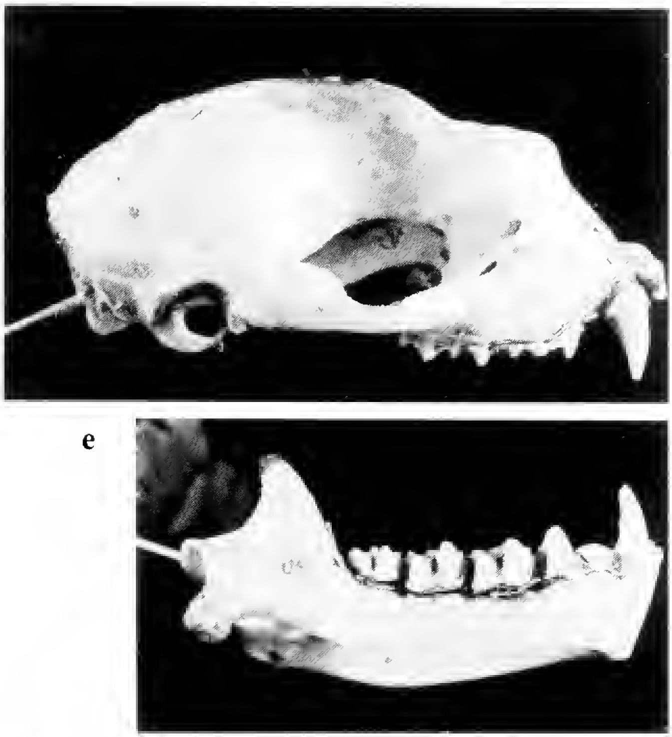
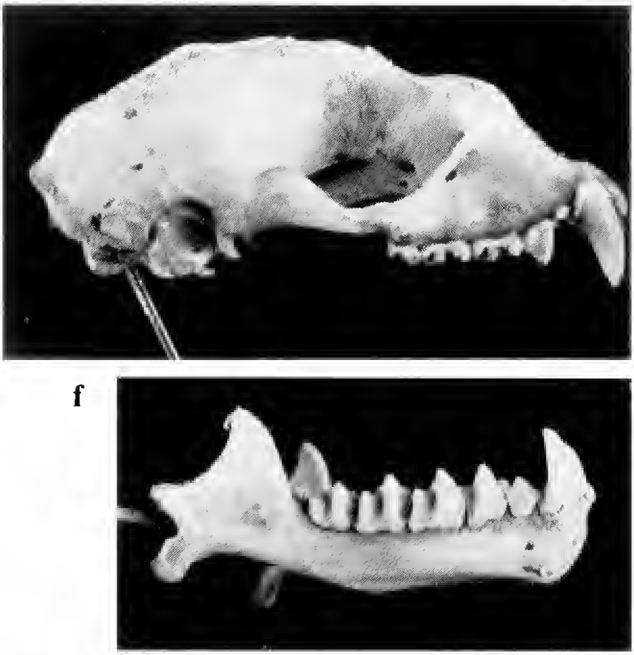


Figure 14 (cont.) Dorsal, ventral and lateral view of skull and dentary of adult female **(e)** *H. d. masoni* (S 259845) and **(f)** *H. d. oceanitis* (AM 20101, Solomon Is).

e



f



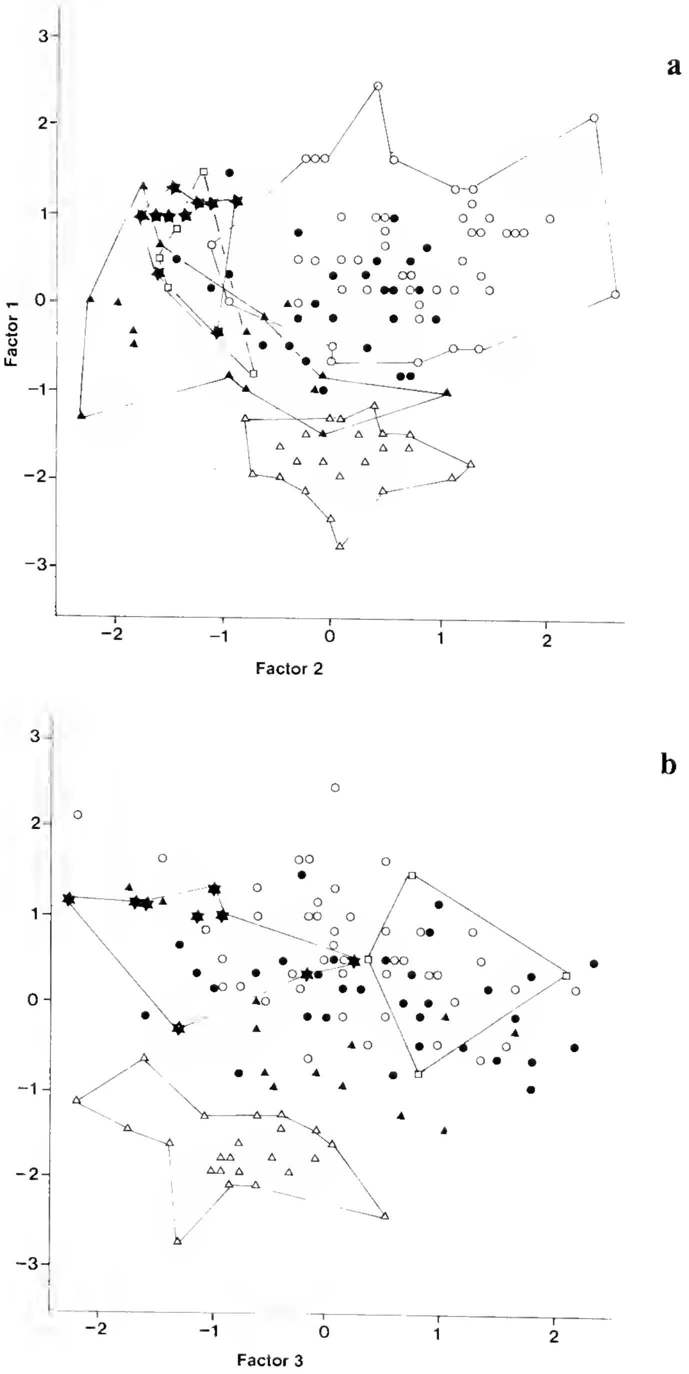


Figure 15 Principal component analysis based on external measurements of *Hipposideros diadema* specimens used in this study. (**a**) Factor 1 *v.* 2 and (**b**) Factor score 1 *v.* 3. Subspecies symbols as for Figure 2.

tibia longer relative to metacarpal 3 length (Figure 5). Most skull, dental and dentary characters average larger, e.g., greatest skull length ♂♂ 31.9 (29.5-33.2) v. 30.4 (30.0-30.7) and ♀♀ 30.8 (29.3-32.3) *v.* 30.0 (29.3-30.7); C^1-M^3 length ♂♂ 12.3 (11.3-13.1) *v.* 11.6 (11.3-11.8) and ♀♀ 11.9 (11.0-12.5) v. 11.4 (11.0-11.7); nasals shorter relative to their breadth (Figure 9a, b).

It differs from *H. d. masoni* in having its anterior noseleaf relatively smaller; averages larger in all external measurements (Table 1) e.g., radius length 88.3 (76.9-97.0) *v.* 85.0 (80.2-90.2); tibia longer relative to both ear length (Figure 3) and metacarpal 3 length (Figure 5). Most skull and dental measurements (except minimum interorbital distance and nasal length) average larger (Table 1) e.g., C^1-M^3 length ♂♂ 12.3 (11.3-13.1) *v.* 11.5 (11.2-11.7) and ♀♀ 11.9 (11.0-12.5) v. 11.6 (11.4-12.0); molar rows further apart relative to greatest skull length (Figure 6a, b); cranial length greater relative to M^3 length (Figure 11a, b).

It differs from *H. d. oceanitis* in having its anterior noseleaf relatively smaller; three rather than two large supplementary nose leaflets; averages much heavier 50.9 (40.0-67.0) *v.* 36.4 (30.2-42.0); larger in all external measurements, often with no overlap (Table 1) e.g., radius length 88.3 (76.9-97.0) *v.* 76.5 (71.7-80.4), tibia length 36.5 (30.1-41.8) *v.* 31.5 (28.6-35.0); tibia longer relative to ear length (Figure 3); radius longer relative to ear length (Figure 4); metacarpal 3 length longer relative to tibia length (Figure 5); larger in all skull measurements (Table 1), e.g., greatest skull length ♂♂ 31.9 (29.5-33.2) *v.* 28.9 (26.4-29.9) and ♀♀ 30.8 (29.3-32.3) *v.* 29.1 (28.5-30.1); C^1-M^3 length ♂♂ 12.3 (11.3-13.1) *v.* 10.7 (9.6-11.3) and ♀♀ 11.9 (11.0-12.5) *v.* 10.7 (10.0-11.2); molar rows wider apart relative to greatest skull length (Figure 6a, b); nasals wider relative to their length (Figure 9a, b); cranial length greater relative to M^3 length (Figure 11 a, b); zygomatic width larger relative to nasal length (Figure 8a, b).

Description

Externals (Table 1, Figures 3, 4, 5)

Heaviest of subspecies considered (40.0-67.0); wing dimensions largest of subspecies with radius 76.9-97.0 and metarcapal digit 5 51.6-62.8; tibia large (30.1-41.8); ear length moderate (25.0-33.1); anterior noseleaf tends to be narrower than *H. d. diadema* (up to 10) and does not project as far anteriorly; posterior leaf with weak median septum and two faint lateral septa. Other descriptions as for *H. d. diadema.*

Pelage

Pattern of colouration similar to *H. d. diadema* but in some specimens the pale lateral dorsal stripe and pale ventral patch at base of humerus indistinct or absent. Also paler area on head and mantle considerably reduced. There is considerable colour variation even on a single island. For example, on Lombok I. predominant darker dorsal colours range from orange brown to dark sepia while lighter colours range from pale cream to dark buff.

Table 1 Measurements, in mm, (see Figure 1 caption for code to characters) for adult *H. diadema diadema; H. d. nobilis; H. d. griseus; H. d. reginae; H. d. masoni; H. d. oceanitis.* N, sample size; X, mean; SD, standard deviation; MIN, minimum; MAX, maximum (a) skull characters (males and females separate); (b) external characters (males and females combined).

Table 1a Males		GSL	CCL	CL	NL	NB	CH	IBW	PBL	MFB	OCL	IOB	ZW
H. d. diadema	N	11	10	11	11	11	11	11	11	11	11	11	11
	X	30.5	27.3	20.6	7.6	9.5	8.2	2.3	5.2	3.7	7.5	3.6	17.6
	SD	0.68	0.69	0.68	0.33	0.31	0.34	0.22	0.42	0.3	0.38	0.2	0.55
	MIN	29.1	25.9	19.3	6.9	9.0	7.7	2.0	4.5	3.3	7.1	3.3	16.7
	MAX	31.5	28.1	21.8	8.0	10.0	8.7	2.7	6.1	4.2	8.4	3.9	18.7
H. d. nobilis	N	27	26	27	27	27	27	27	27	27	27	27	27
	X	31.9	28.3	22.3	7.1	9.4	8.5	2.7	5.7	3.6	8.0	3.4	19.2
	SD	1.01	0.80	0.80	0.45	0.34	0.33	0.28	0.52	0.30	0.52	0.21	0.85
	MIN	29.5	26.3	20.9	6.2	8.9	8.0	2.2	4.5	2.9	6.4	3.1	17.5
	MAX	33.2	29.5	23.6	7.7	9.9	9.6	3.2	7.4	4.2	8.7	4.0	20.5
H. d. griseus	N	6	6	6	6	6	6	6	6	6	6	6	6
	X	29.1	25.5	19.5	7.5	8.5	7.7	2.3	4.8	3.4	6.7	3.5	17.3
	SD	0.59	0.44	0.58	0.39	0.33	0.31	0.28	0.30	0.18	0.24	0.31	0.66
	MIN	28.0	24.7	18.4	7.0	8.1	7.3	1.8	4.3	3.1	6.4	3.1	16.4
	MAX	29.6	26.0	20.0	8.1	8.9	8.2	2.6	5.2	3.7	6.9	3.9	18.3
H. d. reginae	N	4	4	4	4	4	4	4	4	4	4	4	4
	X	30.4	27.4	20.4	8.0	9.6	8.2	2.7	5.3	3.7	7.4	3.8	18.0
	SD	0.31	0.38	0.36	0.45	0.31	0.11	0.26	0.26	0.08	0.34	0.19	0.35
	MIN	30.0	26.9	20.1	7.4	9.4	8.0	2.4	5.0	3.6	7.0	3.6	17.6
	MAX	30.7	27.7	20.9	8.5	10.1	8.2	3.0	5.6	3.7	7.8	4.0	18.4
H. d. oceanitis	N	12	11	12	12	12	11	11	12	11	12	12	11
	X	28.9	25.5	19.7	7.2	8.6	8.0	2.5	5.4	3.4	6.7	3.5	17.1
	SD	0.89	0.78	0.46	0.52	0.41	0.38	0.20	0.62	0.17	0.43	0.18	0.51
	MIN	26.4	23.6	18.6	6.5	7.8	7.4	2.3	4.9	3.0	5.8	3.1	16.0
	MAX	29.9	26.5	20.3	8.2	9.3	8.5	2.9	6.5	3.7	7.5	3.8	17.6
H. d. masoni	N	4	4	4	4	4	4	4	4	3	4	4	4
	X	29.7	26.5	19.6	7.8	9.1	8.1	2.5	5.2	3.6	7.4	3.6	17.6
	SD	0.86	0.43	0.43	0.67	0.29	0.44	0.22	0.53	0.04	0.42	0.50	0.57
	MIN	28.5	26.0	19.1	6.8	8.8	7.5	2.2	4.5	3.6	7.0	2.9	17.1
	MAX	30.5	27.0	20.1	8.3	9.4	8.5	2.8	5.8	3.6	8.0	4.0	18.2

Table 1a Males (cont.)

		BCW	DL	RAL	C^1-C^1W	M^3-M^3W	C^1-M^3L	C_1-M_3L	PM^4L	M^1L	M^2L	M^3L	PML
H. d. diadema	N	11	11	11	11	11	11	11	11	11	11	11	11
	X	12.0	22.6	9.4	8.1	11.7	11.5	13.9	2.2	2.8	2.7	1.7	6.6
	SD	0.44	0.58	0.33	0.26	0.36	0.37	0.30	0.26	0.16	0.33	0.08	0.44
	MIN	11.2	21.8	8.9	7.8	11.1	10.9	13.5	1.8	2.5	2.2	1.6	6.0
	MAX	12.6	23.3	9.9	8.6	12.3	12.2	14.4	2.6	2.9	3.2	1.8	7.2
H. d. nobilis	N	27	27	27	27	26	27	27	27	27	27	27	27
	X	12.5	23.9	9.9	8.5	12.6	12.3	14.9	2.4	3.1	3.0	1.7	6.9
	SD	0.52	0.73	0.57	0.46	0.30	0.44	0.44	0.20	0.13	0.15	0.14	0.47
	MIN	11.5	21.8	9.0	7.6	11.9	11.3	14.0	2.0	2.8	2.7	1.4	6.0
	MAX	13.4	24.8	11.5	9.2	13.0	13.1	15.6	2.8	3.3	3.3	2.0	7.8
H. d. griseus	N	6	6	6	6	6	6	6	6	6	6	6	6
	X	11.6	21.3	9.2	7.5	11.4	10.7	13.1	2.0	2.7	2.7	1.6	6.2
	SD	0.78	0.50	0.50	0.28	0.24	0.27	0.21	0.15	0.1	0.12	0.04	0.21
	MIN	10.4	20.8	8.3	7.0	11.1	10.3	12.9	1.7	2.5	2.5	1.6	6.0
	MAX	12.7	22.0	9.8	7.8	11.8	11.0	13.5	2.1	2.8	2.9	1.7	6.5
H. d. reginae	N	4	3	4	3	4	4	3	4	4	4	4	4
	X	11.9	22.5	9.2	8.0	12.3	11.6	13.9	2.0	2.9	2.9	1.8	6.7
	SD	0.28	0.83	0.21	0.09	0.25	0.23	0.45	0.14	0.16	0.17	0.07	0.26
	MIN	11.6	21.6	9.0	8.0	12.0	11.3	13.5	1.9	2.7	2.6	1.7	6.4
	MAX	12.2	23.3	9.5	8.1	12.5	11.8	14.4	2.2	3.0	3.0	1.8	6.9
H. d. oceanitis	N	11	12	12	12	12	12	12	12	12	12	12	12
	X	11.9	21.3	9.2	7.4	11.1	10.7	13.1	1.9	2.7	2.7	1.5	5.7
	SD	0.31	0.69	0.46	0.35	0.35	0.49	0.44	0.14	0.19	0.15	0.10	0.63
	MIN	11.4	19.6	8.4	7.0	10.6	9.6	12.1	1.7	2.5	2.3	1.4	4.7
	MAX	12.4	22.1	9.8	8.2	11.8	11.3	13.6	2.2	3.1	2.9	1.7	6.6
H. d. masoni	N	4	4	4	4	4	4	4	4	4	4	4	4
	X	11.8	22.4	9.2	7.5	11.7	11.5	13.8	2.2	2.9	3.0	1.6	6.5
	SD	0.62	0.27	0.35	0.37	0.20	0.21	0.12	0.17	0.09	0.09	0.18	0.22
	MIN	11.0	22.1	8.9	7.0	11.6	11.2	13.7	2.0	2.8	2.9	1.4	6.2
	MAX	12.3	22.7	9.6	7.8	11.9	11.7	13.9	2.4	3.0	3.1	1.8	6.8

Table 1a Females		GSL	CCL	CL	NL	NB	CH	IBW	PBL	MFB	OCL	IOB	ZW
H. d. diadema	N	25	25	25	25	25	25	25	25	25	25	25	25
	X	30.0	26.8	20.3	7.5	9.5	8.2	2.4	5.0	3.6	7.2	3.8	17.5
	SD	0.69	0.62	0.42	0.52	0.23	0.32	0.16	0.24	0.24	0.34	0.18	0.46
	MIN	28.7	25.6	19.4	6.7	9.1	7.5	2.0	4.4	3.2	6.6	3.4	16.6
	MAX	31.5	28.1	21.0	8.4	9.9	8.8	2.6	5.6	4.3	7.9	4.0	18.1
H. d. nobilis	N	28	28	28	28	28	28	28	28	28	28	28	28
	X	30.8	27.4	21.3	7.0	9.2	8.3	2.7	5.5	3.6	7.7	3.5	18.6
	SD	0.66	0.63	0.68	0.46	0.29	0.33	0.22	0.32	0.29	0.43	0.24	0.49
	MIN	29.3	26.3	20.3	5.8	8.7	7.6	2.2	4.9	3.0	6.9	3.2	17.6
	MAX	32.3	28.9	22.7	7.8	10.0	9.3	2.9	6.1	4.1	8.6	3.9	19.4
H. d. griseus	N	12	12	12	12	12	11	12	12	12	12	12	12
	X	28.7	25.4	19.5	7.1	8.4	7.9	2.3	4.7	3.2	6.8	3.6	16.9
	SD	0.80	0.76	0.63	0.51	0.39	0.23	0.23	0.33	0.23	0.45	0.19	0.57
	MIN	27.5	24.6	18.4	6.5	7.9	7.5	2.0	4.2	2.8	6.3	3.3	16.1
	MAX	30.1	26.6	20.5	7.8	9.0	8.2	2.7	5.4	3.6	7.7	3.9	17.7
H. d. reginae	N	10	10	10	10	10	10	10	10	10	10	10	10
	X	30.0	26.8	20.0	8.0	9.4	8.1	2.5	5.4	3.6	7.2	3.9	17.7
	SD	0.39	0.49	0.28	0.31	0.21	0.21	0.24	0.56	0.11	0.22	0.18	0.44
	MIN	29.3	26.1	19.6	7.5	9.1	7.8	2.2	4.7	3.4	6.8	3.6	16.9
	MAX	30.7	27.4	20.5	8.5	9.7	8.4	2.9	6.7	3.8	7.5	4.1	18.3
H. d. oceanitis	N	11	11	11	12	12	11	12	12	11	12	12	10
	X	29.1	25.8	19.8	7.0	8.4	7.8	2.5	5.0	3.4	6.7	3.4	17.1
	SD	0.53	0.43	0.60	0.53	0.31	0.18	0.20	0.39	0.21	0.32	0.13	0.47
	MIN	28.5	25.0	18.8	6.1	7.9	7.6	2.2	4.6	3.2	6.0	3.2	16.3
	MAX	30.1	26.6	20.9	7.6	8.9	8.1	2.9	6.0	3.8	7.2	3.6	17.8
H. d. masoni	N	5	5	5	5	5	5	5	5	5	5	5	5
	X	30.1	26.8	20.2	7.7	9.2	8.1	2.6	4.9	3.6	7.4	3.9	18.6
	SD	0.44	0.61	0.69	0.61	0.44	0.18	0.24	0.35	0.24	0.19	0.12	0.33
	MIN	29.4	26.2	19.1	6.9	8.5	7.8	2.2	4.6	3.3	7.2	3.7	18.3
	MAX	30.5	27.6	20.9	8.2	9.6	8.3	2.9	5.4	3.9	7.7	4.0	19.0

Table 1a Females (cont.)

		BCW	DL	RAL	C^1-C^{1}W	M^3-M^{3}W	C^1-M^{3}L	C$_1$-M$_3$L	PM^{4}L	M^{1}L	M^{2}L	M^{3}L	PML
H. d. diadema	N	25	25	25	25	25	25	25	25	25	25	25	25
	X	11.9	22.0	9.2	7.9	11.6	11.2	13.6	2.2	2.8	2.8	1.7	6.8
	SD	0.38	0.57	0.38	0.30	0.25	0.29	0.26	0.18	0.13	0.20	0.11	0.36
	MIN	11.3	20.7	8.5	7.4	11.2	10.4	12.9	1.7	2.5	2.3	1.4	6.0
	MAX	12.6	23.1	10.0	8.3	12.1	11.6	14.0	2.4	3.1	3.1	1.9	7.3
H. d. nobilis	N	28	28	28	28	28	28	28	28	28	28	28	28
	X	12.1	23.0	9.5	8.2	12.4	11.9	14.4	2.3	3.0	3.0	1.7	6.6
	SD	0.48	0.52	0.37	0.35	0.28	0.35	0.39	0.23	0.12	0.14	0.18	0.35
	MIN	11.3	22.1	8.7	7.4	12.0	11.0	13.4	1.9	2.7	2.7	1.4	5.7
	MAX	13.0	24.1	10.3	8.8	12.9	12.5	15.2	2.9	3.2	3.2	2.0	7.2
H. d. griseus	N	12	12	12	12	11	12	12	12	12	12	12	12
	X	11.5	21.1	8.6	7.4	11.4	10.8	13.0	2.0	2.7	2.6	1.6	6.1
	SD	0.45	0.63	0.44	0.48	0.40	0.37	0.43	0.13	0.17	0.23	0.08	0.40
	MIN	10.7	19.9	7.6	6.8	10.8	10.2	12.5	1.7	2.4	2.3	1.5	5.5
	MAX	12.4	21.9	9.0	8.5	11.9	11.4	13.8	2.1	3.0	3.0	1.8	6.9
H. d. reginae	N	10	10	10	10	10	10	10	10	10	10	10	10
	X	11.8	22.3	8.9	7.8	12.1	11.4	13.8	1.9	2.7	2.8	1.7	6.3
	SD	0.20	0.36	0.30	0.17	0.18	0.18	0.19	0.11	0.12	0.10	0.11	0.45
	MIN	11.5	21.7	8.4	7.5	11.7	11.0	13.5	1.7	2.5	2.6	1.5	5.4
	MAX	12.1	22.8	9.3	8.1	12.4	11.7	14.0	2.1	2.9	3.0	1.9	6.8
H. d. oceanitis	N	11	12	12	12	10	12	12	12	12	12	12	12
	X	11.6	21.6	9.1	7.4	11.1	10.7	13.3	1.9	2.7	2.7	1.6	6.0
	SD	0.40	0.44	0.52	0.33	0.37	0.32	0.27	0.16	0.09	0.12	0.06	0.52
	MIN	11.1	20.8	8.0	6.8	10.5	10.0	12.8	1.6	2.6	2.5	1.5	4.9
	MAX	12.4	22.2	9.7	7.9	11.5	11.2	13.8	2.1	2.9	2.9	1.7	6.9
H. d. masoni	N	5	5	5	5	5	5	5	5	5	5	5	5
	X	12.0	22.4	9.4	7.8	12.4	11.6	13.9	2.2	3.0	3.0	1.8	6.4
	SD	0.35	0.73	0.34	0.16	0.36	0.22	0.21	0.15	0.12	0.13	0.13	0.29
	MIN	11.4	21.7	9.1	7.7	11.9	11.4	13.6	1.9	2.9	2.8	1.6	6.0
	MAX	12.4	23.3	9.8	8.1	12.8	12.0	14.1	2.3	3.2	3.2	1.9	6.8

Table 1b:		WT	RL	D2ML	D3ML	D3PL	D4ML	D5ML	TIL	EL
H. d. diadema	N	26	36	36	36	36	36	36	36	34
	X	47.2	85.9	67.1	63.6	28.6	61.6	56.0	34.4	32.1
	SD	6.88	2.17	2.36	1.88	1.28	1.55	1.38	1.46	1.28
	MIN	29.5	81.7	61.1	59.3	25.5	57.8	53.1	31.4	30.0
	MAX	60.0	90.2	71.6	67.0	31.1	64.8	58.4	36.7	34.6
H. d. nobilis	N	37	55	54	54	54	54	54	55	39
	X	50.9	88.3	70.0	66.3	29.1	63.3	58.2	36.5	29.3
	SD	6.36	3.98	2.88	2.67	1.33	2.53	2.35	2.54	2.01
	MIN	40.0	76.9	63.6	61.2	26.5	58.0	51.6	30.1	25.0
	MAX	67.0	97.0	76.0	73.2	32.5	70.0	62.8	41.8	33.1
H. d. griseus	N	11	18	18	18	18	18	18	17	10
	X	38.0	79.2	62.7	59.5	26.6	57.3	52.4	30.3	27.1
	SD	6.81	3.89	3.11	2.53	1.40	2.26	2.20	2.58	1.15
	MIN	27.0	71.6	57.9	56.0	24.5	54.1	49.1	26.5	25.5
	MAX	51.0	85.6	68.6	65.2	29.9	60.8	56.7	35.1	29.1
H. d. reginae	N	2	13	13	13	13	12	13	12	12
	X	46.0	81.2	65.1	62.2	25.9	59.0	54.0	29.8	27.5
	SD	2.83	2.68	1.8	1.5	0.82	1.29	1.49	1.06	1.25
	MIN	44.0	74.1	61.4	58.1	24.7	55.6	50.6	27.4	25.9
	MAX	48.0	84.5	68.0	64.2	27.2	60.4	56.2	31.5	29.3
H. d. oceanitis	N	13	24	24	24	24	24	24	24	24
	X	36.4	76.5	57.3	54.6	25.2	54.0	50.3	31.5	29.5
	SD	3.48	2.14	1.94	1.76	0.92	1.80	1.81	1.54	1.88
	MIN	30.0	71.7	52.2	50.9	23.5	48.7	46.1	28.6	24.9
	MAX	42.0	80.4	60.4	57.0	26.9	56.9	53.6	35.0	33.2
H. d. masoni	N	2	6	8	8	8	8	8	8	3
	X	44.1	85.0	67.2	63.2	28.7	60.5	56.2	31.4	27.0
	SD	2.97	3.76	2.38	2.48	1.72	2.72	2.53	1.31	1.60
	MIN	42.0	80.2	64.3	58.8	25.9	57.3	53.7	29.7	25.2
	MAX	46.2	90.2	71.0	66.9	30.9	66.0	60.7	33.1	28.2

Penis and Baculum

Penis similar to *H. d. diadema*; baculum same general shape as *H. d. diadema* but with flexing on arms variable: almost straight in specimen from Borneo and more 'flexed' in specimen from Lombok; size similar to *H. d. diadema* with total length 2.06-2.51 and basal width 0.52-0.79.

Skull, dentary, dentition (Table 1, Figure 14b)

Large robust skull, greatest skull length (29.3-33.2) with well developed sagittal and lambdoidal crests; supraorbital ridges extending forward from anterior point of sagittal crest usually moderately well developed, terminating anteriorly at posterolateral margin of rostrum as a moderate to marked protuberance which gives rostrum a squarish aspect from dorsal view; posterior triangle of ridge encloses a slight to moderate frontal depression; groove separating rostral eminences moderate; zygomatic width large (17.5-20.5); mastoid moderate; C^1 very large and robust. I^1 bilobed and frequently with a third outer cusplet, inner cusp larger and taller but more vertical than in *H. d. diadema*; toothrows wide apart (M^3-M^3W 10.8-13.0). Other skull characters are as for *H. d. diadema*.

Hipposideros diadema griseus (Meyen, 1833)

Table 1; Figures 3-7, 9-10 and 14

Rhinolophus griseus Meyen, F.J.F., 1833, Beiträge zur zoologie gesammelt auf einer Reise um die Erde. Abh. Nova Acta Akad. Caes. Leop. Carol. Halle 16, 2: 608, Pl. 46.

Hipposideros diadema anderseni Taylor, E.H., 1934, Philippine Land Mammals, Monogr. Philipp. Bureau of Science Manila, 30, 43 Bunguran Island, North Natuna Islands.

Hipposideros diadema pullatus Andersen, K., 1905. *Hipposideros diadema* and its closest allies, Ann. Mag. nat. Hist. (7) 16, 498 — Haveri, Papua New Guinea.

Type: not allocated.

Type locality: Luzon, Philippine islands.

Specimens examined: See Appendix 1.

Diagnosis

Hipposideros d. griseus differs from *H. d. diadema* in averaging smaller in all external and skull measurements (Table 1); nasal breadth absolutely smaller: ♂♂ 8.5 (8.1-8.9) *v.* 9.5 (9.0-10.0) and ♀♀ 8.4 (7.9-9.0) *v.* 9.5 (9.1-9.9); nasals shorter relative to their length (Figure 9a, b).

It differs from *H. d. nobilis* in having a relatively larger anterior noseleaf; external and skull measurements and weight averaging smaller (in some cases without overlap) (Table 1) e.g., radius length 79.2 (71.6-85.6) *v.* 88.3 (76.9-97.0); tibia length 30.3 (26.5-35.1) *v.* 36.5 (30.1-41.8); ear length 27.1 (25.5-29.1) *v.* 29.3 (25.0-33.1); greatest skull length ♂♂ 29.1 (28.0-29.6) *v.* 31.9 (29.5-33.2) and ♀♀ 28.7 (27.5-30.1) *v.* 30.8 (29.3-32.3); C^1-M^3 ♂♂ 10.7 (10.3-11.0) *v.* 12.3 (11.3-13.1) and ♀♀ 10.8 (10.2-11.4) *v.* 11.9 (11.0-12.5). Cranial length smaller relative to nasal length (Figure 7a, b).

It differs from *H. d. reginae* in being generally slightly smaller in external characters (Table 1) e.g., radius length 79.2 (71.6-85.6) *v.* 81.2 (74.1-84.5) and much smaller in skull and dental characters e.g. greatest skull length ♂♂ 29.1 (28.0-29.6) *v.* 30.4 (30.0-30.7) and ♀♀ (28.7 (27.5-30.1) *v.* 30.0 (29.3-30.7); nasal breadth ♂♂ 8.5 (8.1-8.9) *v.* 9.6 (9.4-10.1) and ♀♀ 8.4 (7.9-9.0) *v.* 9.4 (9.1-9.7); C^1-C^1 width ♂♂ 7.5 (7.0-7.8) *v.* 8.0 (8.0-8.1) and ♀♀ 7.4 (6.8-8.5) *v.* 7.8 (7.5-8.1); C^1-M^1 length ♂♂ 10.7 (10.3-11.0) *v.* 11.6 (11.3-11.8) and ♀♀ 10.8 (10.2-11.4) *v.* 11.4 (11.0-11.7); molar row (M^3-M^3W) narrower relative to greatest skull length and cranial length (Figures 6a, b and 10a, b, respectively); and nasals narrower relative to their length (Figure 9a, b).

It differs from *H. d. masoni* in being generally smaller in wing measurements (Table 1) e.g., radius length 79.2 (71.6-85.6) *v.* 85.0 (80.2-90.2) and metacarpal 5 length 52.4 (49.1-56.7) *v.* 56.2 (53.7-60.7); much smaller, skull, dental and dentary characters (Table 1) particularly: nasal breadth ♂♂ 8.5 (8.1-8.9) *v.* 9.1 (8.8-9.4) and ♀♀ 8.4 (7.9-9.0) *v.* 9.2 (8.5-9.6); orbit to canine length ♂♂ 6.7 (6.4-6.9) *v.* 7.4 (7.0-8.0) and ♀♀ 6.8 (6.3-7.7) *v.* 7.4 (7.2-7.7); dentary length ♂♂ 21.3 (20.8-22.0) v. 22.4 (22.1-22.7) and ♀♀ 21.1 (19.9-21.9) v. 22.4 (21.7-23.3), and C^1-M^3 length ♂♂ 10.7 (10.3-11.0) *v.* 11.5 (11.2-11.7) and ♀♀ 10.8 (10.2-11.4) *v.* 11.6 (11.4-12.0); molar row width (M^3-M^3W) much narrower relative to cranial length (Figure 10a, b) and nasals narrower relative to their length (Figure 9a, b).

It differs from *H. d. oceanitis* in having three rather than two large supplementary nose leaflets; averages larger in all wing measurements but shorter in tibia and ear lengths (Table 1) e.g., radius length 79.2 (71.6-85.6) *v.* 76.5 (71.7-80.4); tibia length 30.3 (26.5-35.1) v. 31.5 (28.6-35.0); and ear length 27.1 (25.5-29.1) v. 29.5 (24.9-33.2); ear length generally shorter relative to radius length (Figure 4); and metacarpal 3 longer relative to tibia length (Figure 5).

Description

Externals (Table 1, Figures 3, 4, 5)

Small, body weight 27.0-51.0; radius length 71.6-85.6 and other wing measurements small; tibia short (26.5-35.1); ear short (25.5-29.1); noseleaf large, greatest width up to 11.5, shape of anterior, intermediate and posterior leaves as for *H. d. diadema.* Other descriptions as for *H. d. diadema.*

Pelage

Pattern of coloration very similar to *H. d. diadema* but with shoulder patch a more distinct triangular shape. The darker dorsal colours range from Clove Brown to Snuff Brown while the ventral colours range from cream to pinkish buff.

Penis and Baculum

Both penis and baculum similar in size and shape to *H. d. diadema*; baculum with total length *c.* 2.0 and basal width c. 0.6.

Skull, dentary, dentition (Table 1, Figure 14c)

Moderate length skull (27.5-30.1; cranial length short relative to nasal length; rostrum profile from dorsal aspect varies from rounded (AM 19554) to squarish (FM 80371) with a range of intermediate shapes; rostral eminences more inflated in Papua New Guinea specimens than in *H. d. diadema* but Philippine specimens as for *H. d. diadema*; nasals narrow (7.9-9.0); M^{1-2} with small hypocone; distance between toothrows narrow (M^3-M^3W 10.8-11.9).

Other skull characters are as for *H. d. diadema.*

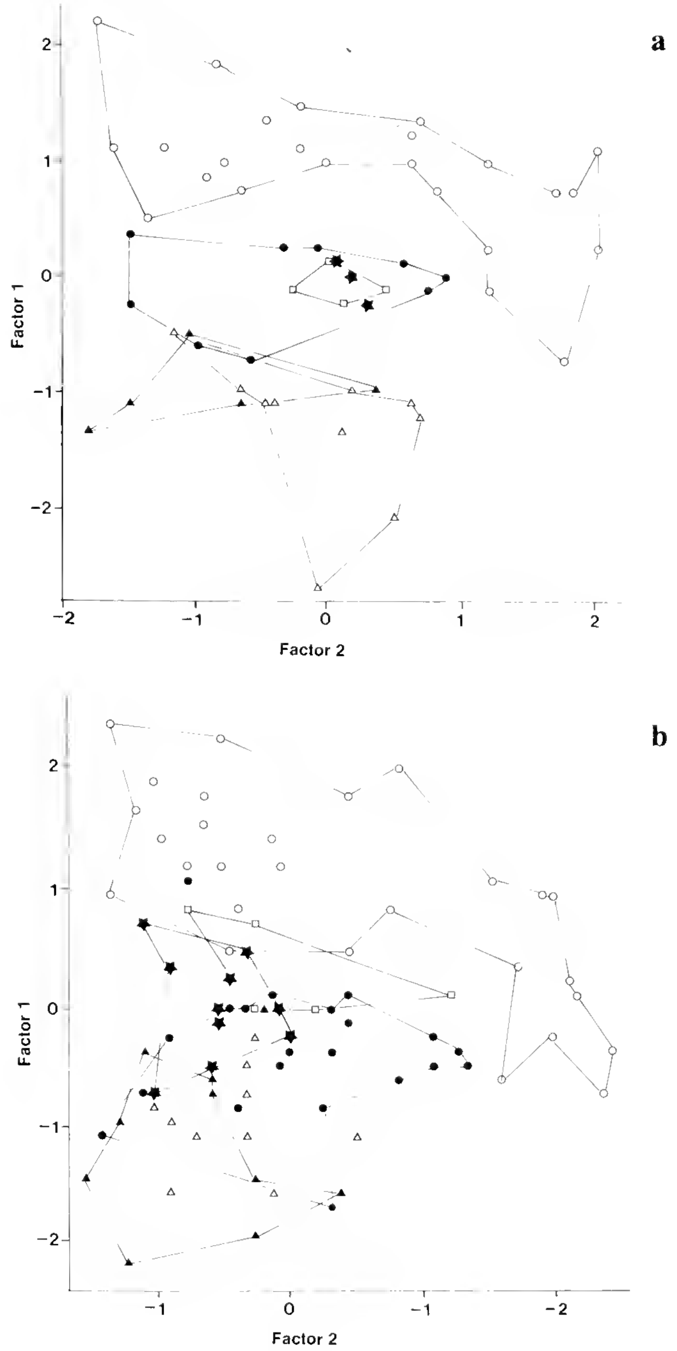


Figure 16 Principal component analysis based on skull measurements of the subspecies of *H. diadema* examined, showing the first two Factors. Subspecies codes as for Figure 2. **(a)** males; **(b)** females.

Hipposideros diadema reginae Troughton, 1937

Table 1; Figures 3-10, 12 and 14

Hipposideros diadema reginae Troughton, E. Le G., 1937. Six new bats (Microchiroptera) from the Australian region, Aust. Zool., 8: 275.

Holotype: Australian Museum AM 1243, male. Wet skin and skull.

Type locality: Bloomfield River, Cooktown area, Queensland.

Specimens examined: See Appendix 1.

Diagnosis

Hipposideros d. reginae differs from *H. d. diadema* by averaging smaller in all external measurements (Table 1) e.g., radius length 81.2 (74.1-84.5) *v*. 85.9 (81.7-90.2); and tibia length 29.8 (27.4-31.5) *v*. 34.4 (31.4-36.7); ear shorter relative to radius length (Figure 4); tibia shorter relative to metacarpal 3 length (Figure 5); distance between molar rows generally wider relative to greatest skull length (Figure 6a, b).

It differs from *H. d. nobilis* in having a relatively larger anterior noseleaf; averages smaller in all external measurements (Table 1) e.g., radius length 81.2 (74.1-84.5) v. 88.3 (76.9-97.0); and tibia length 29.8 (27.4-31.5) v. 36.5 (30.1-41.8); tibia shorter relative to ear length (Figure 3); radius shorter relative to ear length (Figure 4); tibia shorter relative to metacarpal 3 length (Figure 5); most skull characters average smaller e.g., greatest skull length ♂♂ 30.4 (30.0-30.7) *v*. 31.9 (29.5-33.2) and ♀♀ 30.0 (29.3-30.7) *v*. 30.8 (29.3-32.3); C^1-M^3 length ♂♂ 11.6 (11.3-11.8) *v*. 12.3 (11.3-13.1) and ♀♀ 11.4 (11.0-11.7) *v*. 11.9 (11.0-12.5); nasal longer relative to their breadth (Figure 9a, b).

It differs from *H. d. griseus* in being generally slightly larger in external characters (Table 1) e.g. 81.2 (74.1-84.5) *v*. 79.2 (71.6-85.6) and larger in skull and dental characters e.g., greatest skull length ♂♂ 30.4 (30.0-30.7) *v*. 29.1 (28.0-29.6) and ♀♀ 30.0 (29.3-30.7) *v*. 28.7 (27.5-30.1); nasal breadth ♂♂ 9.6 (9.4-10.1) *v*. 8.5 (8.1-8.9) and 9.4 ♀♀ (9.1-9.7) *v*. 8.4 (7.9-9.0); C^1-C^1 ♂♂ 8.0 (8.0-8.1) v. 7.5 (7.0-7.8) and ♀♀ 7.8 (7.5-8.1) *v*. 7.4 (6.8-8.5); C^1-M^3 length ♂♂ 11.6 (11.3-11.8) *v*. 10.7 (10.3-11.0) and ♀♀ 11.4 (11.0-11.7) *v*. 10.8 (10.2-11.4); distance between molar row wider relative to cranial length and greatest skull length (Figures 10a, b and 6a, b, respectively; and nasals wider relative to their length (Figure 9a, b).

It differs from *H. d. masoni* in having externals that average smaller (except ear length) (Table 1) e.g. radius length 81.2 (74.1-84.5) *v*. 85.0 (80.2-90.2); in ♂♂ distance between molar rows wider relative to cranial length and greatest skull length (Figures 10a and 6 a, respectively); ♀♀ zygomatic width smaller relative to nasal length and greatest skull length (Figure 8b and 12b, respectively).

It differs from *H. d. oceanitis* in having three rather than two large supplementary nose leaflets; wing measurements average larger (Table 1), e.g. metacarpal 3 length 62.2 (58.1-64.2) *v*. 54.6 (50.9-57.0) and radius length 81.2 (74.1-84.5) *v*. 76.5 (71.7-80.4); tibia generally shorter relative to ear length (Figure 3); radius longer relative to

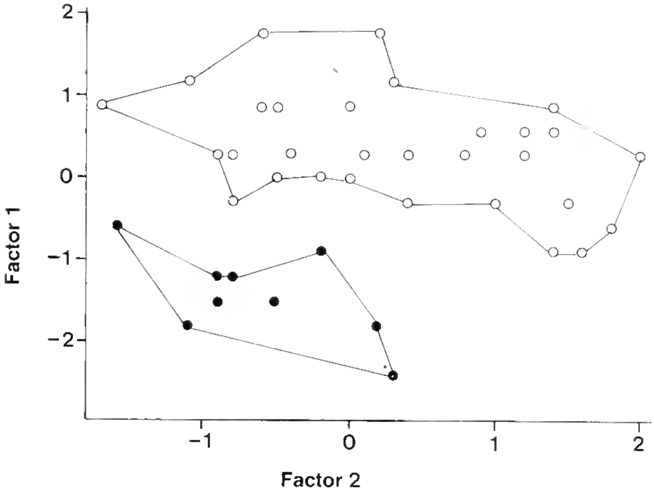


Figure 17 Principal component analysis based on skull measurements of *Hipposideros diadema diadema* from Sumbawa I. and *H. d. nobilis* from Lombok I. showing the first two Factor scores. Subspecies codes as for Figures 2.

ear length (Figure 4); metacarpal 3 longer relative to tibia length (Figure 5); averages larger in almost all skull measurements e.g., greatest skull length ♂♂ 30.4 (30.0-30.7) *v.* 28.9 (26.4-29.9) and ♀♀ 30.0 (29.3-30.7) *v.* 29.1 (28.5-30.1); C^1-M^3 length ♂♂ 12.3 (12.0-12.5) *v.* 11.1 (10.6-11.8) and ♀♀ 11.4 (11.0-11.7) *v.* 10.7 (10.0-11.2); distance between molar rows wider relative to greatest skull length (Figure 6a, b); nasal length greater relative to cranial length (Figure 7a, b) and nasal breadth greater relative to nasal length (Figure 9a, b).

Description

Externals (Table 1, Figures 3, 4, 5)

Moderately heavy (44.0-48.0); radius short (74.1-84.5) and other wing measurements also short; tibia short (27.4-31.5); ear short (25.9-29.3); noseleaf well developed; three large supplementary leaflets but no trace of the fourth leaflet present in *H. d. diadema*; anterior leaf large, greatest width up to 12. Other descriptions as for *H. d. diadema*.

Pelage

Pattern of colouration very similar to *H. d. diadema* but with head, throat and shoulder mantle paler and without darker marking; these paler areas range from Pale Pinkish Cinnamon to Light Pinkish Cinnamon. The lower back is predominantly Saccardo's Umber (brown) marbled with Sepia (dark brown) and Light Pinkish Cinnamon. In contradistinction to the type description of this form by Troughton

(1937), dorsal pale lateral stripes may be prominent, varying from White to Pale Pinkish Buff; occasional patches of these paler colours may also occur on the lower back (e.g. AM 8106). The pelage of the throat is less clearly marked from that of the chest and abdomen which is a slightly darker Isabella Color (light 'pinkish' brown).

Penis and Baculum

Penis with same general shape as *H.d. diadema* but with distal end of glans more pointed and without clearly defined small distal protuberances on lip of urethral groove. Baculum similar shape to *H. d. diadema* but with basin of base slightly deeper so that base in lateral view appears slightly wider, base *c.* 0.6 wide and greatest length *c.* 2.1.

Skull, dentary, dentition (Table 1, Figure 14d)

Moderate length skull (29.3-30.7); posterior triangle of supraorbital ridges enclose moderate to deep frontal depression; nasal profile squarish in dorsal view, long (7.4-8.5) and wide (9.1-10.1); rostal eminences inflated, separated by moderate medial groove; anterior palatal foramina oval, large, with anterior edge of maxilla closing foramina posterior edge, mesopterygoid fossa wide (3.4-3.8). Other characters as for *H. d. diadema.*

Hipposideros diadema masoni (Dobson, 1872)

Table 1; Figures 3-6, 10-11 and 14

Phyllorhina masoni Dobson, G.E. 1872,. Brief descriptions of five new species of Rhinolophine bats, J. Asiat. Soc. Beng. 2: 499.

Holotype: Calcutta Museum. Number 297, body in alcohol, skull separate.

Type locality: Moulmein, Burma.

Specimens examined: See Appendix I.

Diagnosis

Hipposideros d. masoni differs from *H. d. diadema* in that its tibia averages shorter 31.4 (29.7-33.1) *v.* 34.4 (31.4-36.7); ear averages shorter 27.0 (25.2-28.2) *v.* 32.1 (30.0-34.6); tibia shorter relative to metacarpal 3 length (Figure 5); ear shorter relative to radius length (Figure 4); molar rows (M^3M^3W) narrower relative to cranial length (Figure 10a, b).

It differs from *H. d. nobilis* in having a relatively larger anterior noseleaf; averages smaller in all external measurements (Table 1) e.g., radius length 85.0 (80.2-90.2) *v.* 88.3 (76.9-97.0): tibia shorter relative to both ear length (Figure 3) and metacarpal 3 length (Figure 5). Most skull and dental measurements (except minimum interorbital distance and nasal length) average smaller (Table 1) e.g., C^1-M^3 ♂♂ 11.5 (11.2-11.7) *v.* 12.3 (11.3-13.1) and ♀♀ 11.6 (11.4-12.0) *v.* 11.9 (11.0-12.5); molar rows closer (M^3-M^3W) relative to greatest skull length (Figure 6a, b); cranial length shorter relative to M^3 length (Figure 11a, b).

Table 2: ANOVA of *H. diadema* by sex and island for (a) skull and (b) external characters. Significance of F values are as follows $P<.05$*, $P<.01$** and $P<.001$***

Character		Factor	
(a) SKULL	Sex	Island	Interaction
GSL	7.582**	20.411***	1.722
CCL	4.600	26.699***	2.178*
CI	2.840	25.791***	2.947*
NL	1.141	7.192***	1.442
NB	0.000	20.605***	1.076
CH	0.069	7.656***	1.554
IBW	1.095	5.537***	0.747
PBL	1.006	6.524***	0.628
MFB	0.023	7.124***	0.425
OCL	6.301*	13.277***	1.158
IOB	5.964*	8.456***	1.012
ZW	1.104	19.085***	1.733
BCW	6.329*	8.139***	1.401
DL	11.015***	29.460***	2.218*
RAL	6.090*	5.878***	1.087
C^1-C^1W	2.139	13.287***	1.106
M^3-M^3W	1.531	31.523***	1.778
C^1-M^3L	10.470**	27.166***	1.087
C_1-M_3L	14.872***	39.354***	1.881*
PM^4L	0.403	11.432***	0.369
M^1L	0.301	12.148***	1.095
ML	1.038	11.282***	0.972
M^3L	0.036	7.413***	0.567
(B) EXTERNALS			
RL	0.175	29.510***	1.254
D2ML	0.196	39.097***	0.924
D3ML	0.198	42.248***	0.810
D3PL	0.173	20.000***	0.795
D4ML	0.019	32.374***	0.571
D5ML	0.234	26.697***	0.684
TIL	0.927	25.011***	1.023

It differs from *H. d. griseus* in being generally larger in wing measurements (Table 1) e.g., radius length 85.0 (80.2-90.2) *v.* 79.2 (71.6-85.6) and metacarpal 5 length 56.2 (53.7-60.7) — 52.4 (49.1-56.7); much larger skull, dental and dentary characters (Table 1) particularly nasal breadth ♂♂ 9.1 (8.8-9.4) *v.* 8.5 (8.1-8.9) and ♀♀ 9.2 (8.5-9.6) *v.* 8.4 (7.9-9.0); orbit to canine length ♂♂ 7.4 (7.0-8.0) *v.* 6.7 (6.4-6.9) and ♀♀ 7.4 (7.2-7.7) *v.* 6.8 (6.3-7.7); dentary length ♂♂ 22.4 (22.1-22.7) *v.* 21.3 (20.8-22.0) and ♀♀ 22.4 (21.7-23.3) *v.* 21.1 (19.9-21.9); and C^1-M^3 length ♂♂ 11.5 (11.2-11.7) *v.* 10.7 (10.3-11.0) and ♀♀ 11.6 (11.4-12.0) *v.* 10.8 (10.2-10.4); molar row width (M^3-M^3W) wider relative to cranial length (Figure 10a, b); and nasals wider relative to their length (Figure 9a, b).

It differs from *H. d. reginae* in having externals that average larger (except ear length, see Table 1), e.g., radius length 85.0 (80.2-90.2) *v.* 81.2 (74.1-84.5); in ♂♂ molar rows (M^3-M^3W) narrower relative to cranial length (Figure 10a); in ♂♂ molar rows (M^3-M^3W) narrower relative to greatest skull length (Figure 6a); in ♀♀ zygomatic width larger relative to nasal length and greatest skull length (Figures 8b and 12b respectively).

It differs from *H. d. oceanitis* in having three rather than two large nasal leaflets; in being larger in all wing measurements (Table 1) e.g., radius length 85.0 (80.2-90.2) *v.* 76.5 (71.7-80.4); radius longer relative to ear length (Figure 4); metacarpal 3 length longer relative to tibia length (Figure 5); generally larger in skull, dental and dentary characters, particularly nasal length ♂♂ 7.8 (6.8-8.3) *v.* 7.2 (6.5-8.2) and ♀♀ 7.7 (6.9-8.2) *v.* 7.0 (6.1-7.6); zygomatic width ♂♂ 17.6 (17.1-18.2) *v.* 17.1 (16.0-17.6) and ♀♀ 18.6 (18.3-19.0) *v.* 17.1 (16.3-17.8); dentary length ♂♂ 22.4 (22.1-22.7) *v.* 21.3 (19.6-22.1) and ♀♀ 22.4 (21.7-23.3) *v.* 21.6 (20.8-22.2); C^1-M^3 length ♂♂ 11.5 (11.2-11.7) *v.* 10.7 (9.6-11.3) and ♀♀ 11.6 (11.4-12.0) *v.* 10.7 (10.0-11.2); molar rows (M^3-M^3W) wider relative to greatest skull length and cranial length (Figures 6a, b and 10a, b, respectively); in ♀♀ zygomatic width larger relative to nasal length (Figure 8b).

Description

Externals (Table 1, Figures 3, 4, 5)

Medium size; weight 42.0-46.2, radius length 80.2-90.2; tibia short 29.7-33.1; ear short; noseleaf well developed with three only supplementary leaflets in the specimens examined; anterior leaf large, maximum diameter up to 11.5. Other descriptions as for *H. d. diadema.*

Pelage

Pattern of colouration very similar to *H. d. diadema.* Overall dorsal colour Clove Brown to Bister and ventral surface Buffy Brown to Tawny Olive. Shamel (1942) describes two colour phases (i) a pale yellow or buff with reddish brown tips to hairs and (ii) pale buff with dark brown tips to hairs of back with much paler brown with lighter tips to abdomenal hairs.

Penis and Baculum

Penis and baculum as for *H. d. diadema.* Baculum base *c.* 0.7, greatest length *c.* 2.1.

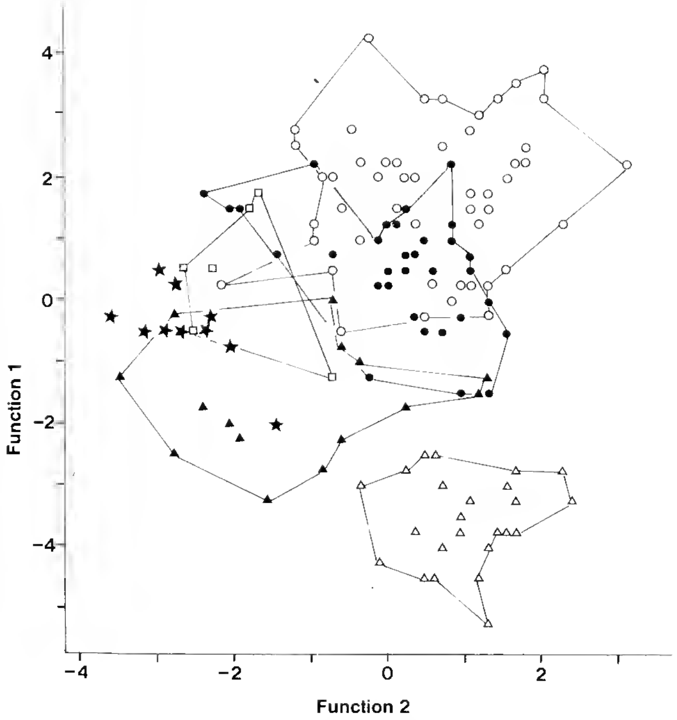


Figure 18 Canonical variate analysis based on external measurements of *Hipposideros diadema* subspecies. Plot of functions 1 and 2 for males and females combined. Subspecies codes as for Figure 2.

Skull, dentary, dentition (Table 1, Figure 14e)

Moderate length skull (28.5-30.5) with well developed sagittal and lambdoidal crests; supraorbital ridges moderately well developed, terminating as slight protuberance at posterolateral margin of rostrum; rostrum profile squarish from dorsal aspect; rostral eminences moderately to well inflated; mesopterygoid width variable; sphenoid bridge partially obscures large sphenorbital foramen; toothrow width variable with females wider than males e.g., M^3-M^3 width ♀♀ 11.9-12.8 and ♂♂ 11.6-11.9; I_1-$_2$ occasionally imbricate (FMNH 98689). Other skull characters as in *H. d. diadema*.

Hipposideros diadema oceanitis Andersen, 1905

Table 1; Figures 3-11 and 14

Hipposideros diadema oceanitis Andersen, K. 1905, On *Hipposideros diadema* and its closest allies, Ann. Mag. nat. Hist. (7)16: 497.

Hipposideros diadema malaitensis Phillips, C.J., 1967, A new subspecies of Horseshoe bat (*Hipposideros diadema*) from the Solomon Islands, Proc. Biol. Soc. Washington 80: 35, — Malaita I.

Holotype: British Museum, Natural History BM 88.1.5.23, adult male, in alcohol.

Table 3 Principal component scores for the first three factors for *Hipposideros diadema* (a) external characters (males and females combined), (b) skull characters (males and females separate).

(a) External characters	Factor 1	Factor 2	Factor 3
RL	0.7149	0.5085	0.3790
D2ML	0.8470	0.3127	0.3920
D3ML	0.8767	0.3056	0.3355
D3PL	0.4658	0.3208	0.8244
D4ML	0.8230	0.3771	0.3808
D5ML	0.7912	0.4642	0.3336
TIL	0.3623	0.8886	0.2655
% variation explained	86.8	5.9	4.0

(b) Factor scores for males, followed by females in brackets

Skull characters	Factor 1	Factor 2	Factor 3
GSL	0.9426 (0.9014)	0.2285 (0.2220)	0.0258 (0.1320)
CCL	0.9426 (0.8790)	0.2153 (0.2589)	0.0549 (0.1872)
CL	0.8774 (0.8171)	0.3200 (0.2772)	−0.2175 (−0.2156)
NL	−0.0403 (−0.0439)	−0.1097 (−0.0717)	0.8062 (0.8167)
NB	0.7126 (0.4266)	0.3746 (0.3596)	0.3333 (0.6229)
CH	0.6133 (0.3400)	0.4925 (0.6600)	0.1051 (0.1616)
IBW	0.2976 (0.4692)	0.5791 (0.3406)	−0.3423 (−0.2031)
PBL	0.5059 (0.6212)	0.1183 (0.0399)	−0.3722 (−0.0949)
MFB	0.2762 (0.1865)	0.7783 (0.6693)	0.2387 (0.4105)
OCL	0.8307 (0.8043)	0.2600 (0.1512)	0.0438 (0.0664)
IOB	−0.1523 (−0.1715)	0.2142 (0.1595)	0.7646 (0.7339)
ZW	0.7986 (0.8054)	0.4438 (0.3941)	−0.1800 (−0.0186)
BCW	0.4728 (0.2325)	0.7699 (0.8448)	−0.0611 (0.1002)
DL	0.9327 (0.8746)	0.2217 (0.2612)	−0.0965 (0.0513)
RAL	0.7054 (0.6526)	0.1868 (0.0922)	−0.1778 (0.0207)
C^1-C^1W	0.8191 (0.6157)	0.2842 (0.4397)	−0.0054 (−0.0032)
M^3-M^3W	0.8686 (0.7713)	0.2605 (0.3900)	−0.0734 (0.0328)
C^1-M^3L	0.8926 (0.8387)	0.2872 (0.3669)	−0.0449 (0.0494)
C_1-M_3L	0.9509 (0.8865)	0.1343 (0.2687)	0.1667 (0.0092)
PM^4L	0.6394 (0.4061)	0.3708 (0.7083)	−0.2487 (−0.0436)
M^1L	0.7018 (0.5932)	0.2215 (0.4393)	−0.3396 (−0.0798)
M^2L	0.7332 (0.5337)	0.1698 (0.4757)	−0.1805 (0.1654)
M^3L	0.5849 (0.6065)	−0.4127 (−0.5559)	0.4515 (0.1622)
% variation explained	58.5 (49.8)	9.3 (10.5)	6.7 (7.2)

Type locality: Guadalcanar (= Guadalcanal), Solomon Islands.

Specimens examined: See Appendix 1.

Diagnosis

Hipposideros d. oceanitis differs from *H. d. diadema* in having two rather than three large supplementary nose leaflets; averages smaller in almost all external and skull measurements and weight (Table 1) e.g., radius length 76.5 (71.7-80.4) *v.* 85.9 (81.7-90.2), metacarpal 4 length 54.0 (48.7-56.9) *v.* 61.6 (57.8-64.8); greatest skull length ♂♂ 28.9 (26.4-29.9) *v.* 30.5 (29.1-31.5) and ♀♀ 29.1 (28.5-30.1) *v.* 30.0 (28.7-31.5); C^1-M^3 length ♂♂ 10.7 (9.6-11.3) *v.* 11.5 (10.9-12.2) and ♀♀ 10.7 (10.0-11.2) *v.* 11.2 (10.4-11.6); radius shorter relative to ear length (Figure 4); metacarpal 3 length shorter relative to tibia length (Figure 5); nasals narrower relative to their length (Figure 9a, b).

It differs from *H. d. nobilis* in having two rather than three large supplementary nose leaflets; proportionally larger anterior noseleaf; averages much lighter 36.4 (30.2-42.0) *v.* 50.9 (40.0-67.0); smaller in all external measurements (often with no overlap) (Table 1) e.g., radius length 76.5 (71.7-80.4) *v.* 88.3 (76.9-97.0), tibia length 31.5 (28.6-35.0) *v.* 36.5 (30.1-41.8); tibia shorter relative to ear length (Figure 3); radius shorter relative to ear length (Figure 4); metacarpal 3 length shorter relative to tibia length (Figure 5); smaller in all skull measurements (Table 1), e.g., greatest skull length ♂♂ 28.9 (26.4-29.9) *v.* 31.9 (29.5-33.2) and ♀♀ 29.1 (28.5-30.1) *v.* 30.8 (29.3-32.3); C^1-M^3 length ♂♂ 10.7 (9.6-11.3) *v.* 12.3 (11.3-13.1) and ♀♀ 10.7 (10.0-11.2) *v.* 11.9 (11.0-12.5); molar rows (M^3-M^3W) narrower relative to greatest skull length (Figure 6a, b); nasals narrower relative to their length (Figure 9a, b); cranial length smaller relative to M^3 length (Figure 11a, b); zygomatic width small relative to nasal length (Figure 8a, b).

It differs from *H. d. griseus* in having two rather than three large supplementary nose leaflets; averages smaller in all wing measurements but longer in tibia and ear length (Table 1) e.g., radius length 76.5 (71.7-80.4) *v.* 79.2 (71.6-85.6), tibia length 31.5 (28.6-35.0) *v.* 30.3 (26.5-35.1) and ear length 29.5 (24.9-33.2) *v.* 27.1 (25.5-29.1); ear length generally longer relative to radius length (Figure 4) and metacarpal 3 length shorter relative to tibia length (Figure 5).

It differs from *H. d. reginae* in having two rather than three large supplementary nose leaflets; wing measurements average smaller (Table 1) e.g., metacarpal 3 length 54.6 (50.9-57.0) *v.* 62.2 (58.1-64.2) and radius length 76.5 (71.7-80.4) *v.* 81.2 (74.1-84.5); tibia generally longer relative to ear length (Figure 3); radius shorter relative to ear length (Figure 4); metacarpal 3 shorter relative to tibia length (Figure 5); molar rows (M^3-M^3W) narrower relative to greatest skull length (Figure 6a, b); nasal length shorter relative to cranial length (Figure 7a, b) and nasals narrower relative to their length (Figure 9a, b).

It differs from *H. d. masoni* in having two rather than three large supplementary nose leaflets; smaller in all wing measurements (Table 1), e.g., radius length 76.5

Table 4 Standardised and unstandardised (in brackets) canonical variates from the six subspecies of *Hipposideros diadema* considered (a) for external characters (males and females combined, WT and EL excluded) and (b) for skull characters (males and females separate).

(a)

External characters	Function 1	Function 2	Function 3
RL	0.2242 (0.0743)	—0.1900 (—0.0629)	0.5366 (0.1777)
D2ML	0.3174 (0.1228)	—0.6905 (—0.2671)	—0.3461 (—0.1339)
D3ML	0.6869 (0.3005)	—0.0942 (—0.0412)	—0.9451 (—0.4135)
D3PL	0.1452 (0.1165)	0.2772 (0.2225)	0.6969 (0.5593)
D4ML	—0.0760 (—0.0358)	0.1577 (0.0744)	1.5580 (0.7349)
D5ML	—0.2312 (—0.1149)	—0.1540 (—0.0765)	—0.9185 (—0.4564)
TIL	0.0371 (0.0187)	1.2214 (0.6146)	—0.4253 (—0.2140)
Constant	(—28.5045)	(—1.7211)	(—7.6778)
% Variation explained	70.4	22.6	4.4

(b) Skull — (males)

Characters	Function 1	Function 2	Function 3
GSL	—1.9247 (—2.2962)	—1.7695 (—2.1111)	1.1040 (1.3170)
CCL	0.9763 (1.4313)	1.4317 (2.0989)	—2.3769 (—3.4847)
CL	1.1511 (1.7132)	—0.7962 (—1.1850)	0.6982 (—1.6571)
NL	0.1305 (0.3022)	—0.2603 (—0.6029)	—0.2341 (1.6174)
NB	—0.2979 (—0.8450)	1.3318 (3.7771)	—0.3220 (—0.6640)
CH	—0.0041 (—0.0126)	—0.3314 (—1.0124)	0.0596 (—0.9838)
IBW	0.3999 (1.5854)	—0.0252 (—0.0998)	0.1748 (0.2363)
PBL	—0.3295 (—0.7022)	0.3357 (0.7154)	0.3834 (0.3726)
OCL	0.6439 (1.3945)	0.1297 (0.2808)	0.5340 (0.8303)
ZW	—0.6460 (—0.9326)	0.0533 (0.0769)	1.4823 (0.7710)
DL	0.5649 (0.8916)	0.1617 (0.2552)	0.7032 (2.3396)
M^1-M^3W	0.8535 (2.7876)	—0.1150 (0.3756)	0.6095 (2.2970)
C^1-M^3L	—0.4427 (—1.0885)	0.5647 (1.3887)	—0.4815 (1.4987)
C_1-M_3L	0.6480 (1.6709)	—0.6502 (—1.6766)	0.1250 (—1.2415)
PM^4L	0.2542 (1.3063)	0.1563 (0.8031)	—0.2417 (0.6423)
M^2L	—0.7735 (—3.9982)	—0.1518 (—0.7846)	0.1755 (—1.2492)
M^3L	0.1554 (1.3205)	0.8406 (7.1411)	—2.3769 (1.4910)
Constant	—50.8880	—1.5300	—12.2906
% variation explained	70.9	16.0	7.6

Table 4 cont.

(**b**) Skull (females)

Character	Function 1	Function 2	Function 3
CCL	−0.5966 (−0.9904)	0.4946 (0.8210)	0.1534 (0.2546)
CL	0.0220 (0.0390)	−0.3757 (−0.6667)	0.5771 (1.0241)
NL	−0.1653 (−0.3471)	−0.0063 (−0.0132)	−0.4230 (−0.8881)
NB	−0.3782 (−1.3289)	0.9007 (3.1648)	0.2135 (0.7501)
PBL	0.3864 (1.1029)	−0.0656 (−0.1873)	−0.2026 (−0.5782)
MFB	−0.1423 (−0.5764)	−0.0278 (−0.1125)	0.3464 (1.4032)
IOB	−0.0168 (0.0840)	0.1928 (0.9654)	−0.2098 (−1.0507)
ZW	0.5746 (1.2218)	−0.4504 (−0.9576)	−0.3578 (−0.7608)
DL	0.8122 (1.5054)	−0.2406 (−0.4460)	−0.8968 (−1.6621)
RAL	−0.2762 (−0.6874)	0.0267 (0.0664)	0.4455 (1.1089)
C^1-C^1W	−0.1282 (−0.3941)	0.0611 (0.1880)	0.4555 (1.4006)
M^3-M^3W	0.4333 (1.4427)	0.4910 (1.6347)	−0.8882 (−2.9573)
C_1-M_3L	−0.0167 (0.0505)	−0.0537 (−0.1630)	0.6123 (1.8576)
PM^4L	0.1349 (0.7104)	0.1427 (0.7513)	0.4276 (2.2513)
M^1L	0.2999 (2.3243)	−0.1379 (−1.0684)	0.3483 (2.6989)
M^3L	0.0207 (0.1593)	0.3695 (2.8410)	0.0484 (0.3721)
Constant	−33.6239	−34.9333	−0.5045
% Variation explained	44.6	28.6	17.9

(71.7-80.4) *v.* 85.0 (80.2-90.2), radius shorter relative to ear length (Figure 4); metacarpal 3 length shorter relative to tibia length (Figure 5); generally smaller in skull, dental and dentary characteristics, particularly nasal length ♂♂ 7.2 (6.5-8.2) *v.* 7.8 (6.8-8.3) and ♀♀ 7.0 (6.1-7.6) *v.* 7.7 (6.9-8.2); zygomatic width ♂♂ 17.1 (16.0-17.6) *v.* 17.6 (17.1-18.2) and ♀♀ 17.1 (16.3-17.8) *v.* 18.6 (18.3-19.0); dentary length ♂♂ 21.3 (19.6-22.1) *v.* 22.4 (22.1-22.7) and ♀♀ 21.6 (20.8-22.2) *v.* 22.4 (21.7-23.3); C^1-M^3 length ♂♂ 10.7 (9.6-11.3) *v.* 11.5 (11.2-11.7) and ♀♀ 10.7 (10.0-11.2) *v.* 11.6 (11.4-12.0); molar rows (M^3-M^3W) narrower relative to greatest skull length and cranial length (Figures 6a, b and 10a, b, respectively); in ♀♀ only zygomatic width smaller relative to nasal length (Figure 8b).

Description

Externals (Table 1, Figures 3, 4, 5)

Smallest of the subspecies examined: weight 30.0-42.0, radius length 71.7-80.4, tibia moderately long 28.6-35.0; ear moderately long 24.9-33.2; noseleaf well developed with two large and one small supplementary leaflets; anterior leaflet of the same shape as *H. d. diadema*, greatest width up to 10. Other descriptions as for *H. d. diadema*.

Pelage

Basic pattern of colouration similar to *H. d. diadema* but with much less contrast between the paler and darker parts. In some specimens the paler dorsal lateral stripes are very indistinct as is the posterior margin of the pale shoulder mantle which merges indistinctly with the marbling of the lower back region. The predominant darker colours of dorsal and ventral pelage is Natal Brown (dark orange brown) and Buffy Brown (pale brown), respectively. The paler head, throat and mantle pelage a pinkish brown, and ranges from Avellaneous to Wood Brown. Occasional indistinct paler spots on dorsum, particularly at base of femur and humerus.

Penis and Baculum

Penis and baculum as for *H. d. diadema.* Baculum base *c.* 0.75, greatest length 2.0-2.3.

Skull, dentary, dentition (Table 1, Figure 14f)

Small skull with greatest length (26.4-30.1), well developed sagittal and lambdoidal crests; supraorbital ridges poorly developed, terminating anteriorly in a very low protuberance, posterior triangle encloses moderate frontal depression; rostral profile from dorsal aspect oval, small; rostral eminences well inflated; mastoid triangular shaped in dorsal profile; M^3 posterior cusp obsolescent, prematacristid most reduced of *H. diadema* subspecies considered, represented by a small nub only.

Statistical Analysis: Results and Discussion

(a) Sexual dimorphism

Only the following islands were used in this analysis. They had both males and females well represented.

Island	No. of individuals Skulls		Externals	
	♂♂	♀♀	♂♂	♀♀
Sumbawa Moyo	4	6	4	6
Flores	2	6	2	8
Roti	1	1	2	1
Borneo	2	2	2	2
Java	5	6	5	6
Lombok	16	17	18	17
Nusa Penida	1	1	1	1
Papua New Guinea	4	5	4	4
Philippines	2	5	2	7
Queensland (Aust)	3	10	3	8
Ysabel	2	2	3	—
New Britain	5	7	5	8
Thailand	3	2	1	1

A two factor ANOVA was run for subspecies, sex and island for skull and external characters. From Table 2 there was significant sexual dimorphism in 8 of the 23 skull characters. These were GSL, OCL, IOB, BCW, DL, RAL, C^1-M^{3}L, C^1-M^{3}L. The most pronounced dimorphism was in greatest skull length, dentary length, and C1-M3 length. There was no significant dimorphism in external measurements (Table 2). There were very significant ($p<<.001$) differences for all measurements between islands for the combined sexes and a weakly significant interaction between sex and island for four skull characters (CCL, CL, DL and C^1-M^3L). The MANOVA also indicated that there was a significant difference between both the sexes (Hotellings Test = 0.577, P = 0.03) and the islands (Hotellings Test = 19.846, $P<<.001$), but did not show a significant interaction between these effects (Hotellings Test = 3.940, P = 0.486).

As a consequence, subsequent analysis of *H. diadema* subspecies will combine males and females when external characters are being considered, but will treat males and females separately for skull characters.

(b) Principal component analysis (all specimens)

External characters — seven external characters were used (weight and ear length excluded). The analysis (males and females combined) extracted three factors (Table 3a) which together explained 96.6 percent of the variation (Factor 1 — 86.8, Factor 2 — 5.9 percent and Factor 3 — 4.0 percent). The plot of Factors 1 and 2 (Figure 15a) shows that *H. d. oceanitis* clusters distinctly from the other subspecies, with the separation on Factor 1. This Factor is strongly influenced by the majority of external measurements, except phalanx 1 digit 3 and tibia length and probably reflects its smaller overall body size. Separation between the other species is largely on Factor 2; on this Factor *H. d. nobilis* clusters distinctly from *H. d. griseus, H. d. reginae* and *H. d. masoni* — but these latter three subspecies merge on this Factor. However, *H. d. reginae* and *H. d. masoni* separate on Factor 3 (Figure 15b) which is most strongly influenced by phalanx 1 digit 3 (averages longer in *H. d. masoni*, 28.7 *v.* 25.9). *H. d. nobilis* and *H. d. diadema* cluster together on all Factors; the latter subspecies also are not separable from *H. d. griseus, H. d. reginae* or *H. d. masoni.*

Skull characters. Twenty-three skull characters were used in this analysis (males and females separately).

Males — the PCA extracted three Factors (Table 3b) which combined explained 74.4 percent of the variation (Factor 1 — 58.5 percent, Factor 2 — 9.3 percent and Factor 3 — 6.7 percent). The plot of Factors 1 and 2 (Figure 16a) indicates that several of the subspecies cluster distinctly. Only *H. d. diadema, H. d. reginae* and *H. d. masoni* cluster together; these are not separated by other combinations of Factors 1, 2 or 3. The separation between these subspecies is mainly on Factor 1. Most characters load heavily and positively on this Factor, except nasal length, minimum interorbital distance and distance between cochlea (Table 3b). This suggests that overall size of skull, teeth and dentary are important in separating these groups.

Females — The 3 Factors extracted by the PCA combined explained 67.5 percent of the variation (Factor 1 — 49.8 percent; Factor 2 — 10.5 percent; Factor 3 — 7.2

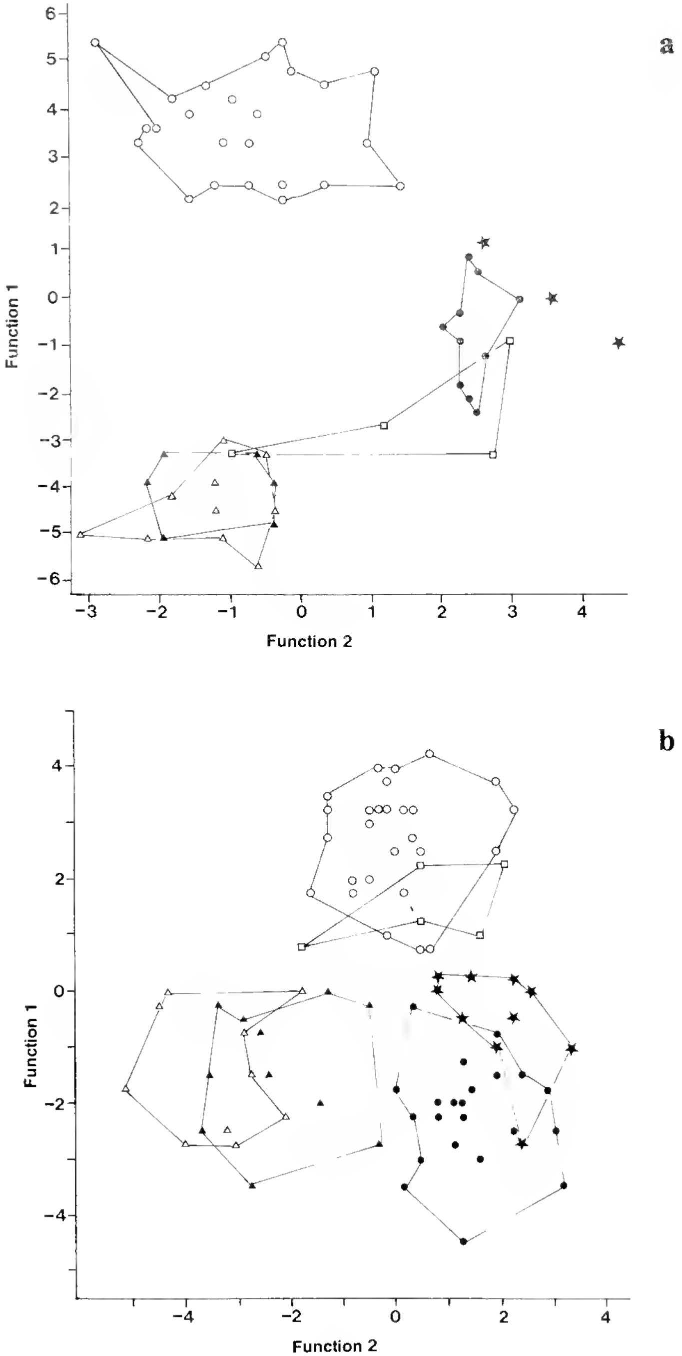


Figure 19 Canonical variate analysis based on skull measurements of *Hipposideros diadema* subspecies. Plot of functions 1 and 2 for (**a**) males and (**b**) females. Subspecies codes as for Figure 2.

percent, Table 3b). The plot of Factors 1 and 2 (Figure 16b) indicate a similar trend to Figure 16a but with the clusters less discrete. Again the separation between these groups is mainly on Factor 1 with characters loading on this Factor as for the males (Table 3b).

(c) Principal Component Analysis (Lombok and Sumbawa specimens only)

The two subspecies of *H. diadema* in the Lesser Sunda Islands interface between the narrow, (14 km) shallow strait between Lombok and Sumbawa (Selat Alas).

The PCA analysis of 23 skull characters (males and females combined) for the Lombok and Sumbawa specimens, representing respectively *H. d. nobilis* immediately to the west and *H. d. diadema* immediately to the east of Selat Alas, extracted three factors. These factors combined explained 73 percent of the variation (Factor 1 — 56.7 percent,; Factor 2 — 10.8 percent; Factor 3 — 5.4 percent). The plot of Factor 1 and Factor 2 (Figure 17) indicates that the closely adjacent Lombok and Sumbawa populations cluster separately and maintain their distinct morphological identity.

(d) Descriminant Function Analysis

(i) *External characters* (males and females combined, excluding weight and ear length)

The first three canonical variate functions, combined explained 97.4 percent of the variance (Table 4a). Function 1, which explained 70.4 percent of the variance, appeared to be most influenced by metacarpal 3 length (D3ML) and then metacarpal 2 length (D2ML); Function 2 (22.7 percent) appeared to be most influenced by tibia length (TIL); and Function 3 (4.4 percent) appeared influenced most by metacarpal 4 (D4ML) but the other characters were also important (Table 4a).

The plot of Functions 1 and 2 (Figure 18) provided the best separation of the *H. diadema* subspecies considered. Plots of Functions 1 and 2 separately with Function 3 did not provide noted further clarification or separation of the groups.

A plot of the first two discriminant functions (Figure 18) reveals separation of *H. d. oceanitis* from the other subspecies. Also *H. d. reginae* is separate from both *H. d. diadema* and *H. d. nobilis* and *H. d. griseus* is separate from *H. d. nobilis*. Function 1 provided complete separation only for *H. d. oceanitis*, but *H. d. nobilis* was also reasonably separate from *H. d. griseus* on that Function. Function 2 provided almost complete separation of *H. d. reginae* from *H. d. oceanitis* and *H. d. nobilis*, it also allowed complete separation between *H. d. masoni* and *H. d. oceanitis*.

Of the cases, 76.4 percent were correctly classified. With *H. d. diadema* 63.9 percent were correctly classified; incorrect classifications were: 16.7 percent as *H. d. nobilis*, 5.6 percent as *H. d. griseus*, 2.8 percent as *H. d. oceanitis* and 11.1 percent as *H. d. masoni*. With *H. d. nobilis* 79.6 percent were correctly classified; incorrect classifications were: 13.0 percent as *H. d. diadema*, 3.7 percent as *H. d. griseus* and 3.7 percent as *H. d. masoni*. With *H. d. griseus* 58.8 percent were correctly classified; incorrect classifications were: 11.8 percent as *H. d. diadema*, 5.9 percent as *H. d.*

nobilis, 17.6 percent as *H. d. reginae* and 5.9 percent as *H. d. oceanitis*. With *H. d. reginae* 81.8 percent were correctly classified; incorrect classifications were: 18.2 percent as *H. d. griseus*. With *H. d. oceanitis* 100 percent were correctly classified. With *H. d. masoni* 66.7 percent were correctly classified; incorrect classifications were: 16.7 percent as both *H. d. griseus* and *H. d. reginae*.

(ii) *Skull characters (*male and female analyses separate, excluding premaxilla length).

Males — The first three canonical variate functions combined explained 94.5 percent of the variation (Table 4b). Function 1 which explained 70.9 percent of the variance, appeared to be most influenced by characters GSL, CCL, CL, OCL, ZW, DL, M^3-M^3W, C^1-M^3L, M^2L. These are characters related to overall size of the skull, teeth and dentary. Function 2 (16.0 percent) appeared most influenced by GSL, CCL, CL, NB, C_1-M_3L, M^3L which relate to overall length of the skull, nasal breadth and length of teeth. Function 3 (7.6 percent) was most influenced by GSL, ZW, DL, M^3-M^3W and M^3L which again relate to overall length and width of skull and dentary and M^3 length (Table 4b).

The plot of Functions 1 and 2 (Figure 19a) provided the best separation of *H. diadema* subspecies. Plots of other combinations of Functions 1, 2 and 3 did not notably clarify the clusters. From Figure 19a it is apparent that *H. d. nobilis* males separated from the other subspecies on Function 1, suggesting that it is distinguished from them by its much larger and more robust skull and dentition. The other subspecies are arranged as a continuum of clusters that separate partially on Function 2. For example, *H. d. oceanitis* separate from *H. d. masoni, H. d. diadema* and *H. d. reginae* but not from *H. d. griseus*. *H. d. masoni* is not separated from either *H. d. diadema* or *H. d. griseus*. Again these would appear to be separated by length of skull, nasal shape and length of teeth.

Of the cases considered, 94.8 percent were classified to their correct subspecies when all three Factors were considered. With *H. d. diadema, H. d. nobilis, H. d. reginae* 100 percent were correctly classified. With *H. d. griseus* 83.3 percent were correctly classified; 16.7 percent were incorrectly classified as *H. d. oceanitis*. With *H. d. oceanitis* 90.9 percent were correctly classified; 9.1 percent were incorrectly classified as *H. d. griseus*. With *H. d. masoni* 75.0 percent were correctly classified; 25.0 percent were incorrectly classified as *H. d. diadema*.

Females — The three canonical variate Functions produced explained 91.1 percent of the variance. Function 1 which explained 44.6 percent of the variance appeared to be most influenced by characters related to overall skull and dentary length (DL, CCL) (Table 4b). Function 2 (28.6 percent) appeared most influenced by characters related to shape of nasal (NB)) and, length and width of skull (CCL, ZW, M^3-M^3W) Function 3 (17.9 percent) appeared most influenced by characters related to length of dentary (DL), cranial length (CL), distance between molar rows (M^3-M^3W) and length of part of lower tooth row (C_1-M_3L).

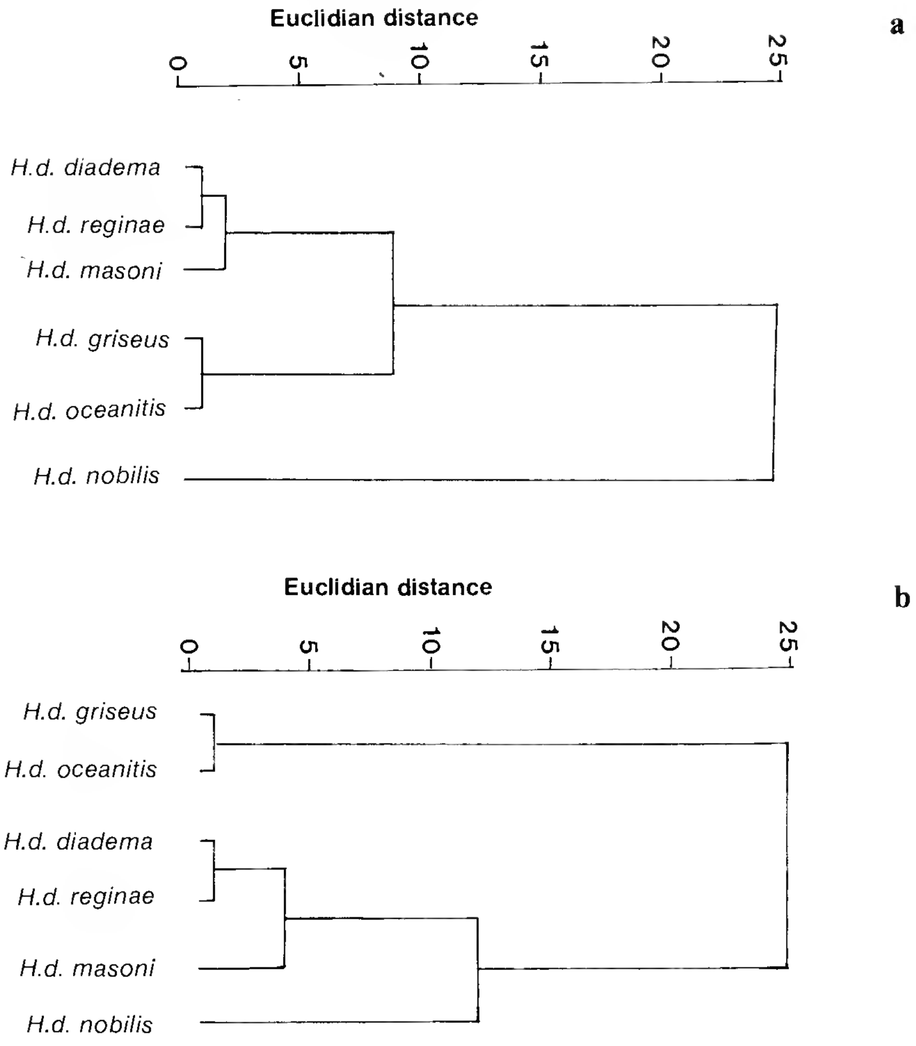


Figure 20 Phenetic relationships of the subspecies of *Hipposideros diadema* examined derived by UPGMA analysis on skull plus external measurements for (**a**) males and (**b**) females.

The plot of Functions 1 and 2 for females (Figure 19b) is similar to males (Figure 19a) (*H. d. masoni* separates from *H. d. nobilis* in discriminant function space when Factor 3 is also considered).

Using all three canonical variate functions 92.0 percent of all cases were correctly classified to their subspecies. With *H. d. diadema* and *H. d. reginae* 100 percent were correctly classified. With *H. d. nobilis* 92.9 percent were correctly classified; 7.1 percent were incorrectly classified as *H. d. masoni*. With *H. d. griseus* 81.8 percent were correctly classified; 18.2 percent were incorrectly classified as *H. d. oceanitis*. With *H. d. oceanitis* 80.0 percent were correctly classified; 20.0 percent were

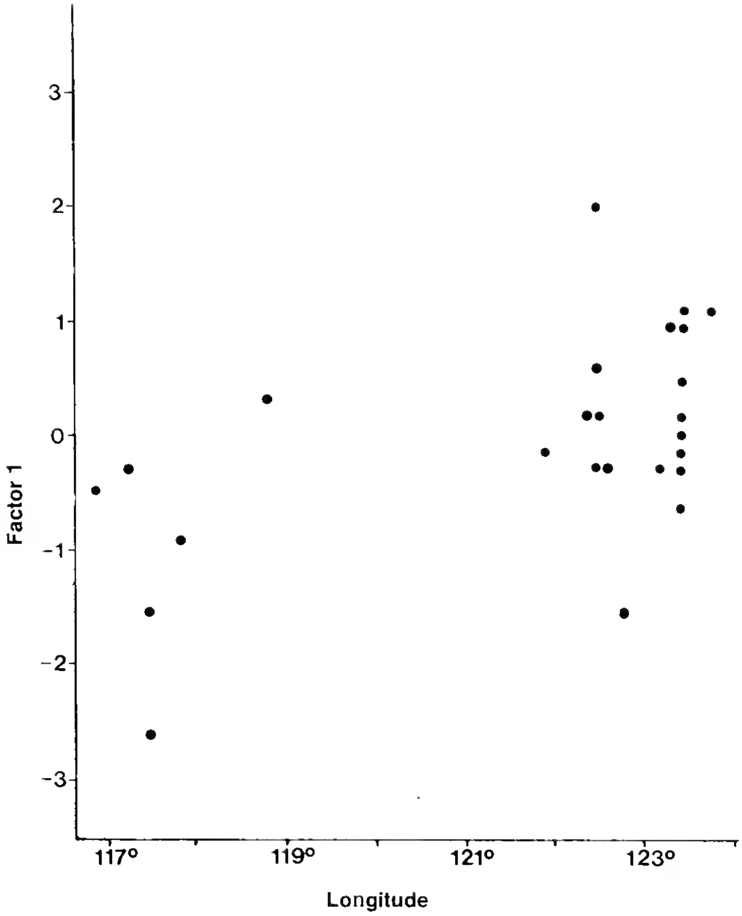


Figure 21 Plot of the first principal component factor score based on skull measurements of individual female *Hipposideros d. diadema* against the longitude of their collection sites.

incorrectly classified as *H. d. griseus.* With *H. d. masoni* 80.0 percent were correctly classified; 20.0 percent were incorrectly classified as *H. d. griseus.*

It appears that *H. d. nobilis* separates from most other subspecies on characters strongly influenced by overall skull and dentary length, but separates from *H. d. masoni* on Factor 3, which is also influenced by C_1-M_3 and width between molar rows (M^3-M^3W). The other subspecies are likely to be separated by the size and shape of their dorsal skull, particularly the nasal region.

Phenetic relationships

The UPGMA analysis of *H. d. diadema* subspecies was run for males and females separately against both skull and external characters separately and combined. These

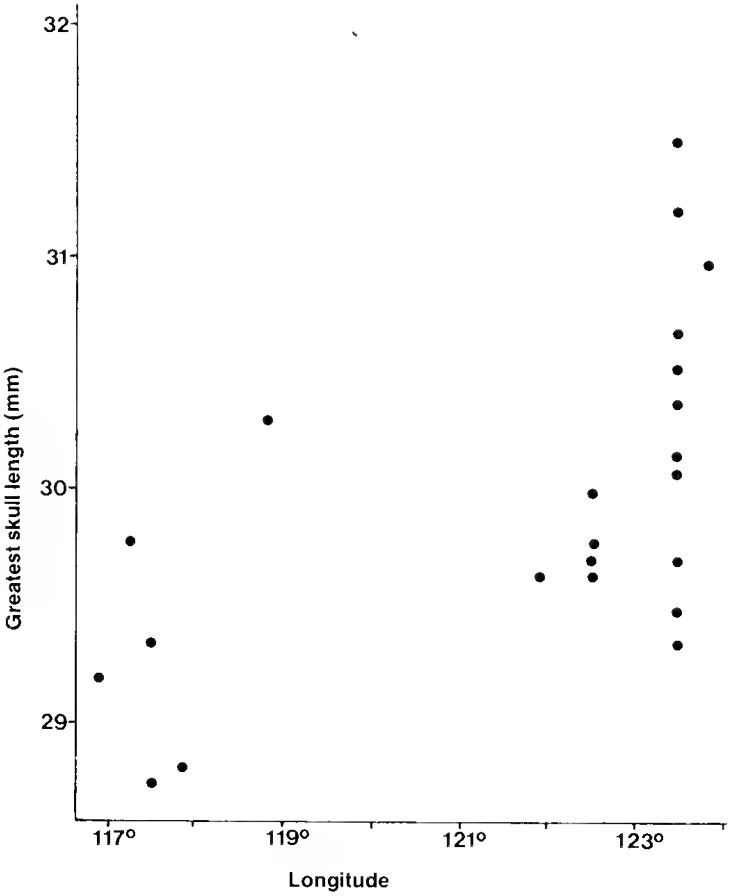


Figure 22 Plot of the greatest skull length of individual female *Hipposideros d. diadema* against the longitude of their collection sites.

two treatments produced very similar dendrograms so we present only the latter results. For males (Figure 20a), *H. d. nobilis* is phenetically very distinct from the other subspecies. The other subspecies fall into two groups. One group closely linking *H. d. griseus* and *H. d. oceanitis* and the other group closely linking *H. d. diadema, H. d. reginae* and *H. d. masoni* but with the latter subspecies slightly less closely related. The relationships for females (Figure 20b) are very similar, to the situation in the males. Once again it closely links *H. d. griseus and H. d. oceanitis* but places this group as distant from the other subspecies. *H. d. nobilis* is again separated from *H. d. diadema, H. d. regina* and *H. d. masoni;* these latter three subspecies again form a tight group, especially *H. d. diadema* and *H. d. reginae.*

Geographic variation in H. d. diadema

Factor 1 of the PCA analysis in the *H. diadema* subspecies considered appears to reflect in large part overall size in skull and external characters of specimens. For this reason the PCA Factor 1 scores of individual specimens was used as a measure of the specimen's overall size. This score was then associated with the specimen's latitude and longitude using stepwise multiple regression analysis. Skulls of males and females were analysed separately. External measurements were combined for males and females. The same analyses were then repeated using greatest skull length, radius length and body weight as direct measurements of size.

Skull characters

Females

Longitude is significantly correlated with the skull Factor scores obtained from PCA of *H. d. diadema* specimens only. ($F_{1,21}$ = 12.745, P = 0.0018) (Figure 21). The equation representing this relationship is Factor 1 score = 0.247 longitude — 29.944 (R^2 = 0.378).

Only longitude is significantly correlated with greatest skull length ($F_{1,23}$ = 12.395, P = .0018) (Figure 22). The equation representing this relationship is greatest skull length = 0.166 longitude + 9.709 (R^2 = 0.350).

These data strongly suggest that in female *H. d. diadema* there is a clinal trend in overall skull size, with greatest skull length increasing from west to east.

Males

There was no significant correlation between Factor scores and longitude (P = 0.22) or latitude (P = 0.97).

Nor is there a significant correlation between greatest skull length and longitude (P = 0.48) and latitude (P = 0.99).

These data suggest that males do not show the cline in skull size which is apparent in females. However, there were only 11 males in this analysis. A larger sample may indicate the same trend in males that is present in females.

External characters

The analysis of external Factor scores against latitude and longitude included ear length as an external characters. There was no significant correlation between Factor scores and longitude (P = 0.30) or latitude (P = 0.45).

Nor was there a significant correlation between weight and longitude (P = 0.18) or latitude (P = 0.76) or between radius length and longitude (P = 0.15) or latitude (P = 0.51).

Discussion

This study clearly demonstrates the existence of at least two morphological forms of *Hipposideros diadema* in the Lesser Sunda Islands. The eastern form (*H. d. diadema*), which ranges from at least Timor to Sumbawa, is smaller and easily diagnosed by skull and external characters from the western form (*H. d. nobilis*). The *a priori* principal component analysis separates *H. d. diadema* and *H. d. nobilis* into distinct clusters. Their morphological distinction is still clear when PCA is applied to populations on Lombok and Sumbawa which are the islands on either side of the distributional interface between these two subspecies. These two islands are separated by a narrow (14 km) shallow strait (Selat Alas). They would have been broadly connected during the late Pleistocene (Kitchener *et al.* 1990a) allowing ready interchange between their populations of *H. diadema*. Further, evidence from Kitchener *et al.* (1990b) suggests that water gaps of this nature are not a barrier to most species of bat in this region. This coupled with the observation that *H. diadema* (? *nobilis*) crossed a 50 km water gap to recolonise Krakatau only 45 years after that island had been sterilised by volcanic eruption (Dammerman 1948), supports the belief that Selat Alas would not constitute a substantial barrier to movement of *H. diadema* between these two islands. Despite the probability of gene exchange between these close populations of *H. diadema nobilis* and *H. d. diadema* these juxtaposed subspecies retain a morphological distinctiveness that placed their males at opposite extremes of the phenetic relationships amongst the closely related subspecies examined. Their females are also considerably separated phenetically.

There is a trend within *H. d. diadema* females for overall skull size to decrease from east to west. This suggests some overall factor such as climate may be operating, because there is a trend towards moister environments from east to west as this island chain emerges from the rain shadow cast by the Australian continent. An increase in size in response to increasing climatic severity (especially aridity) is a trend observed in other bats (Findley and Jones 1967; Findley and Traut 1970; Stebbings 1973).

The westwards step from Sumbawa to Lombok results in *H. d. nobilis* on Lombok having a skull considerably larger than the Sumbawan *H. d. diadema*. This is in spite of the trend which places the Sumbawan population at the smaller end of an east-west cline in overall skull size. Clearly the selection factors operating within *H. d. diadema* to reduce its size from east to west do not have a similar influence on the Lombok *H. d. nobilis*. Perhaps this finding is in keeping with studies (Kitchener and Caputi 1985) on morphological clines in tropical Australian *Scotorepens*. That study indicated that *S. sanborni* shows a strong trend to increase in measures of overall size from west to east. However, in *S. greyii* the trend is reversed. These authors concluded that morphological clines in these species result from a complex interplay of environmental patterns.

In combination, the above observations indicate that the morphological distinctiveness between *H. d. diadema* and *H. d. nobilis* over such a narrow gap may warrant their recognition as separate species. A concurrent electrophoretic study carried out by colleagues at the South Australian Museum, on tissue collected from populations of *H. diadema* on Sumbawa and Lombok may assist with such a taxonomic decision. For the present, we tentatively retain *nobilis* as a subspecies of *H. diadema*.

This study of the taxonomy of the Lesser Sunda *H. diadema* required examination of some morphologically and geographically closely related subspecies. As a consequence, the conclusions of this study have a wider bearing on the subspecific taxonomy of *Hipposideros diadema*. In particular, we differ from most recent authors by placing the New Guinea form, *H. d. pullatus*, in synonymy with *H. d. griseus* from the Philippines. This is because we are unable to distinguish between these subspecies on size and shape, apart from the observation that the paired eminences on the nasal swelling appeared less inflated in specimens from the Philippines. Also we agree with Shamel (1942) that Thailand *H. d. masoni* have slightly longer skulls than those from the Javan form of *H. diadema* (we included some of the same specimens examined by Shamel in this study of *H. d. masoni*). However, we do not agree with Hill (1963) that *H. d. masoni* is consubspecific with the Javan form (*H. d. nobilis*).

The taxonomy of *H. diadema* in the Bismarck and Solomon Is is confused. A number of small subspecies have been described from that region (*H. d. trobrius, H. d. malaitensis, H. d. mirandus, H. d. oceanitis* and *H. d. demissus*). Additionally, Koopman (1982) notes the presence of another distinct form from Misima Island. Phillips (1967), Hill (1968) and Koopman (1982) have all commented on the distributional mosaic of smaller and larger subspecies in this region. We have examined specimens of *H. d. oceanitis* and the smaller *H. d. demissus*. These, and the other smaller forms referred to above, are not closely related to the subspecies of *H. diadema* considered in this paper — nor is the small *H. d. inornatus* from Northern Territory, Australia. The taxonomic status of these smaller forms will be examined in a separate paper.

Hipposideros diadema oceanitis from the Solomon islands is quite distinct from the other subspecies examined in both the Principal Component and Discriminant Function Analyses. However, the UPGMA analysis indicate that it is very closely related to *H. d. griseus* from Papua New Guinea and the Philippines.

Hipposideros diadema reginae from Queensland, Australia is very closely related phenetically to *H. d. diadema* of Nusa Tenggara. This conflicts with the statement by Koopman (1984: 11) that neither of the Australian *H. diadema* subspecies "has any close affinity with the still larger *H. d. diadema* of the Lesser Sundas". It is also reasonably closely related to *H. d. masoni* from Thailand and Malaysia. Together, these populations of *H. diadema* stand apart from those of New Guinea and the Solomon forms. The relationships of *H. d. reginae* suggests that it reached Australia from the Lesser Sundas rather than from the New Guinea-Cape York route.

Koopman (1982) correctly cautioned against the naming of island forms of *H. diadema* without first considering variation within the species over a wide range. *H. diadema* subspecies vary in their morphology over their distribution as demonstrated in this study with *H. d. diadema*. This variation may be expected to be emphasised by the requirement of this species for large caves which presumably restrict their general movements to the locality of such caves — although we have mentioned their ability to move substantial distances on occasions.

Evidence from the Lesser Sundas indicates that these subspecies may have a wide distribution and occupy a number of islands that have never been connected; e.g., the inner and outer Banda island groups. Consequently many small island populations of the subspecific *H. diadema* in the Moluccas, Solomons, Bismarcks and other islands: Nicobar, Engano, Bungaran, Kalao, Kei may, after a comprehensive revision of the species, result in a number of them being recognised as consubspecific with the forms considered herein. This is particularly likely with subspecies on islands on or close to the Sunda Shelf e.g., (*H. d. nicobarensis; H. d. enganus; H. d. natunensis*). If this proves to be the case, then the stability of some of the subspecies names used in this paper may be affected. For example, if the Nicobar I. population were shown to be consubspecific with that from Burma, then *H. d. masoni* would be replaced by *H. d. nicobarensis*. However, other populations of *H. diadema* on small islands were named after 1900. Consequently, the nomenclature of the other subspecies considered here are unlikely to be affected by such synonymy because their names would have priority.

A principal reason for carrying out our series of mammal surveys on islands throughout the Lesser Sundas was to examine distributional trends of species along this island chain and, with selected species, also examine morphological and genetic changes that occur between their populations on different islands. These data, coupled with comparisons between island mammal faunas in the region, will be used to examine the nature of the interface between the Australian and Oriental Biogeographic Regions — traditionally placed between Lombok and Bali. However, a great deal of systematic work remains to be done on mammals of this region before we can clarify its mammalian biogeography. Recent studies suggest that there is much more mammal endemicity in the Lesser Sundas than was previously supposed (Kitchener *et al.* 1990a, b; Kitchener *et al.* 1991a-d); Kitchener and Maharadatunkamsi (1991).

Kitchener *et al.* (1990a, b) suggested that the water gap between Bali and Lombok was not a barrier to the distribution of bats and did not mark an important biogeographic boundary for bats. This study would tend to support this view, with the demarcation between subspecies of *H. diadema* in this region being placed to the east of Lombok.

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Appendix I: Specimens examined. All adults, 'alcoholic' specimens except where the numbers are affixed with S — which are 'cabinet' skins.

Hipposideros d. diadema

INDONESIA	
Flores I.:	Ratulodong, 8°11'S, 122°52'E, WAM 32557, WAM 32560, WAM 32562, WAM 32565-7, WAM 32581-2, WAM 32558, WAM 32583 (8 ♀♀, 2 ♂♂).
Moyo I.:	Tanjung Pasir, 8°23'15S, 117°31'30"E, WAM 31950, WAM 31993 (2 ♀♀).
Roti I.:	Baa, 10°44'S, 123°06'E, WAM 35430 (♀); Oeseli, 10°51'S, 123°05'E, WAM 35495-96 (2 ♂♂).
Savu I.:	Menia, 10°29'S, 121°55'E, WAM 35210 (♀).
Sumba I.:	Waikabubak, 9°38'S, 119°31'30"E, WAM 30353-4 (2 ♂♂).
Sumbawa I.:	Batu Dulang, 8°35'S, 117°17'20"E, WAM 31756 (♀); Batu Tering, 8°48'S, 117°22'E, WAM 31138, WAM 31466-7 (3 ♂♂); Desa Bela, 8°52'S, 116°50'E, WAM 31302 (♀); Merente, 8°33'10"S, 117°01'15"E, WAM 31177 (♂); Teluk Santong, 8°43'40"S, 117°53'30"E, WAM 31411 (♀); Waworada, 8°42'30"S, 118°47'30"E, WAM 31672 (♀).
Timor I.:	Lifuleo, 10°18'S, 123°30'E, WAM 38039, WAM 38080-83, WAM 38086, WAM 38087-90 (9 ♀♀, ♂).

Hipposideros d. nobilis

INDONESIA	
Bali I.:	c. 8°15'S, 115°00'E, WAM 16170-71 (2 ♀).
Java I.:	Cibodas, 6°45'S, 107°00'E, MZB 10374, MZB 9429, MZB 10375 (♂, 2 ♀♀); Cidalog, 7°14'S, 106°54'E, MZB 12786 (♀); Liampea, 6°32'S, 106°40'E, MZB 9426, MZB 9428 (2 ♀♀); Sukambumi, 7°15'S, 106°50'E, WAM 30022 (♀); Gua Ciampea, 6°32'S, 106°40'E, MZB 14787 (♂); Guharatu (C. Java) MZB 9415, MZB 9410, MZB 943 (3 ♂♂).
Lombok I.:	Kuta, 8°55'S, 116°17'E, WAM 31105, WAM 33765-75, WAM 33900-03 (8 ♂♂, 8 ♀♀); Suranadi, 8°33'30"S, 116°14'E, WAM 33761-4, WAM 35738 (2 ♂♂, 3 ♀♀);

Pringgasela, 8°36'S, 116°29'E, WAM 35741, WAM 35744 (2 ♂♂); Lendi, 8°35'S, 116°31'E, WAM 35729, WAM 35742-3 (2 ♀♀, ♀); Lenele 8°37'S, 116°30'E, WAM 35733, WAM 35747 (2 ♂♂); Tebabian, 8°37'S, 116°30'E, WAM 35736-7 (2 ♀♀); Terowangan Air 8°37'S, 116°30'E, WAM 35731-2, WAM 35735 (1 ♂, 2 ♀♀); Lombok, WAM 35740, WAM 35745 (2 ♂♂).

Nusa Penida I.: 8°45'S, 115°30'E, MZB 14828, MZB 14845 (♂, ♀).

BORNEO

Sabah,

Bode River: Sepagaya Forest Reserve, 5° S52'N, 118°04'E, FMNH 76960 S (♂); Kalimantan, Ritan River (*c.* 0°50'N, 115°45'E), FMNH 44125-6 (♂♀); S. Kalimantan, WAM 27605 S (♀); N. Borneo, AM 6242 (♂).

Hipposideros diadema griseus

PAPUA

NEW GUINEA: Doido, 6°32'S, 144°51'E, AM 15103 (♀); Lawarere, 9°25'S, 147°26'E, AM 15089-90, AM 15095 (2 ♂♂, ♀); Mt Missim, 7°15'S, 146°47'E, AM 19554 (♂); Tedebeoi Village, AM 19102 S (♀); Waro Swamp, 6°31'S, 143°11'E, AM 15200 S (♂); Baiteta, 5°20'S, 145°44'40"E, WAM 27484, WAM 27486 (2 ♀♀).

PHILIPPINES: Busuanga I., 6 km NE of San Nicolas, 12°10'N, 120°05'E, S 477700 S, S 477703 S, S 1477715 S (2 ♂♂, 1♀); Luzon I., 4 mi W of Ipo Dam, 14°53'N, 121°08'E, S 304073 S (♀); Clark Air Base, 14°50'N, 120°30'E, S 304074 S, 51304076 S (♂ ♀); Mindanao I., Matam Sapinit Cave, 8°28'N, 123°07'E, FMNH 80371 S (♀); Negros I. c. 9°N, 123°00'E, WAM 29051-2 (2 ♀♀); Palawan I. St Pauls Cave, 10°12'N, 118°50'E, AM 12412 (♀).

Hipposideros diadema reginae

AUSTRALIA

Queensland: Bourne Creek, 13°39'S, 143°03'E. JM 3505 (♀); Buthen Buthen, 13°23'S, 143°27'E, JM 2452-3, JM 2468 (3 ♀♀); c. 5 km WSW of Buthen Buthen, 13°24'S, 143°25'E, JM 2472 (♀); Rocky Scrub, 13°44'S, 143°22'E, JM 3504 (♀); Steenes Shack, 13°46'S, 143°12'E, JM 2411 (♀); West Claudie River, 12°44'S, 143°19'E, JM 2383, JM 2402, JM 3507, AM 8106 S, AM 13337, JM 9492 (4 ♂♂, 2 ♀♀); Attack Creek, 13°30'S, 143°15'E, JM 2419 (♀).

Hipposideros diadema masoni

MALAYSIA: Batu Caves, 3°16'N, 101°39'E, FMNH 109556 (♀); Bentong, 3°35'N, 101°54'E, FMNH 98689-90 S (2 ♀♀); Kepong Forest Reserve, 3°12'N, 101°38'E, FMNH 82278 (♂).

THAILAND: Koh Lak, nr Prachuap Khiri Khan, (11°50'N, 99°49'E): S 258945-6 S (2 ♀♀); Seechol, (= Ban Sichon, 9°00'N, 99°56'E, S 255767 S (♂); Thailand, FMNH 48848, (♂).

Hipposideros diadema oceanitis

SOLOMON ISLANDS

NEW GUINEA Ysabel I.:

c. 8 km E Mufu Point, *c.* 8°00S, 159°00'E, AM 3579, AM 3969-71, AM 3974 (3 ♂♂, 2 ♀♀).

Florida Is: Mboli Caves *c.* 9°00'S, 160°00'E, AM 7857 (♂);

Guadalcanal I.: Lavaro Platations, *c.* 9°30'S, 160°00'E, AM 3496 AM 3498 (♀, ♂).

New Ireland I.: nr Lakuramau, 2°54'S, 151°16'E, AM 20089 AM 20091 (2 ♂♂).

New Britain I: Melai, nr Fulleborn, 6°6'S, 150°40'E, AM 20092 (♀); nr Waipo, 5°58'S, 150°43'E, AM 20093 (♀), AM 20095-7 (3 ♀♀), AM 20099-101 (3 ♀♀), AM 20104-5 (2 ♂♂), AM 20107, AM 20109, AM 20111 (3 ♂♂).

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New species and new records of genus Tamopsis Baehr & Baehr, (Arachnida, Araneae, Hersiliidae).

Third supplement to the revision of the Australian Hersiliidae.

Barbara Baehr* and Martin Baehr*

Abstract

Three new *Tamopsis* species from Western Australia and Victoria are described: *Tamopsis depressa* sp. nov., *T. distinguenda* sp. nov., and *T. transiens* sp. nov. and their relationships within the genus *Tamopsis* are discussed. New records of several other *Tamopsis* species are presented, and the ranges of some species are considerably extended.

Introduction

Soon after having finished the second supplement (Baehr & Baehr 1989) to our revision of the Australian Hersiliidae (Baehr & Baehr 1987) we received another sample of Hersiliidae from the Western Australian Museum (courtesy of Miss J. M. Waldock) that included a further three new species of *Tamopsis* from Western Australia, together with specimens of some other recently described species. While working on this material, we received additional Hersiliidae from the Museum of Victoria, Melbourne (courtesy of Dr. M. S. Harvey, Mr. G. Milledge), from the C.S.I.R.O., Canberra (courtesy of Dr. R. B. Halliday), and from Naturhistorisches Museum, Wien (courtesy of Dr. J. Gruber). These samples include an additional specimen of a new species described herein and some specimens which considerably extend the range of species described earlier by us. This material is recorded in the present paper which is regarded a third supplement to our revision. It is again evidence of the insufficient knowledge of taxonomy and distribution of the Australian Hersiliidae, especially in Western Australia.

The sequence of the species follows the systematic order of our revision. Descriptions and measurements were taken as indicated previously (Baehr & Baehr 1987, 1988, 1989). Eye ratio was taken in the following order: AME:ALE:PME:PLE. Maps are provided for the newly described species and for species in which the range has been significantly extended in the present paper.

The samples contain several juvenile specimens which could not positively identified and that are therefore not included in the present paper.

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Abbreviations

ACT	Australian Capital Territory
ALE	anterior lateral eye
AME	anterior median eye
ANIC	Australian National Insect Collection, Canberra
bS	basal segment of posterior lateral spinneret
CBM	Collection B. Baehr, München
LB	total length of body
LL	total length of legs
NHMW	Naturhistorisches Museum, Wien
NMV	Museum of Victoria, Melbourne
NSW	New South Wales
PLE	posterior lateral eye
PLS	posterior lateral spinneret
PME	posterior lateral eye
QLD	Queensland
tS	terminal segment of posterior lateral spinneret
VIC	Victoria
WA	Western Australia
WAM	Western Australian Museum, Perth
I	1st leg
II	2nd leg
III	3rd leg
IV	4th leg

Systematics

In our revision (Baehr & Baehr 1987) all known species of the former genera *Chalinura* or *Tama,* respectively, were transferred to a new genus *Tamopsis.* Except for the singular *Hersilia australiensis* Baehr & Baehr, all other Australian species of Hersiliidae are included in the genus *Tamopsis* (for the generic diagnosis, see revision). Most important characters for species differentiation in genus *Tamopsis* are the structure of the male palpus and of the female epigyne and vulva.

Tamopsis depressa sp. nov.

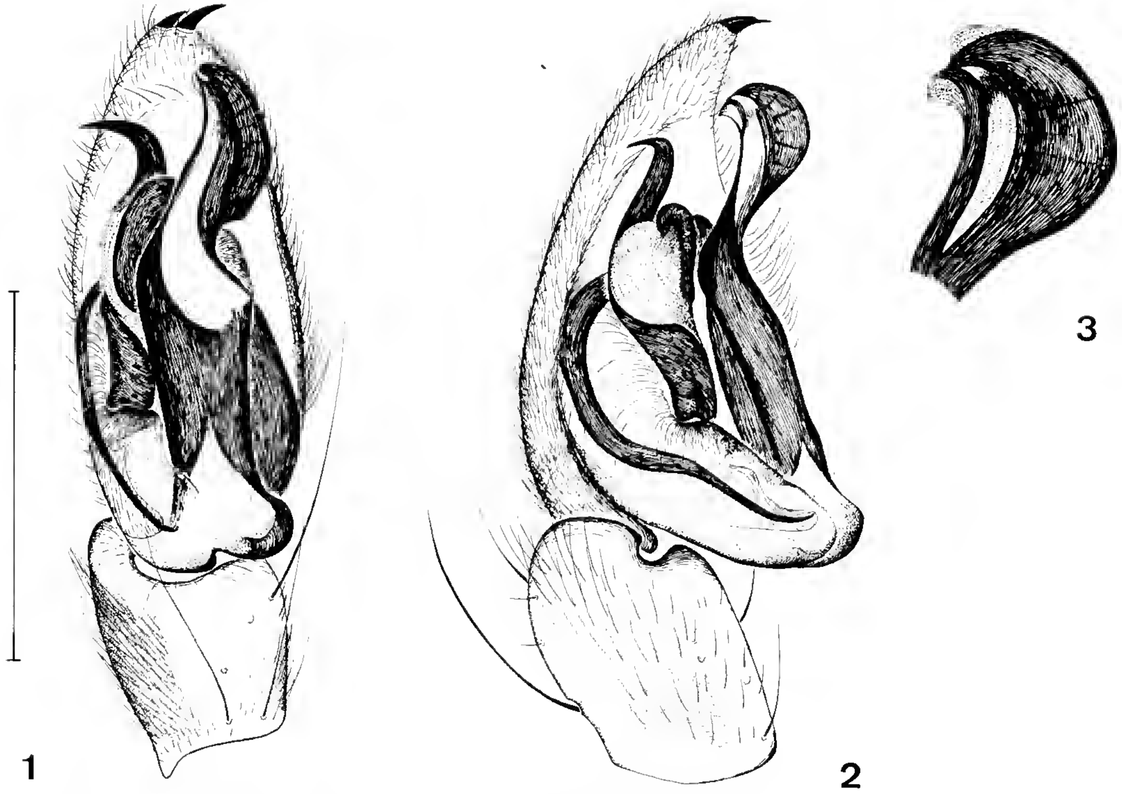
Figures 1-3, 12

Holotype

Male, W.A. 12 km E of Badja H.S., D. Mead-Hunter & G. Harold, 30.X.1988, Field No. 60 (WAM 890/91).

Diagnosis

Species of the *platycephala*-group, characterized by depressed eye area and



Figures 1-3 *Tamopsis depressa* sp. nov. Holotype. Male palpus. 1. ventral view, 2. lateral view, 3. apex of lateral apophysis. Scale for figs 1 and 2: 0.5 mm.

elongate, falciform dorsal muscular pits. Distinguished from related species by the markedly widened and strongly hollowed apex of lateral apophysis of male palpus.

Description

Measurements: Length: 4.3 mm; cephalothorax length: 1.8 mm; width: 1.6 mm; abdomen length: 2.6 mm; width: 1.56 mm. Legs: I: 11.24 mm, II: 10.32 mm, III: 3.56 mm, IV: 9.50 mm; ratio: 1:0.92:0.32:0.85. Ratio LB/LL: 0.38. PLS length: 2.24 mm; bS: 0.52 mm; tS: 1.72 mm. Eye ratio: 1:0.32:0.70:0.79.
Colour: Cephalothorax dark yellowish, eye area, clypeus, lateral border, and some radial spots blackish. Sternum dark piceous. Abdomen very dark, mottled, a lancet-shaped median stripe, the wide lateral border, and the areas around the dorsal muscular pits piceous. Ventral surface light. Legs light yellowish, outer and inner surface of femora black, apical parts of leg III and IV annulate. Palpus with dark spot on apical part of femur. PLS yellow, medially and laterally with dark stripe.
Cephalothorax: Approximately circular, slightly longer than wide, c. as wide as abdomen. Eye area not raised, clypeus c. 1/3 as high as eye area. AME by far largest,

PLE slightly larger than PME. Distances AME/AME and AME/ALE slightly less than diameter of AME. Distance PME/PME c. half of diameter of PME, distance PME/PLE almost twice the diameter of PME. Chelicerae almost twice as long as wide. Sternum pentagonal, hirsute.

Abdomen: Elongate, rather parallel, much longer than wide and c. as wide as cephalothorax. Dorsally with 3 pairs of elongate, falciform and one posterior pair of circular muscular pits. Ventral muscular pits in a narrow, slightly v-shaped arrangement. PLS but slightly shorter than abdomen, tS comparatively short.

Legs: Measurements see above. Rather short, III comparatively elongate.

Palpus: Median apophysis with very large, elongate, sharply bent, hook-like apex. Lateral apophysis basally rather wide, apex markedly widened and hollowed, though not cup-shaped, concealing the embolus completely.

Female: Unknown.

Variation: Variation of male genitalia unknown, of non-genitalic characters apparently feeble.

Additional material examined: The following juvenile is tentatively assigned to this species: 1 juvenile male, Western Australia, 21 km NE. of Denham, 23 July 1987, W. F. Humphreys (WAM 89/92).

Etymology

Derived from the markedly depressed eye area.

Distribution

Known so far from central western area of Western Australia.

Habits

According to label data holotype "active on ground (PM). Open *Acacia* over stony brown clay", the juvenile collected by "beating tray". This species lives perhaps not on bark of tree trunks, but on branches, like most low-eyed species of which observations have been made. The adult specimen caught in October, the juvenile in July.

Relationships

The very depressed eye area as well as the elongate, falciform dorsal muscular pits, and the structure of male palpus allude *T. depressa* to the *platycephala*-group of revision which includes so far only *T. platycephala* Baehr & Baehr from eastern Queensland and *T. amplithorax* Baehr & Baehr from southern Western Australia. In view of the rather similar male palpus of both species, *T. depressa* is certainly more closely related to the eastern *T. platycephala* than to the other Western Australian species.

Identification

For identification the key to species in our revision (Baehr & Baehr 1987) should be extended and altered as following:

Couplet 3(2) delete "Eastern central Queensland" 3a

3a(3) Apex of lateral apophysis cup-shaped, convexly tapering. Eastern central Queensland .... *platycephala*

Apex of lateral apophysis hollowed, apically widened. Central western part of Western Australia ...... *depressa sp.* nov.

Tamopsis eucalypti (Rainbow)

Tama eucalypti Rainbow, 1900: 487.
Tamopsis eucalypti, Baehr & Baehr 1987: 364; 1988: 13.

New records: **ACT:** 2 females, 35° 16′S 149°06′E, Black Mtn., 29 Dec 1984, M. S. Harvey, R. J. Moran, A. Hastings (ANIC). — **NSW:** 1 female, 35°38′S 150°18′E, Durras North, nr. Batemans Bay, 23.I.1980, D. C. F. & B. G. F. Rentz. Stop 6 (ANIC).

This is a widespread species in southeastern Australia, though few records on habits are available. The specimens are identified by the conspicuous shape of the female epigyne.

Tamopsis centralis Baehr & Baehr

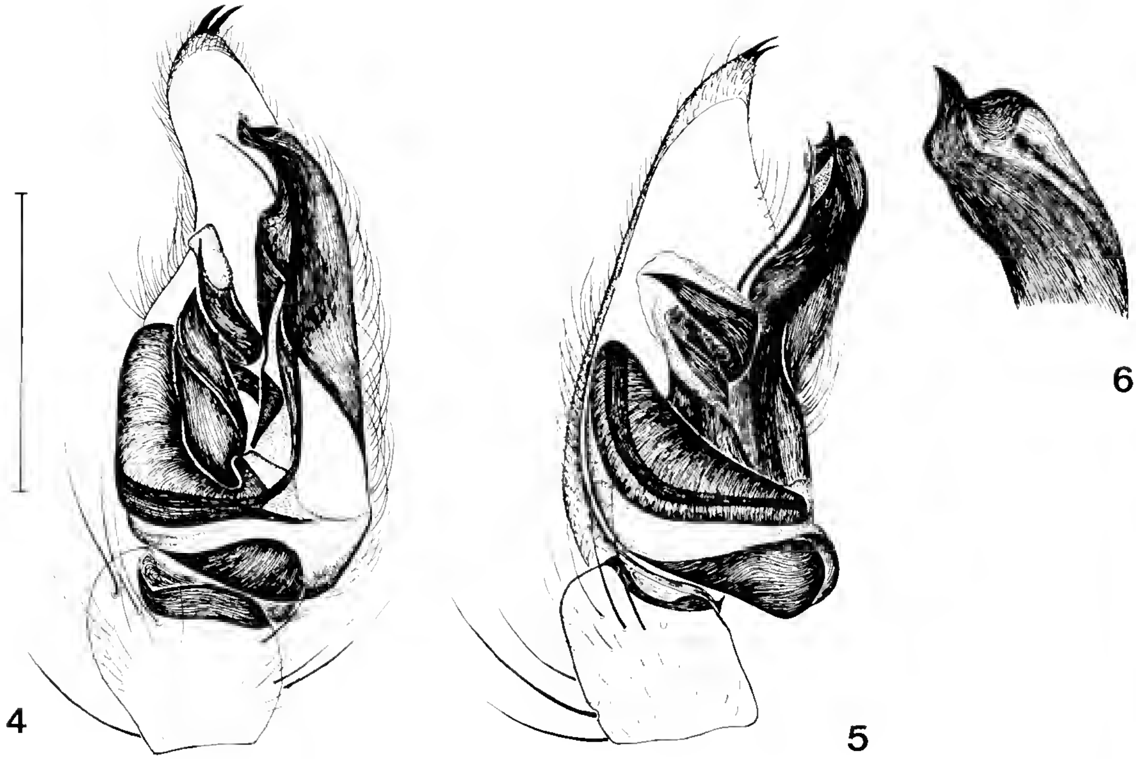
Figure 12

Tamopsis centralis Baehr & Baehr, 1987: 369

New records: **QLD:** 1 male, ? 3 juveniles, Peak Downs, A.D. 1884, 1882, A.N. I.275, II.154, leg. Steindachner, "*Tama novae-hollandiae* L. K.", Inv.No.466 (NHMW).

This species was described from a slightly damaged male from Winton, central Queensland (Baehr & Baehr 1987), and two juveniles from the Godeffroy collection, presumably from Peak Downs, were tentatively included in this species. We now assign to this species the three present juveniles. *T. centralis* is easily recognized by the deeply excised median apophysis of male palpus.

A note of J. Gruber and our own reexamination of the original description revealed that Fickert and not L. Koch is the author of *Chalinura novaehollandiae*. Although the single male mentioned above was determined by L. Koch, it is not a type of *Chalinura novaehollandiae* Fickert which should be located in the museum of Breslau (now Wroslav) and which has been probably lost during World War II (see Baehr & Baehr 1987). Although it seems reasonable to believe that *T. centralis* might be the original *T. novaehollandiae* Fickert, the description of the latter contains no argument for that supposition, the more, as only the female genitalia are figured, and several other species equally compete for that synonymization.



Figures 4-6 *Tamopsis distinguenda* sp. nov. Holotype. Male palpus. 4. ventral view, 5. lateral view, 6. apex of lateral apophysis. Scale for figs 4 and 5: 0.5 mm.

Tamopsis distinguenda sp. nov.

Figures 4-8, 12

Holotype

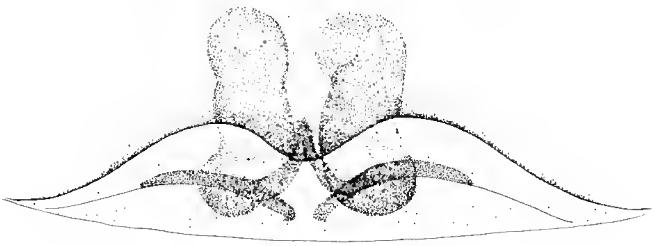
Male, Western Australia, Grass Patch, 33° 14′S 121°43′E, 25 Nov. 1978, A. F. Longbottom, Fitz. Loc. 41, Under wooden plank. On beach (WAM 89/104).

Paratypes

1 female, W.A., Grass Patch, 33°14′S 121°44′E, 10.XII.1981, C. Longbottom, Fitz loc. 81, While harvesting (WAM 89/105); 1 male, W.A., Ludlow Tuart Forest, Ludlow, Day Trap No.1, 11.XI.1980, S. S. Curry, open canopy tuart forest (WAM 89/106); 1 male, W.A. Ludlow Tuart Forest, Ludlow, Malaise Trap No.2, 4.XII.1981, S. S. Curry, replanted tuart. No burning (CBM).

Diagnosis

Species of the *queenslandica*-group. Medium sized species with low eye area, distinguished from related species by male palpus with apical excision of median apophysis narrow, lateral apophysis channelled, barely sinuate and contorted, by female epigyne with dorsal receptaculum seminis markedly smaller than ventral and by introductory ducts coiled twice.



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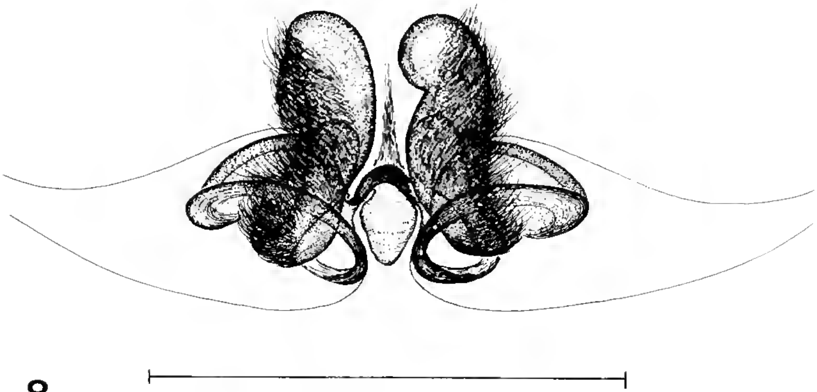

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Figures 7 and 8 *Tamopsis distinguenda* sp. nov. Female genitalia. 7. epigyne, 8. vulva. Scale: 0.5 mm.

Description

MALE HOLOTYPE

Measurements: Length: 3.8 mm; cephalothorax length: 1.55 mm; width: 1.60 mm; abdomen length: 2.25 mm; width: 1.85 mm. Legs: I: 9.42 mm, II: 9 mm, III: 3.68 mm, IV: 9.24 mm; ratio: 1:0.96:0.39:0.98. Ratio LB/LL: 0.40. PLS length: 1.62; bS: 0.38; tS: 1.24. Eye ratio: 1:0.42:1.14:1.24.

Colour: Cephalothorax dark yellow, eye area, anterior surface of chelicerae, and lateral border dark. Almost no dark radial spots visible. Abdomen white, slightly mottled, a lancet-shaped median spot and the narrow lateral borders dark. Legs yellowish, almost without pattern. Terminal segment of palpus brown. PLS whitish, median border with dark stripe. Sternum yellowish, ventral surface of abdomen grey.

Cephalothorax: Circular, slightly wider than long, narrower than abdomen. Eye area rather low, clypeus c. half as high as eye area. PLE largest, PME larger than AME.

Distance AME/AME c. half of diameter of AME, distance AME/ALE distinctly larger than diameter of AME, distance PME/PME c. 1/3 of diameter of PME, distance PME/PLE slightly larger than diameter of PLE. Chelicerae c. twice as long as wide. Sternum pentagonal, hirsute.

Abdomen: Short, wide, widest in posterior third, clearly wider than cephalothorax. Dorsally with 5 pairs of circular muscular pits. Ventral muscular pits in a wide v-shaped arrangement. PLS rather short, considerably shorter than abdomen.

Legs: Measurements see above. Rather short, III comparatively elongate.

Palpus: Median apophysis oblique, strongly contorted, apex deeply excised, though narrow. Apical part of lateral apophysis channelled for reception of embolus, barely contorted nor sinuate.

FEMALE HOLOTYPE

Measurements: Length: 4.1 mm; cephalothorax length: 1.64 mm; width: 1.72 mm; abdomen length: 2.46 mm; width: 2.50 mm. Legs: I: 9.46 mm, II: 9.06 mm, III: 3.46 mm, IV: 8.96 mm; ratio: 1:0.96:0.37:0.95. Ratio LB/LL: 0.43. PLS length: 2.4 mm; bS: 0.48 mm; tS: 1.92 mm. Eye ratio: 1:0.52:1.35:1.46.

Colour: Cephalothorax dark yellow, eye area, lateral parts of clypeus, anterior surface of chelicerae, and lateral borders blackish, a triangular spot behind eye area and three spot above the leg bases white. Abdomen whitish, strongly mottled, a lancet-shaped median spot and the wide lateral borders dark. Legs and palpus conspicuously annulate, median surface of femora with dark stripe. PLS with two indistinct dark rings.

Cephalothorax: Circular, wider than long, much narrower than abdomen. Size of eyes and distances between them almost similar to male, but AME comparatively smaller.

Abdomen: Considerably wider than cephalothorax. Arrangement of dorsal and ventral muscular pits as in male. PLS slightly longer in relation to abdomen than in male.

Legs: Measurements see above. Shorter than in male, III relatively shorter.

Epigyne: Without lateral openings. Parts of vulva closely adjacent.

Vulva: With two receptacula seminis of different size, the dorsal one being much smaller. Ventral receptaculum glandular along whole lateral surface. Introductory ducts two times coiled, laterally sharply bent.

Variation: Some variation in colour and in relative length of legs noted.

Etymology

Alludes to the high similarity to some other species of same group.

Distribution

Known from southwestern corner of Western Australia.

Habits

According to label data holotype "under wooden plank on beach", paratypes on "tuart" and "while harvesting". These records are not very useful for fixing the habitat of *T. distinguenda*. However, this is perhaps another species living rather on branches than on tree trunks. Collected so far in November and December.

Relationships

The species belongs to the *queenslandica*-group of revision. Male and female genitalia are most similar to *T. queenslandica* Baehr & Baehr from central eastern Queensland and New South Wales, though differ in the less wide apex of median apophysis and the rather straight lateral apophysis of male palpus, and in the small dorsal receptaculum seminis of female vulva. Female genitalia of *T. distinguenda* are also fairly similar to those of *T. darlingtoniana* Baehr & Baehr from southwestern Australia, though differ in the more complicately coiled introductory ducts. With regard to systematic position, *T. distinguenda* is closely related to *T. queenslandica*, but is perhaps slightly more plesiomorphic.

Identification

For identification the key to species in our revision (Baehr & Baehr 1987) should be altered and extended as follows:

Couplet 11(10) MA very deeply excised. LA deeply channelled at apex 11a

(11) MA with wide excision. LA sinuate. Southeastern Queensland, eastern New South Wales .... *queenslandica*

MA with narrow excision. LA barely sinuate. Southwestern Australia .... *distinguenda* sp. nov.

Couplet 25(24) V with ID posteriorly sharply bent outwards and produced laterally 25a

V with ID posteriorly not bent outwards, nor produced laterally... 26

25a(25) AME almost as large as PME. Dorsal RS as large as ventral RS. Southeastern Queensland, eastern New South Wales .... *queenslandica*

AME considerably larger than PME. Dorsal RS half as large as ventral RS. Southwestern Australia .... *distinguenda* sp. nov.

Tamopsis circumvidens Baehr & Baehr

Figure 12

Tamopsis circumvidens Baehr & Baehr, 1987: 378

New records: **VIC:** 1 male, 13.3 km NW of Lascelles, 35° 33′S 142° 27′E, Site 43, A. L. Yen, Jan.1986 (NMV); 1 male, 15.2 km NW. of Lascelles, 33° 33′S 142° 26′E, Site 45, A. L. Yen, Jan.1986 (NMV); 1 male, 8.2 km N. of Culleraine, 34° 12′S 141° 36′E, Site 119, A. L. Yen, Feb.1986 (NMV); 1 male, 9.0 km ESE of Hattah, 34° 48′S 142° 22′E, Site 3, A. L. Yen, Jan.1986 (NMV); 1 female, 8.4 km SE of Hattah, 34° 48′S 142° 21′E, Site 6, A. L. Yen, Jan.1986 (NMV); 1 male, 18.9 km SW of Hattah, 34° 54′S 142° 09′E, Site 31, A. L. Yen, Jan.1987 (CBM); 1 male, 6.7 km SSW of jnct MV Hwy & Annuello Rd., 34° 51′S 142° 36′E, Site 14, A. L. Yen, Jan.1986 (NMV); 1 female, 8.3 km SE of confluence of Lindsay R. & Mullaroo Creek, 34° 11′S 141° 10′E, Site 103, A. L. Yen, Nov.1985 (NMV); 2 females, 16.8 km SSW of Murrayville, 35° 25′S 141° 10′E, Sites 67 and 68, A. L. Yen, 18-24 Feb.1986 (CBM, NMV). All specimens collected in "Drift fence pitfall trap".

T. circumvidens is a characteristic, easily recognized species known so far from central-southern Western Australia only. It is perhaps a typical species of the Mallee region. The new records extend the range considerably through arid southern Australia to northwestern Victoria, where *T. circumvidens* inhabits also semiarid areas.

Tamopsis transiens sp. nov.

Figures 9-11, 13

Holotype

Male, W.A., WAM Goldfields Survey, MT Jackson, 30° 15′00″S, 119° 15′20″E. MJR6 Pit fall(s), 24.-30.XI.1981, W. F. Humphreys et al. (WAM 89/109).

Paratype

Male, Vict., 19.7 km NE of Patchewollock, 35° 14′S 142° 19′E, Site 54, Drift fence pitfall trap, Jan.1986, A. L. Yen, "*Tamopsis fickerti, Tamopsis* sp." (NMV).

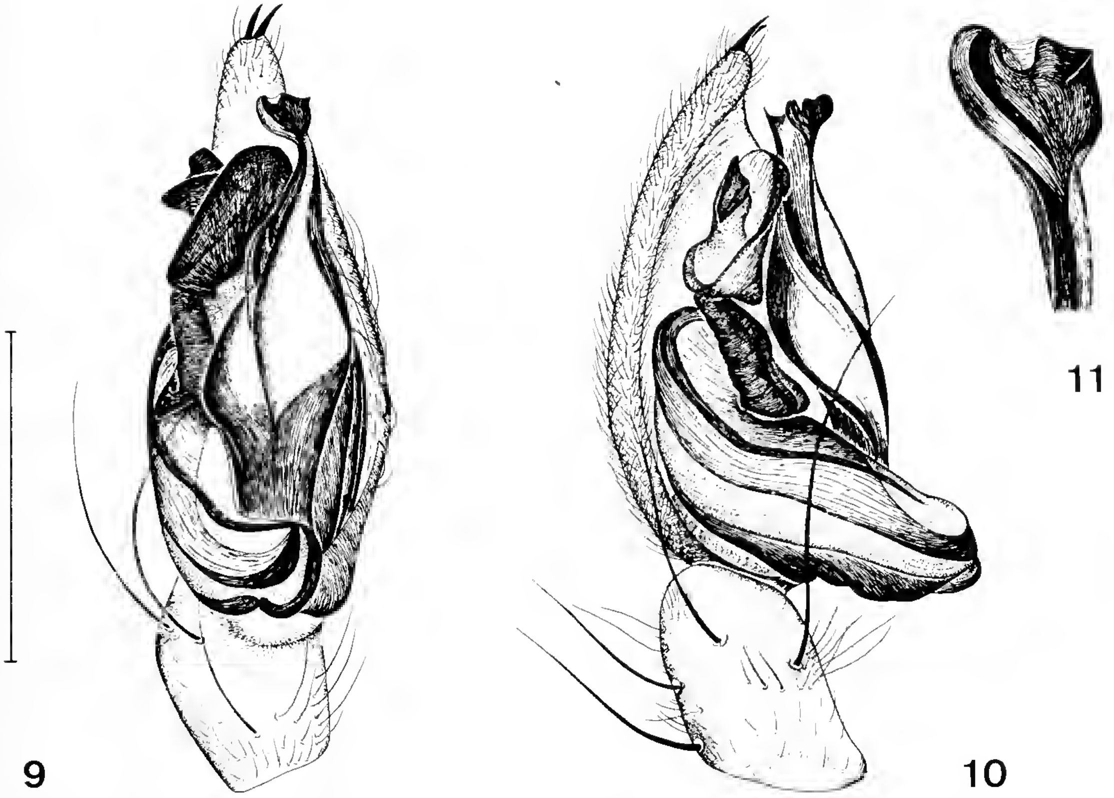
Diagnosis

Species of *nanutarrae*-group (Baehr & Baehr 1989) by means of high eye area, large AME, and structure of median apophysis of male palpus. Distinguished from *T. nanutarrae* Baehr & Baehr by median apical process of median apophysis of male palpus longer, and lateral part of apical excision of lateral apophysis widened and with deep excision.

Description

HOLOTYPE

Measurements: Length: 3.54 mm; cephalothorax length: 1.44 mm; width: 1.32 mm; abdomen length: 2.12 mm; width: 1.42 mm. Legs: I: 12.34 mm, II: 10.74 mm, III: 3.80



Figures 9-11 *Tamopsis transiens* sp. nov. Holotype. Male palpus. 9. ventral view, 10. lateral view, 11. apex of lateral apophysis. Scale for figs 9 and 10: 0.5 mm.

mm, IV: ?; ratio: 1:0.87:0.31:?. Ratio LB/LL: 0.29. PLS length: 1.56 mm; bS: 0,52 mm; tS: 1.04 mm. Eye ratio: 1:0.31:0.76:0.80.

Colour: Cephalothorax dark yellowish, eye area, middle of clypeus, anterior basal surface of chelicerae, lateral border, and some radial spots dark brown. Abdomen whitish, laterally and posteriorly slightly mottled, lateral borders and a lancet-shaped median stripe indistinctly dark. Ventral surface light. Legs whitish-yellowish, femora on outer and inner surface with dark stripe. PLS with a basal and a subapical dark spot on tS.

Cephalothorax: Circular, c. as wide as long, and almost as wide as abdomen. Eye area strongly raised, clypeus c. as high as eye area. AME largest, PME almost als large as PLE. Distances AME/AME and AME/ALE clearly less than diameter of AME. Distance PME/PME c. 1/3 of diameter of PME, distance PME/PLE slightly larger than diameter of PLE. Chelicerae almost twice as long as wide. Sternum pentagonal, hirsute.

Abdomen: Elongate, rather parallel, much longer than wide and c. as wide as cephalothorax. Dorsally with five pairs of circular muscular pits. Ventral muscular pits in a narrow, v-shaped arrangement. PLS short, considerably shorter than abdomen.

Legs: Measurements see above. Rather elongate, III moderately elongate.

Palpus: Median apophysis contorted, apex widened, with wide, membraneous area within. Lateral rim of apex simply bordered. Within membraneous area with a thickly sclerotized, contorted, apically excised process directed outwards. Lateral apophysis slightly contorted, apex excised, lateral part of apex widened, with deep excision. Embolus hidden.

Female: Unknown.

Variation: Paratype slightly more vividly patterned, otherwise little variation noted.

Etymology

Derived from transient distribution from Western Australia to northwestern Victoria.

Distribution

Known so far from interior of southwestern Australia and from northwestern Victoria.

Habits

Both specimens collected in pitfall traps, the holotype in "shrubland". As the closely related species *T. nanutarrae* Baehr & Baehr and most other species with high eye area live on bark of tree trunks, this might be also the habit of *T. transiens.*

Relationships

In view of the very similar male palpus this species is certainly very closely related to *T. nanutarrae* Baehr & Baehr from northern Western Australia. In *T. transiens,* however, the palpus is slightly more complicately built, and therefore, this species is perhaps more evolved than the northern *T. nanutarrae.*

Identification

For identification the extended key to the species in Baehr & Baehr (1989) should be altered and extended once more as following:

Couplet 13a(13) delete: "Northwestern Australia south of Great Sandy Desert" 13aa

13aa(13a) Apical process of median apophyis shorter. Lateral part of apex of lateral apophysis not widened nor excised. Northwestern Australia south of Great Sandy Desert .... *nanutarrae*

Apical process of median apophysis longer. Lateral part of apex of lateral apophysis distinctly widened and excised. Southwestern Australia, northwestern Victoria .... *transiens* sp. nov.

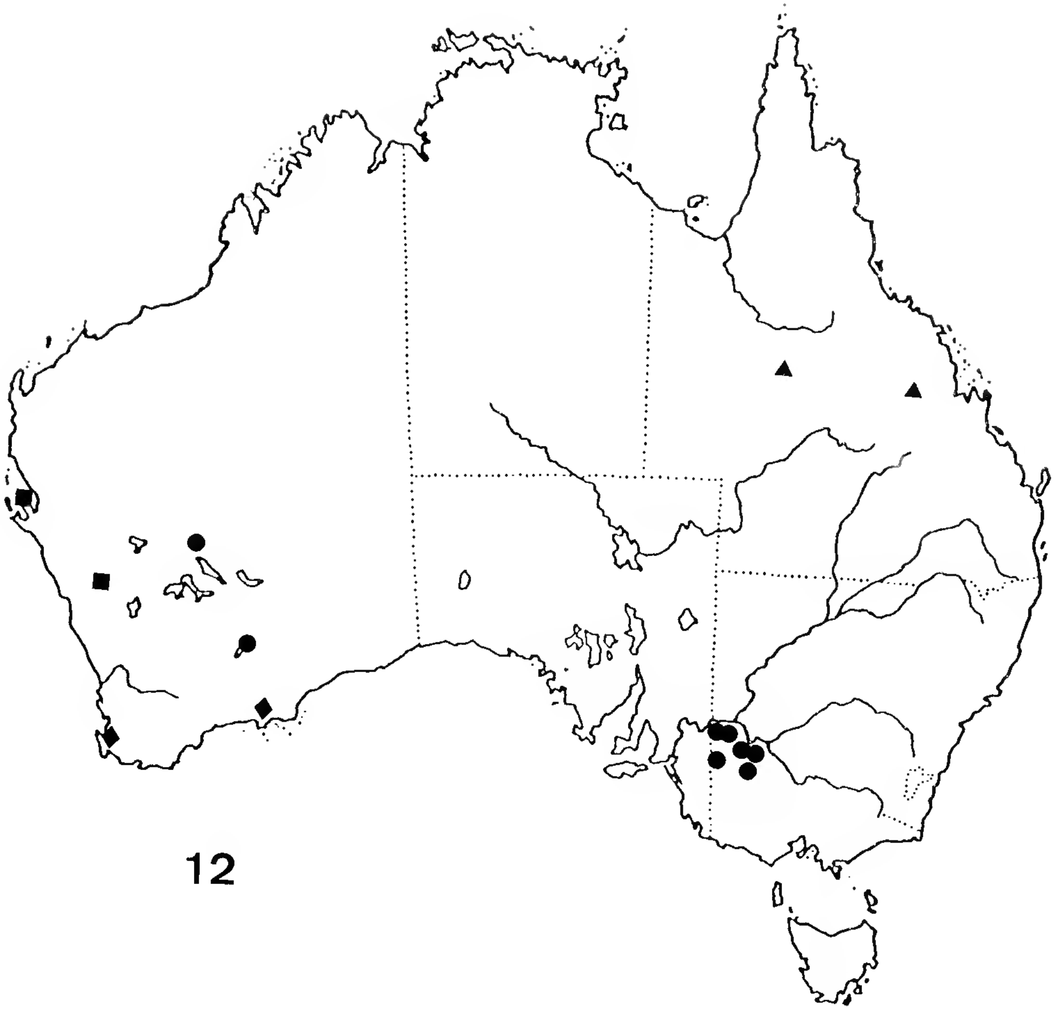


Figure 12 Distribution of *Tamopsis depressa* sp. nov.: ■, *T. distinguenda* sp. nov.: ◆, *T. circumvidens* Baehr & Baehr: ●, and *T. centralis* Baehr & Baehr: ▲.

Tamopsis tropica Baehr & Baehr

Tamopsis tropica Baehr & Baehr, 1987: 379.

New record: **QLD:** 1 female, Pallarenda, 7 m N of Townsville, 7.VIII.1967, F. J. Day (ANIC).

A northeastern species, easily identified by the high eye area, simple lateral apophysis of male palpus, and median apophysis with scopula-like organ.

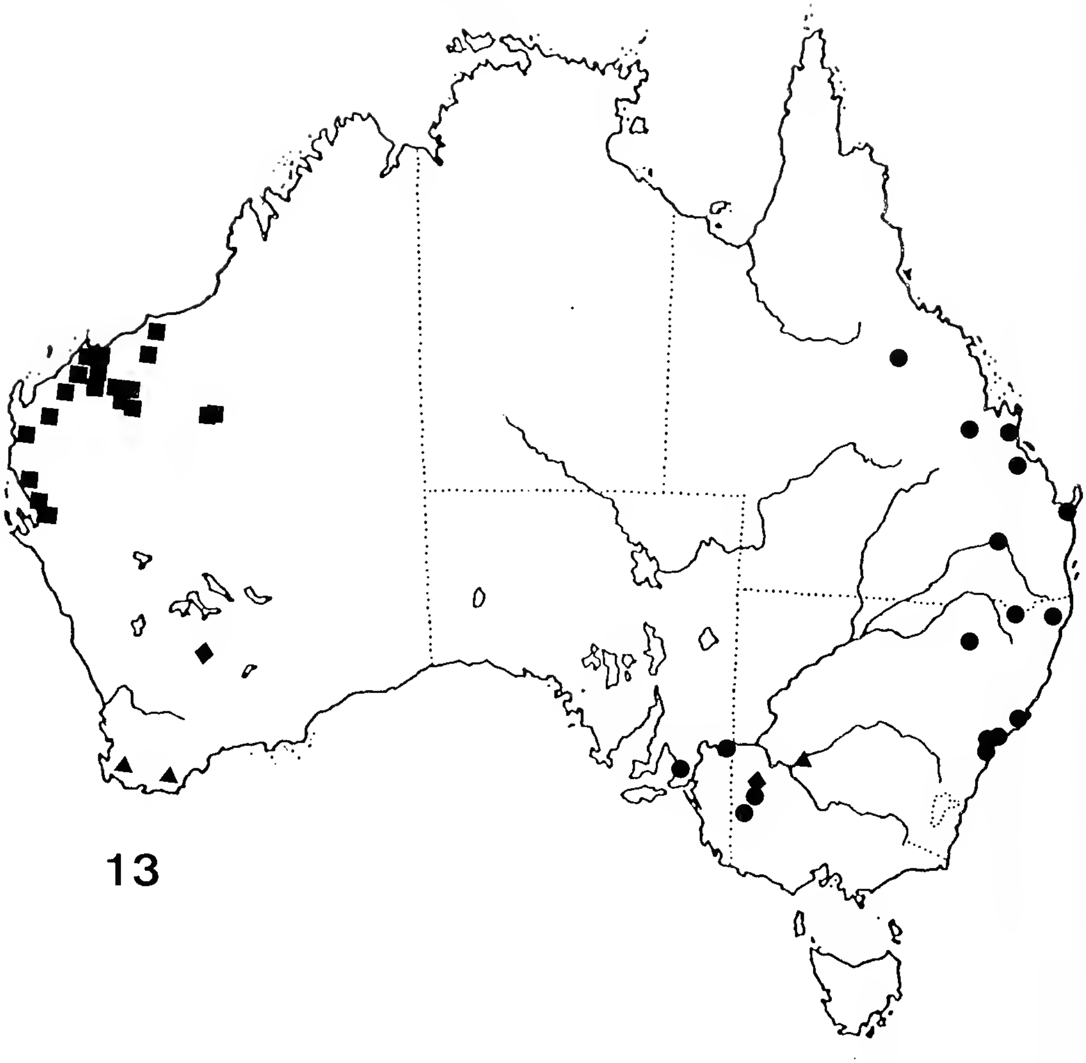


Figure 13 Distribution of *Tamopsis transiens* sp. nov.: ◆, *T. fickerti* (L. Koch): ●, *T. marri* Baehr & Baehr: ▲, and *T. occidentalis* Baehr & Baehr: ■.

Tamopsis fickerti (L. Koch)

Figure 13

Chalinura fickerti L. Koch, 1876: 830.
Tamopsis fickerti, Baehr & Baehr 1987: 384; 1988: 16.

New records: **VIC:** 1 male, 2 juv., Horseshoe Bend, Little Desert Nat. Park, 6. July 1982, M. S. Harvey & B E. Roberts (WAM 89/245-7); 1 male, 1 juv. female, near junction of Freeway Tk & Everard Tk, Wyperfeld Nat. Park, 4 July 1982, M. S. Harvey & B. E. Roberts (WAM 89/254-5); 1 male, 15 km WNW of Jaapet, Lake Albacutya Park, 3 July 1982, M. S. Harvey & B. E. Roberts (WAM 89/252). The specimens were collected "under bark of *Eucalyptus largiflorens* and *Eucalyptus camaldulensis*". There are several additional juveniles from the same or nearby localities which are tentatively alluded to, this species. — **NSW:** 1 female, 28.37 S 153.23 E, Mongaburra Lookout, nr. Minyon Falls, Whian, NNE of Lismore, 18 Nov.1983, D. C. F. Rentz & M. S. Harvey, Stop 54 (ANIC). — **QLD:** 1 female, 29.00 S 151.05 E, 18 km SSW. of Texas, 24 Nov.1983, D. C. F. Rentz & M. S. Harvey, Stop 66 (ANIC); 1 female, 28.56 S 151.08 E, 9 km SSW. of Texas, 24 Nov.1983, D. C. F. Rentz & M. S. Harvey, Stop 68 (ANIC); 1 female, 20.44 S 145.11 E, Burra, 2.X.1977, Rentz & White, Stop 24 (ANIC).

Tamopsis fickerti is common and widespread in southeastern Australia, but has not yet been reliably recorded from Victoria. The new records close the range of this species in Victoria and extend it into the semiarid region. The record from Burra in inland Queensland is also evidence of occurrence of *T. fickerti* in rather dry areas. *T. fickerti* is a typical bark-inhabiting species, living in crevices on tree trunks. Females of this species are easily recognized by the heart-shaped median plate in the epigyne.

Tamopsis perthensis Baehr & Baehr

Tamopsis perthensis Baehr & Baehr, 1987: 386.

New records: **WA:** 1 female, 4 km S. of Nannup, 3 Dec.1979, M. S. Harvey (WAM 89/257); 2 females, Mundaring Weir, 31°58′S 116°10′E, 16 Sept.1988, J. M. Waldock, M. Zabka (WAM 89/96, 89/101); 1 male, Parmelia, nr. Kwinana, 32°14′S 115°48′E, 14 Dec.1988, A. E. de Jong (WAM 89/103); 1 male, Ludlow Tuart Forest, J. Curr 4, 11.XII.1981 (WAM 89/108). The specimens were collected "on bark of *Eucalyptus*", "on smooth burnt (black) trunk of dead tree", "under bark", in "bush area, in jarrah tree", in "Malaise trap, replanted tuart. No burning".

This is perhaps the most common species in southwestern Australia which lives mainly on the bark of tree trunks, but has been found also on walls and fences.

Tamopsis marri Baehr & Baehr

Figure 13

Tamopsis marri Baehr & Baehr, 1989: 312.

New records: **NSW:** 4 females, ca. 8 km WNW. of Balranald, N.S.W., 5.11.1978, D. C. F. Rentz. Stop 7 (ANIC, CBM).

This species was originally described from two localities in southwestern Australia, where it has been found on Marri eucalypts. The new record extends the range of this species across southern Australia into western Riverina country. The species is recognized by the conspicuous black and light face pattern and by the female vulva having two heavily sclerotized bridges in middle. These are rather larger in the eastern specimens than in the western females. Otherwise, however, the specimens are very similar, so that we do not hesitate to assign them to *T. marri.*

Tamopsis occidentalis Baehr & Baehr

Figure 13

Tamopsis occidentalis Baehr & Baehr, 1987: 387; 1989: 319.

New records: **WA:** 2 males, 1 juvenile female, Rudall River Camp, 22.19S, 122.58E, 17 July 1988, A. E. de Jong (WAM 89/290-2); 1 female, Poonemerlarra Ck., 22.37S, 122.22E, 20 July 1988, A. E. de Jong (WAM 89/289).

This species was hitherto known from northwestern Australia south of Great Sandy Desert to about Shark Bay in the south. It is an arid country species that is collected almost exclusively on the trunks of river eucalypts. The present records are also from river gum, and they extend the range of this species considerably inland into the southern part of Great Sandy Desert.

Remarks

The three newly described species belong to three rather different groups, and altogether, they do not much help explain the phylogenetic relations and the difficult biogeographical questions within the Australian Hersiliidae, but they render them rather more difficult.

The evolution of the peculiar *platycephala*-group is still enigmatic, because this group is so far distributed in eastern Queensland and southwestern Australia only and the two Western Australian species are less closely related one to another than eastern *T. platycephala* and western *T. depressa*.

For the biogeographic problems raised by the occurrence of another species of the *queenslandica*-group in Western Australia (*T. distinguenda*) that is apparently more closely related to the eastern Australian *T. queenslandica* than to any western species, we have at present no conclusive explanation. We think, however, that the actual number and distribution of the low-eyed species of *Tamopsis* is even less known than those of the high-eyed species. The former live perhaps chiefly on smaller branches and are thus less easily and more randomly collected. We increasingly tend to believe that any conclusion on distribution in these species-groups is premature.

The *nanutarrae*-group which is perhaps the sister group of most other high-eyed species with exception of the northern *arnhemensis*-group is no longer restricted to Western Australia, but occurs also in western Victoria (*T. transiens*). This distribution suggests that the ancestor of this group immigrated into Western Australia from the southeast, right across the Nullarbour plain, in the same direction we assume for the other species-groups (Baehr & Baehr 1987).

The discovery of the formerly exclusive western species *T. circumvidens, T. marri* and of the new species *T. transiens* in western Victoria and adjacent southwestern New South Wales, respectively, is evidence of closer relations of the southeastern and western faunas, than we believed. In all three species, however, the eastern localities are in semiarid areas, and thus they are perhaps "mallee species" being restricted to the mallee zone that extends through most of southern Australia. This distribution pattern could be evidence of a very young, presumably late glacial invasion of dry adapted southeastern species into similar southwestern habitats.

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Geographical and stratigraphical distribution of the echinoid *Echinometra mathaei* (Blainville) in Western Australia

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Abstract

The distribution of the camarodont echinoid *Echinometra mathaei* (Blainville, 1825) in Western Australia is discussed. Being restricted to inhabiting intertidal reef platforms, the species does not lend itself to being readily fossilised. However, its discovery in a Late Pleistocene reef limestone at Cape Burney, south of the mouth of the Greenough River, provides the first geological record of the species in Australia. The stratigraphic record of this widespread Indo-West Pacific species suggests that, like a number of other echinoids, it has undergone an easterly spread across the Indian Ocean during the Neogene and probably reached south-west Australia during the Pleistocene following the initiation of the warm water Leeuwin Current.

Introduction

The camarodont echinoid *Echinometra mathaei* (Blainville, 1825) (Figure 1A) has been described (Clark 1946) as perhaps the most abundant living echinoid in the world. Very common on coral reefs and intertidal reef flats (Negretti *et al.* 1990), *E. mathaei* has a widespread Indo-West Pacific distribution, occurring in the Gulf of Suez, Red Sea, Persian Gulf, East Africa, Bay of Bengal, Australia, Papua New Guinea, Japan, Guam, Taiwan, Solomon Islands, Indonesia, American Samoa, East China Sea and French Polynesia (Mortensen 1943).

The aim of this paper is to document the geographical distribution of the species off the Western Australian coast and to record for the first time its occurrence in the fossil record in Australia. This is of particular importance in the light of a recent paper by Negretti *et al.* (1990) who document an eastward spread of this species across the Indian Ocean during the Neogene. The presence and absence of this species from different fossil deposits in Western Australia is dependent partly on the rate of this easterly spread, but also on the occurrence of suitable lithologies for preservation.

Present distribution of *Echinometra mathaei* off the Western Australian coast

In his analysis of the distribution of echinoderms in Australia, Clark (1946) records *Echinometra mathaei* off the Western Australian coast only at Shark Bay, the Abrolhos Islands and Rottnest Island. However in the collections of the Western Australian Museum specimens are present from a wide range of localities along and off the coast (Figure 2; Table 1), ranging between latitudes 12°S and 32°S. The most southerly record of the species in Western Australia is at Rottnest Island, where it occurs in shallow burrows on wide intertidal reef platforms (Hodgkin *et al.* 1959). Individuals here tend to reach larger sizes than those occurring in tropical populations (Pearse and Phillips

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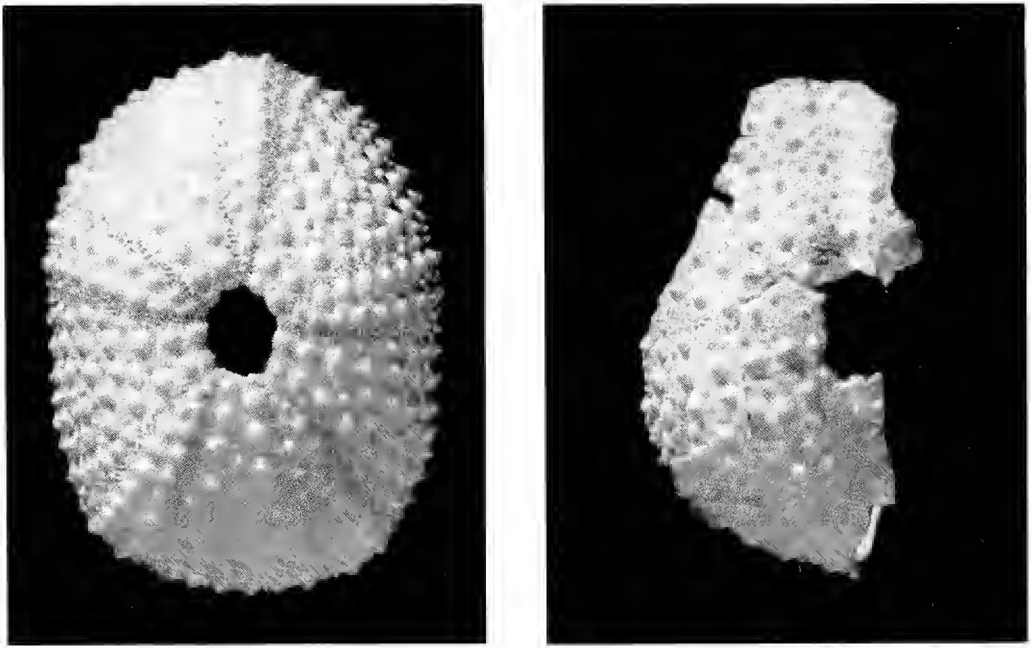

Figure 1 *Echinometra mathaei*. **A**, WAM 850-82, Recent, Barrow Island, W.A.; **B**, WAM 86.731, Late Pleistocene, Cape Burney, W.A.; both x1.

1968).The largest specimen recorded by Pearse and Phillips (1968) was an individual with a maximum test length of 67 mm. *E. mathaei* reaches a similar large size on the Houtman Abrolhos, one specimen in the collections of the Western Australian Museum (507-76) having a maximum test length of 68.5 mm. While *E. mathaei* populations off central Japan and the Gulf of Suez exhibit summer spawning periods, at Rottnest Island they reproduce throughout the year, probably on account of higher winter temperatures (Pearse and Phillips 1968).

Along the mainland coast *E. mathaei* does not extend as far south as Rottnest Island (32° 00'S), the southerly most mainland coastal record being of a single specimen from Port Gregory, some 450 km further north (28° 12'S). *E. mathaei* has also been found at Shark Bay (off Dorre Island); in the region of North West Cape at Coral Bay, Ningaloo Reef and Exmouth Gulf; around Barrow Island; and in the Dampier Archipelago region at Kendrew, Delambre and Rosemary Islands. However, *E. mathaei* has not been found on the nearshore Kimberley coast or reefs (L.M. Marsh, pers. comm.). Further off the coast the species has been collected from the Houtman Abrolhos (Teichert 1947), Rowley Shoals, Scott and Seringapatam Reefs (Marsh 1986), Cartier Island and Ashmore Reef (Table 1). Further out in the Indian Ocean *E. mathaei* has been found at Christmas Island and Cocos Keeling Islands.

Clark (1946) was surprised that he found only one record of the species from the northern Australian coast, a specimen from the Gulf of Carpentaria. The extent of the range of *E. mathaei* off the northern coast is not known. However, it is known to extend down the Queensland coast to Lord Howe Island. Specimens are present in the Western Australian Museum collections from Darnley, Murray and Yorke Islands in the Torres Strait; Green, Heron, Lizard and Reef Hook Islands in the Great Barrier Reef, Queensland, as well as from Lord Howe Island. Dakin (1987) records it as far south on the mainland as Coffs Harbour, New South Wales. Consequently, it is likely that wherever there is a suitable reefal or rocky habitat, in a region of moderately high hydrodynamic activity, *Echinometra mathaei* can be expected to be found, from Lord Howe Island on the eastern coast, around the northern coast of Australia, and south down the western coast to Rottnest Island.

Fossil distribution of *Echinometra mathaei* in Western Australia

In September 1985 Mr Alan Rowe collected two specimens (WAM 86.504, 86.731) of *Echinometra mathaei* from a fossil reef deposit in low cliffs at Cape Burney, about 200 metres south of the mouth of the Greenough River (28°52'S 114°38'E), near Geraldton. Although both specimens are incomplete (Figure 1B) there is no doubt that they belong to the living species. Like the living specimens from Rottnest Island and the Houtman Abrolhos, these two specimens are both relatively large, one (WAM 86.731: Figure 1B) probably having had an original test length in the region of about 70 mm.

The outcrop from which the specimens were collected is about 2m above present day sea level and forms part of the Tamala Limestone. The unit probably formed as a small, offshore patch reef over a pre-exisiting calcarenite (G.W. Kendrick, pers. comm.) and closely resembles the contemporaneous Rottnest Limestone that outcrops on the southern shores of Rottnest Island at Fairbridge Bluff. From its geological setting, the nature of the accompanying mollusc fauna and its degree of weathering, it is likely that the Cape Burney deposit was one of a number formed during the Late Pleistocene along the western Australian coast (Teichert 1947, 1967; Fairbridge 1954; Playford 1988; Kendrick *et al.* 1991), probably during the Last Interglacial (Oxygen Isotope Substage 5e)(G.W. Kendrick, pers. comm.). In addition to *E. mathaei* two other echinoid species occur in this unit: *Protenaster australis* (McNamara 1985) and *Phyllacanthus irregularis*. The former species is represented by three specimens, the latter by a single interambualcral plate and a number of radioles. *Phyllacanthus irregularis* has hitherto not been reported from the fossil record.

A number of Western Australian formations that range in age from Early Miocene to Middle Pleistocene contain reasonably large echinoid faunas. However despite extensive searching over the last decade *Echinometra* has not been found in any of these deposits. For instance material collected from a large number of boreholes in the Perth Basin that derive from shallow marine deposits of the Pliocene-Early Pleistocene Ascot Formation (Kendrick *et al.* 1991) have yielded abundant echinoid remains, in particular species of *Echinocyamus* and *Ammotrophus*. Yet no evidence of *Echinometra mathaei* has been found. Similarly, it has not been found in the Middle Pleistocene Carbla Oolite that outcrops in Shark Bay (Logan *et al.* 1970) despite the presence of shallow water echinoids such as *Breynia desorii* Gray and *Peronella ricta* Gregory. However, these

Table 1 The recent distribution of *Echinometra mathaei* around Western Australia

Lat.(S) / Long.(E)	Locality	No. of specimens
10°30' 105°35'	Christmas Island	35
12°05' 96°55'	Cocos Keeling Islands	4
12°15' 123°00'	Ashmore Reef	3
12°32' 123°33'	Cartier Island	1
14°05' 122°11'	Scott and Seringapatam Reefs	2
17°30' 119°00'	Rowley Shoals	5
20°33' 116°32'	Dampier Archipelago	7
20°46' 115°24'	Barrow Island	8
21°47' 114°10'	North West Cape	4
22°05' 114°15'	Exmouth Gulf	1
22°40' 113°40'	Ningaloo Reef	22
23°07' 113°45'	Coral Bay	4
25°00' 113°07'	Dorre Island, Shark Bay	5
28°12' 114°15'	Port Gregory	1
28°35' 113°40'	Houtman Abrolhos	31
32°00' 115°30'	Rottnest Island	11

infaunal burrowers would not have shared the same habitat as *E. mathaei*. Coral-dominated assemblages from the Shark Bay Pleistocene, within which the species might be expected to occur, have not been adequately collected. The absence of *E. mathaei* from some of these older units may reflect, in part, the lack of a suitable habitat for the species. Its absence, despite extensive searching, from the Late Pleistocene Rottnest Limestone on Rottnest Island suggests that during the Late Pleistocene it did not range as far south as it does today on the offshore islands. However, along the mainland coast at this time it extended further south that it does today.

Its occurrence with *Protenaster australis* at Cape Burney is interesting, because today the only site at which the tropical *E. mathaei* occurs with the southern Australian *P. australis* is on Rottnest Island. While the Late Pleistocene occurrence of *E. mathaei* at Cape Burney is the southerly most known record of the species along the mainland coast, this site represents the most northerly known occurrence of *P. australis*. The slight overlap in geographic ranges of these two species on the mainland coast in the Late Pleistocene is in contrast to the present day situation, with the ranges of the two being widely disjunct, the range of *P. australis* having contracted to the south.

The shift from predominantly siliciclastic to mainly carbonate sedimentation along the inner shelf of southwestern Australia during the Middle Pleistocene (Kendrick *et al.* 1990), as represented by the formation of the Tamala Limestone, was possibly associated with a current/temperature regime that ought to have been favourable to the presence in local waters of *E. mathaei*, at least during transgressive episodes. This has been interpreted as reflecting the initiation of the warm water Leeuwin Current (Kendrick *et al.* 1991) during the Middle Pleistocene. Severe oceanic cooling during terminal Pleistocene Stage 2 in the south-east Indian Ocean (Prell *et al.* 1980) probably caused a

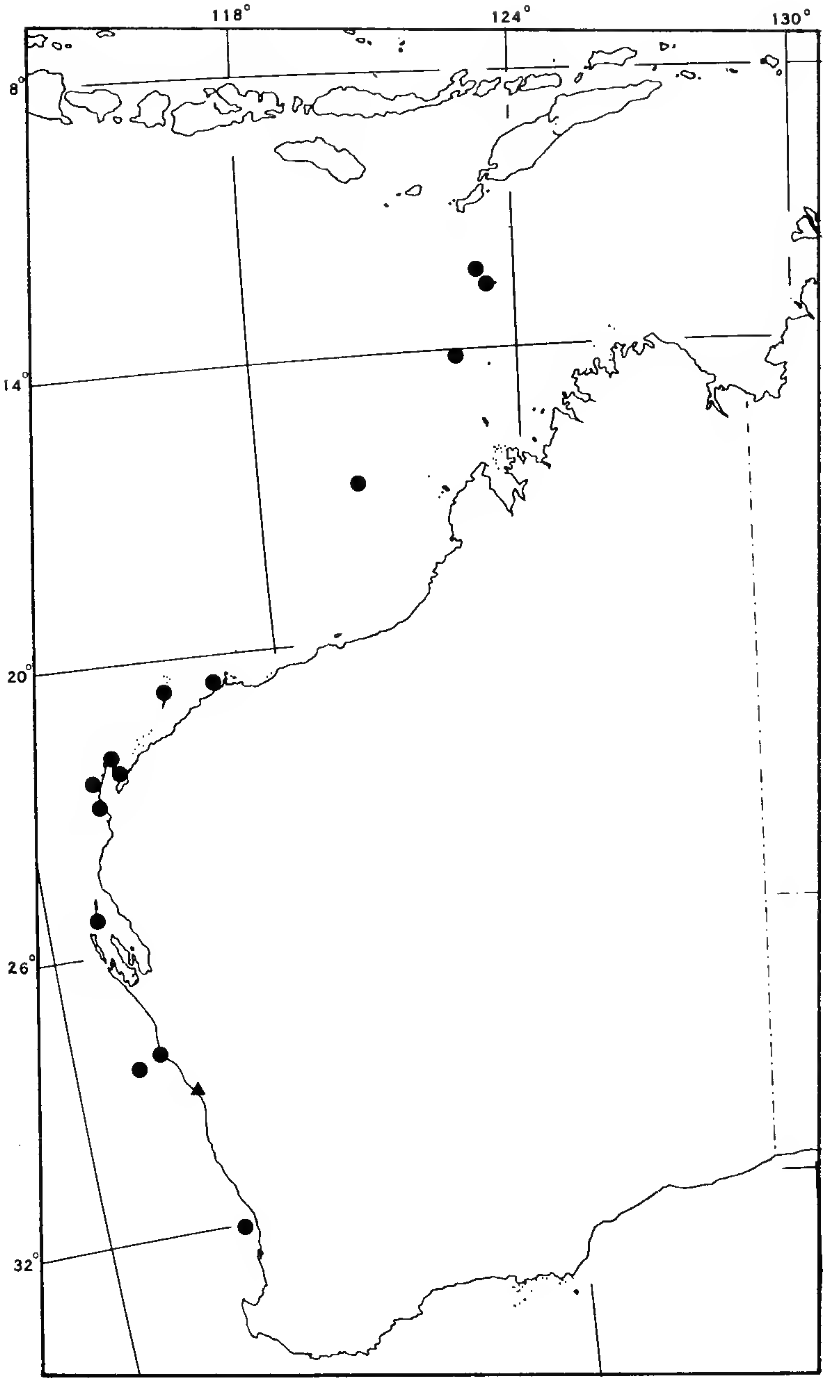

Figure 2 Map of Western Australia showing the distribution of living (●) and fossil (▲) *Echinometra mathaei.*

Table 2 Times of known occurrence of *Echinometra mathaei* in the Mediterranean Sea, Red Sea and eastern Indian Ocean.

Mediterranean Sea[1]	Red Sea[2]	Eastern Indian Ocean[3]
Miocene	Miocene	—
—	Pliocene	—
—	Pleistocene	Pleistocene
—	Recent	Recent

[1] Negretti *et al.* (1990); [2] Ali 1985; Brighton 1931; [3] W.A.Museum collections

contraction of range toward the equator of temperature-sensitive, tropical and subtropical species, such as *E. mathaei*. If this were the case, then the modern stocks of this, and other such species, that now inhabit extra-tropical waters, would represent post-Pleistocene re-colonisation from the north, presumably as plankton via the Leeuwin Current. It is known that *E. mathaei* is a planktotrophic species and, in this part of Western Australia, breeds all year (Pearse and Phillips 1968). The absence of *E. mathaei* from the Late Pleistocene Rottnest Limestone, despite it being a typical lithology for the species, suggests that at this time the species had spread no further south than the mouth of the Greenough River.

The present day concentration of *E. mathaei* at the West End of Rottnest Island, and its apparent absence from the opposite end, is considered to reflect the effect of the Leeuwin Current. NAOO satellite imagery of the Leeuwin Current (see cover photograph of *The Leeuwin Current: an influence on the coastal climate and marine life of Western Australia*: Jl. Roy. Soc. W.A., vol. 74) clearly shows a tongue of the Leeuwin Current extending past the western end of Rottnest Island, and cooler water of the West Australian Current wedging north between this tongue of the Leeuwin Current and the coastline. It is probably this cooler, near coastal water originating from northerly flowing cooler currents, that is responsible for the absence of *E. mathaei* along coastal shorelines between Perth and Port Gregory.

Neogene dispersal of *Echinometra mathaei* across the Indian Ocean

In a recent restudy of *Echinometra miocenica* Loriol from the Early Miocene of southern France, Negretti *et al.* (1990) found no evidence to support the view that this species was any different from the living species *E. mathaei*. Consequently they placed *E. miocenica* in synonymy with *E. mathaei*. Thus this species has existed for about 17 million years. However, of particular interest is evidence from the fossil record that indicates a changing distribution of this species through the Neogene.

The earliest, Early Miocene, specimens of *E. mathaei* occur in the south of France at Sériège, Hérault and in northern Sardinia in the Mediterranean Sea, and along the Suez Gulf and Red Sea coasts of Egypt (Negretti *et al.* 1990). However, as Negretti *et al.* (1990) have reported, the range of *E. mathaei* retracted eastwards into the Pliocene as it became locally extinct in the Mediterranean Sea at the time of the Messinien crisis during the Late Miocene. There is ample evidence, however, that it persisted in the Red Sea, having been recorded in Pliocene and Pleistocene deposits at Mersa Alam along the Red Sea coast of Egypt (Ali 1985) and in the Pleistocene of Farsan Island, south of the Red Sea (Brighton 1931).

Its appearance in Late Pleistocene deposits at the eastern end of the Indian Ocean implies that between the Miocene and Pleistocene it spread eastwards from its centre of origin in the Mediterranean region to the eastern Indian Ocean and into the western Pacific (Table 2). Negretti *et al.* (1990) report a similar pattern of migration for *Echinoneus cyclostomus* through the Neogene. McKinney *et al.* (1992) have likewise described the same eastwards migration of nine genera of echinoids across the Indian Ocean during the Tertiary.

Conclusions

The presence of *E. mathaei* at Cape Burney during the Late Pleistocene, outside of its modern day range along the coast, is probably indicative of past oscillations in the strength of the Leeuwin Current, as the present day geographical distribution of the species appears to be closely linked to the course of the Leeuwin Current. It has been suggested (Collins *et al.* 1991) that the existence of Late Pleistocene coral reefs on the Houtman Abrolhos, at Cape Burney and on Rottnest Island reflects a period of more vigorous Leeuwin Current activity at that time than at present (Collins *et al.* 1991). While it could be argued that the apparent absence of *E. mathaei* in the Rottnest Limestone, and the more northerly extension of the cool water spatangoid *P. australis* during the Late Pleistocene implies that the intensity of the Leeuwin Current was less then than it is now off the coast, the existence of Late Pleistocene coral reefs on Rottnest Island does not support this view. The presence of *E. mathaei* at Cape Burney during the Late Pleistocene, argues for perhaps a stronger influence of the Leeuwin current along the mainland coast during the Late Pleistocene, because today along the mainland coast *E. mathaei* extends only as far south as Port Gregory, some 80 km north of Cape Burney.

It is likely that *E. mathaei* would not have existed this far south during glacial stages 2,4, and 6, when sea temperatures were appreciably lower than at present (G.W. Kendrick pers. comm.). It probably persisted farther north in warmer, tropical waters at these times. The initiation of the Leeuwin Current, probably in the Middle Pleistocene (Kendrick *et al.* 1991) may well have been the event that allowed *E. mathaei* to extend south from its normal tropical range, down the south-west Australian coast. Initially, during the Late Pleistocene, it appears to have only reached as far south as Cape Burney (28° 52'S). Following its probably northwards contraction of range during the last glacial stage, it has spread further south with the Holocene rejuvenation of the Leeuwin Current, reaching Rottnest Island (32° S). The geographical range of the species is therefore likely to have been appreciably different during periods of transgressions from its range during regressions.

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Oniscidea (Crustacea, Isopoda) from caves of Cape Range in Western Australia. I. The genus *Buddelundia.*

H. Dalens*

Abstract

Oniscidae, Philosciidae and Armadillidae have been collected in caves of Cape Range. Armadillidae of the genus *Buddelundia* are the most represented with five species and one subspecies. Four of them new to science are described. None is a true troglobite.

Introduction

For some years explorations have been carried out in caves of the semi-arid Cape Range in Western Australia (Humphreys 1990, 1991; Humphreys, Adams & Vine 1989). The Oniscidea crustaceans collected during 1988 and 1989 belong to the three families Oniscidae, Philosciidae and Armadillidae. This first note deals with the genus *Buddelundia* (Armadillidae) which is, by the number of species, the best represented in caves. This genus is well distinguished by its pleopods which are coadapted and fit together except the fifth which is without pseudotracheae and hidden by the fourth This form is unique among Oniscidea and a good account of it, at the same time as a guide of the described species, was given by Wahrberg (1922, p.198-200 & 203-204).

Numbers with a C- prefix denote caves in the Cape Range Karst region. Holotypes of new species and the greater number of paratypes are lodged in the Western Australian Museum, Perth (WAM); specimens prefixed by the letters DH are in the personal collection of the author.

Systematics

Buddelundia cinerascens (Budde-Lund, 1912)

Figure 1

Armadillo (Buddelundia) cinerascens Budde-Lund, 1912, p.26, fig.IX.

Buddelundia cinerascens .-Wahrberg, 1922, p.204 & 229.

Buddelundia cinerascens .-Vandel, 1973, p.148.

Buddelundia cinerascens .-Bunn & Green, 1982, p.147 & 149.

Syntypes: Budde-Lund coll., British Museum (Natural History), 1921 10.18.2464-2465, 1 male & 1 female; Wahrberg coll., Swedish Museum of Natural History, n°6189, 1 male & 2 broken specimens.

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Figure 1 *Buddelundia cinerascens* (Budde-Lund), whole animal in lateral view.

Other material examined: C-118, 12.VIII.1989, WAM 51-91 1 female.

This species was described from Rottnest Island (Budde-Lund, 1912) and later found on Carnac Island (Wahrberg, 1922) both in Western Australia. It is not necessary to redescribe this species, well described by Wahrberg and it is only illustrated here (fig.1). This species is not a troglobite and it was collected in a "pitfall trap placed around the outside of the doline containing the cave entrance" (Humphreys pers. comm.).

Buddelundia grisea sp.nov.

Figures 2-9

Holotype

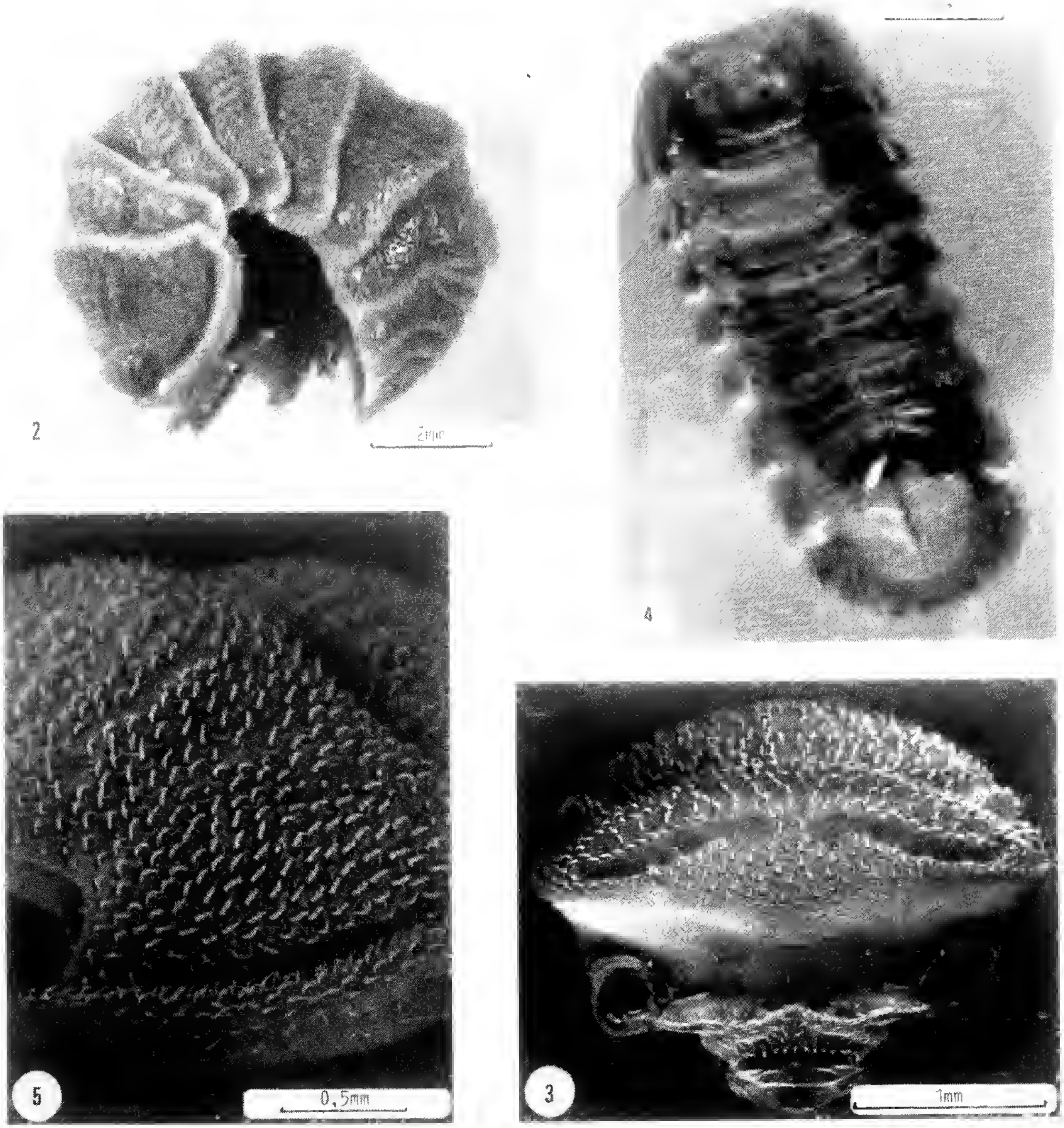
C-162 (= Rock Bench Cave), 12.IX.1988, WAM 972-88 1 male.

Paratypes

C-15, 25.VI.1989, WAM 52-91 1 juvenile; C-21, 10.VII.1989, WAM 53-91 1 female; C-60, 9.VII.1989, WAM 54-91 1 female; C-64 (= Shot-Hole Tunnel), 27.VI.1989 & 3.VII.1989, WAM 55-91, 56-91 & 57-91 1 male and 7 females, DH 1 male and 3 females; C-68, 26.VI.1989, WAM 58-91 2 males and 1 female, DH 1 male; C-96 (= Anomaly Cave), 30.VI.1989, WAM 59-91 1 female; C-118, 8.IX.1988, WAM 964-88 1 female; C-156, 23.VI.1989 & 16.VIII.1989, WAM 60-91, 61-91, 62-91 & 63-91 4 males; C-162 (= Rock Bench Cave), 6.IX.1988, WAM 469-92 1 male; 12.IX.1988, WAM 64-91 1 male, DH 1 male and 1 female; 20.VI.1989, 21.VI.1989, WAM 65-91 & 66-91 5 males & 5 females, DH 2 males & 2 females.

Diagnosis

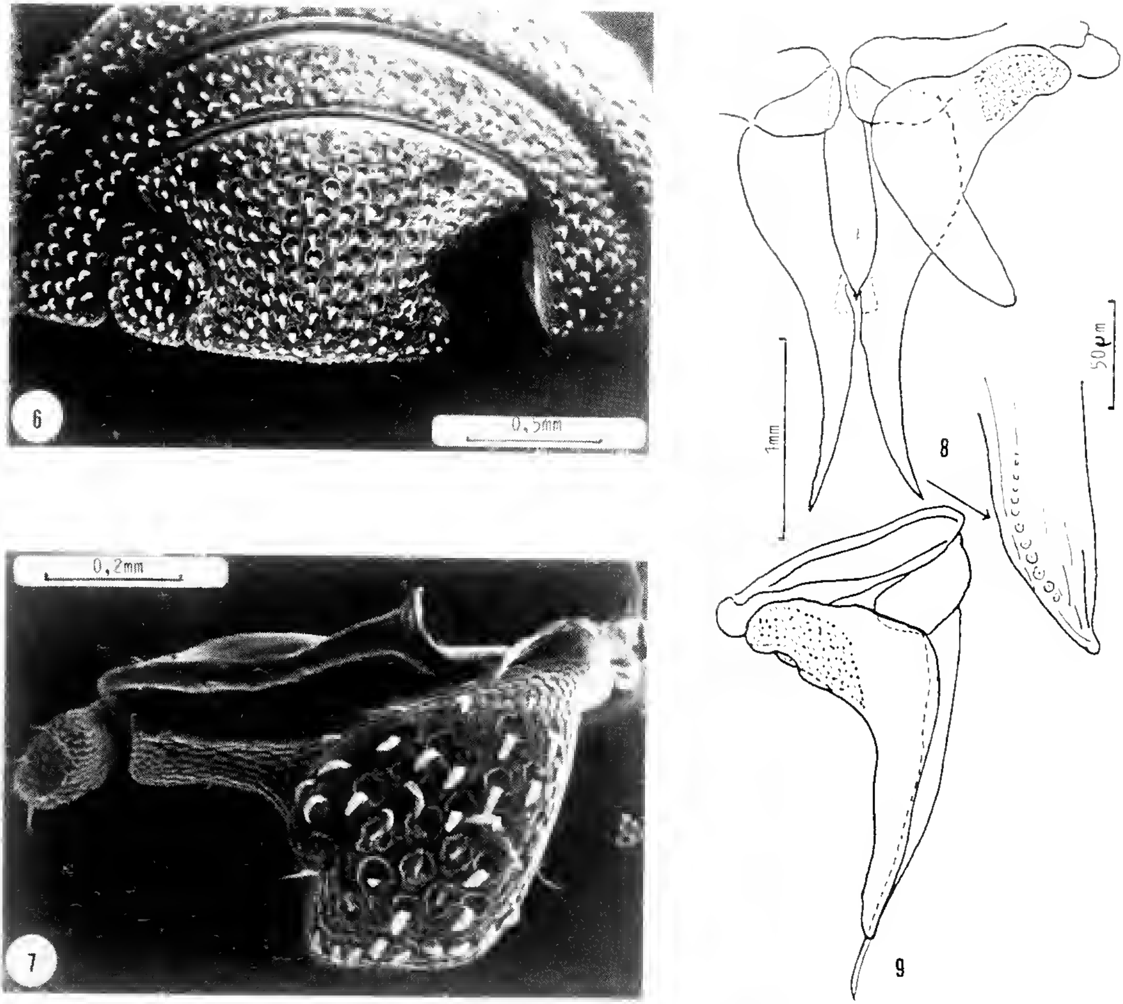
Conglobating species with lateral sides of the body vertical. A secondary frontal line well developed, while frontal line is discrete. Exterior lobe of the schisma larger than



Figures 2-5 *Buddelundia grisea* sp.nov. **2:** whole animal in lateral view; **3:** cephalon in frontal view (S.E.M.); **4:** whole animal in ventral view; **5:** surface of the first peraeonite (S.E.M.).

internal. *Sulcus arcuatus* on first peraeon segment and interlocking system present as far as the third pleon segment.

By its frontal line, the parallel pleura of the fifth pleonite and the relative size of external and internal lobes of the first peraeon segment, *B. grisea* is to be compared with *B. bulbosa* Wahrberg, 1922 and *B. frontosa* (B.-L., 1912). From the first, *B. grisea*



Figures 6-9 *Buddelundia grisea* sp.nov. **6:** telson (S.E.M.); **7:** right uropod (S.E.M.); **8:** first male pleopod; **9:** second male pleopod.

differs in many characters and in particular by the shape of both the secondary frontal line and frontal line, by the *sulcus arcuatus* being more developed in *B. grisea*, by the sinuosity of the posterior margin of the first peraeon segment being more marked in *B. bulbosa* and by the shape of the telson and uropods. From *B. frontosa*, the differences are related to the secondary frontal line and frontal line, the shape of the anterior parts of first peraeon epimeron which are slightly turned up in *B. grisea* and also the telson and uropods which are different between the two species.

Description

Size of holotype 10.6x4.2mm. Lead grey colour with sites of muscle attachment paler. Black eyes with 15 ommatidia. Conglobating (fig.2) with lateral sides of the body vertical. Cephalon (fig.3) with frontal line discrete and which disappears in the middle part, where it is just concave. Secondary frontal line well developed and overhanging vertex. Lateral ocular tubercles present. Clypeal line split and clypeal lobes rounded and horizontal.

First peraeon segment with posterior margin sharp sinuated. Lateral margins slightly thickened and turned up. *Sulcus arcuatus* present. Schisma with external lobe protruding backward compared to internal lobe. A discrete groove extends anterior to the schisma. Process well developed on ventral surface of second peraeonite epimeron; indications of folds on the ventral face of fourth to seventh peraeon segments (fig.4).

Well developed fold belonging to interlocking system, present on ventral face of pleura of third pleon. Pleura of fifth segment parallel. Telson hour-glass shaped with distal part short and with apex slightly rounded (fig.6).

Body smooth but covered by setae in close order. These setae curved backwards and, in the paramedian part of peraeon, arranged in rib-like parallel rows (fig.5). A1 (antennule) three-jointed, with about 10 aesthetascs on the apex of the distal article. A2 (antennae) with two jointed flagellum, ratio distal joint / proximal joint = 2.

Mx1 (first maxilla) with 10 teeth. Uropod with distal part of protopodite rectangular and minute exopodite (figs 6 & 7). No sexual dimorphism apparent in peraeopods. Pleopods 1 and 2 of male as in figs 8 & 9.

Distribution

This species is known only from caves of Cape Range but it is not considered to be a troglobite as there is no depigmentation, nor anophthalmy or elongation of appendages. It will probably be found outside caves when investigated. It is a facultative troglobite like *B. albomarginata* Wahrberg, 1922 described from Broome in Western Australia but often found in caves on the Nullarbor Plain in South Australia.

Derivation of name

From the old german language *gris*, in allusion to its coloration.

Buddelundia hirsuta sp.nov.

Figures 10-16

Holotype

C-162 (= Rock Bench Cave), 10.IX.1988, WAM 967-88 1 male.

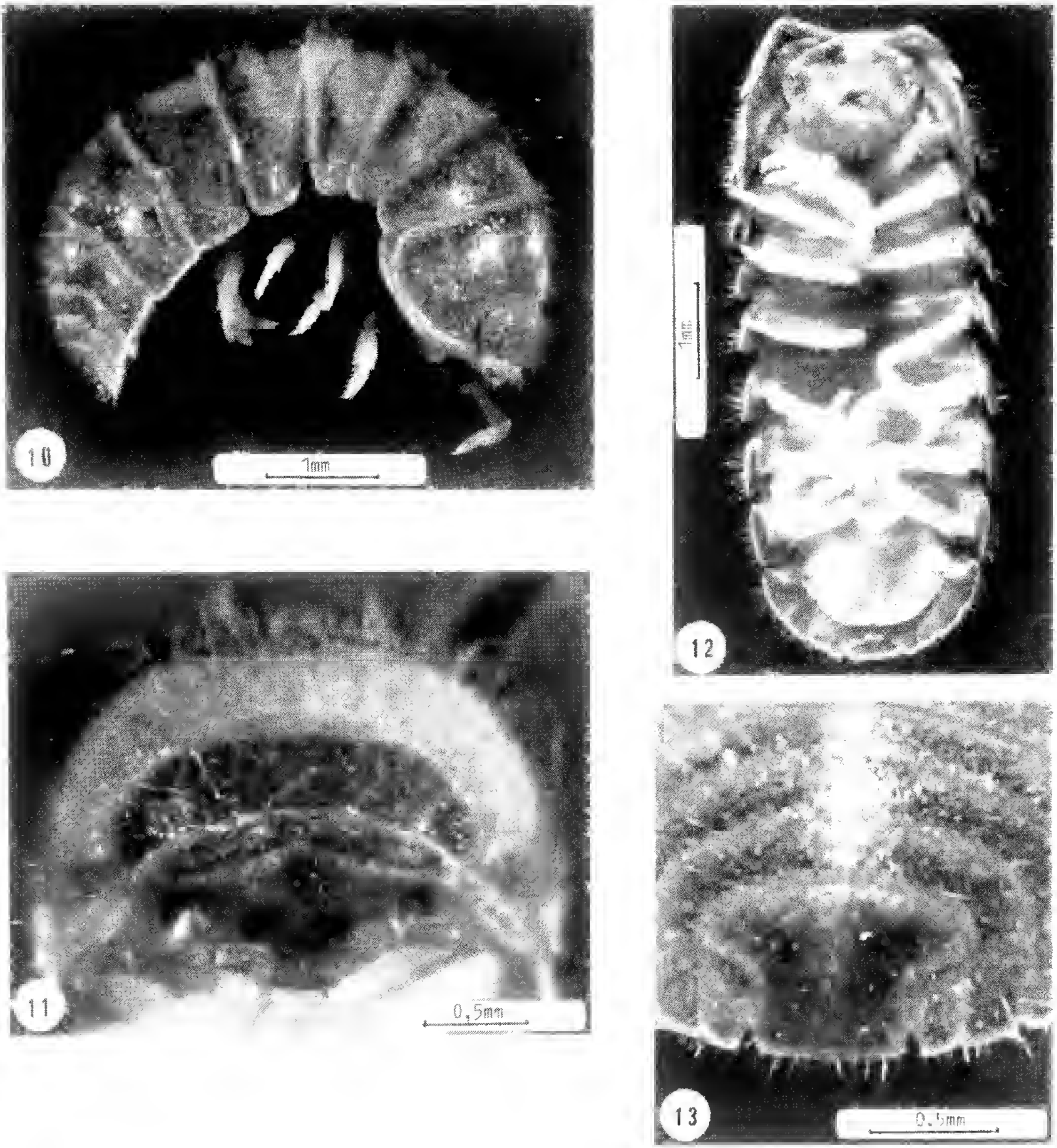
Paratype

C-118 ,18.VIII.1989, pitfall trap near entrance, WAM 67-91 1 female.

Diagnosis

Frontal line and secondary frontal line well developed. A slight groove in place of *sulcus arcuatus*. Internal lobe of the schisma greater than external. Interlocking system present on all the peraeon segments and on the third segment of pleon.

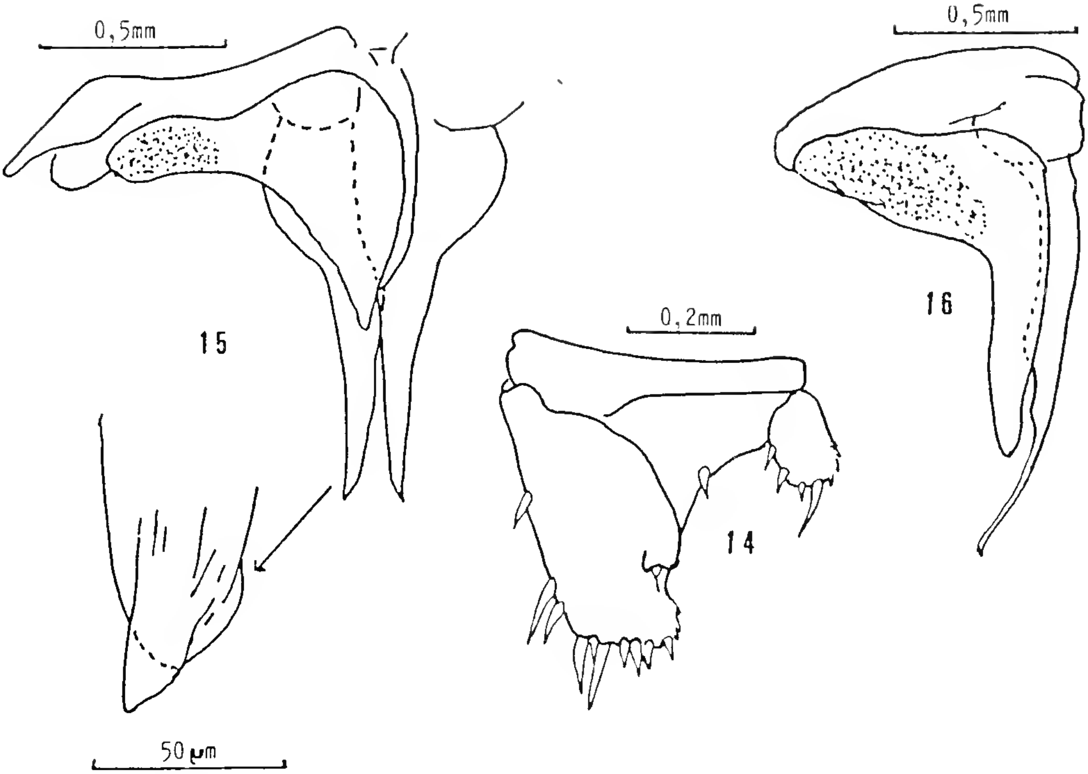
This species is near *B. monticola* (B.-L., 1912) and closest to *B. grisea*.



Figures 10-13 *Buddelundia hirsuta* sp.nov. **10:** whole animal in lateral view; **11:** cephalon in frontal view; **12:** whole animal in ventral view; **13:** telson and uropods.

From *B. monticola* it differs in the shape of the secondary frontal line, of the lateral margin of the first peraeon segment, of the protopodite of uropod, by the hairy appearance and by the pigmentary patterns.

From *B. grisea*, it differs in the hairy appearance, in the sinuosity of the posterior



Figures 14-16 *Buddelundia hirsuta* sp.nov. **14:** left uropod; **15:** first male pleopod; **16:** second male pleopod.

margin of the first peraeon segment, and in the shape and respective size of external and internal lobes of the schisma of the first peraeon segment.

Description

If the specimens are adult, this species is small for the genus *Buddelundia*. Size 6.9x2.9mm. Lead grey colour with places of muscular attachment paler. Clear spot on each epimeron of peraeon. Black eyes with 13-14 ommatidia.

Congoblating species with lateral sides of body vertical (fig.10). Cephalon with secondary frontal line well developed, in arc of a circle (fig.11). Frontal line distinct and uninterrupted. Lateral ocular tubercles absent. Clypeal line uninterrupted and clypeal lobes rounded and horizontal.

First peraeon segment with posterior margin not sinuate and with lateral margins slightly thickened and revolute. *Sulcus arcuatus* not well differentiated but a slight groove present. Schisma with internal lobe greater than external. Internal process of second peraeon segment well developed. Internal face of epimera with processes progressively more developed from third to seventh peraeon segment (fig.12).

Pleuron of third pleon segment with distinct process in relation to interlocking system. Pleuron of fifth segment parallel. Telson with apex subrectangular (fig.13).

Body smooth with long, upright setae making animal seem hairy. A1 with 7 to 8 aesthetascs at tip. A2 with two jointed flagellum; ratio distal joint/proximal joint = 2.9. Mx1 with 10 teeth. Uropod with distal part of protopodite rounded and very minute exopodite (fig.14).

Male pleopods 1 and 2 (figs 15&16) without distinctive features.

Distribution

This species is not a troglobite as it was collected also in pitfall trap on the surface near C-118.

Derivation of name

From the latin *hirsutus* in allusion to the upright setae which made the animal hirsute.

***Buddelundia humphreysi* sp.nov.**

Figures 17-23

Holotype

Learmonth near Cape Range, outside of cave, 1.VII.1989, WAM 68-91 1 male.

Paratypes

Learmonth, outside of caves, 5.IX.1988, WAM 984-88 1 female; 9.IX.1988, WAM 985-88 3 males and 10 females, DH 3 males and 5 females; 1.X.1988, WAM 986-88 1 male, WAM 987-88 1 male and 2 females, DH 1 female; C-162 (= Rock Bench Cave), 6.IX.1988, WAM 963-88 1 female; C-203, 19.VII.1989, WAM 69-91, 70-91 & 71-91 4 females, DH 1 female; C-328, 28.VIII.1989, WAM 72-91, 73-91, 74-91 & 75-91 5 males and 3 females, DH 2 males and 1 female.

Diagnosis

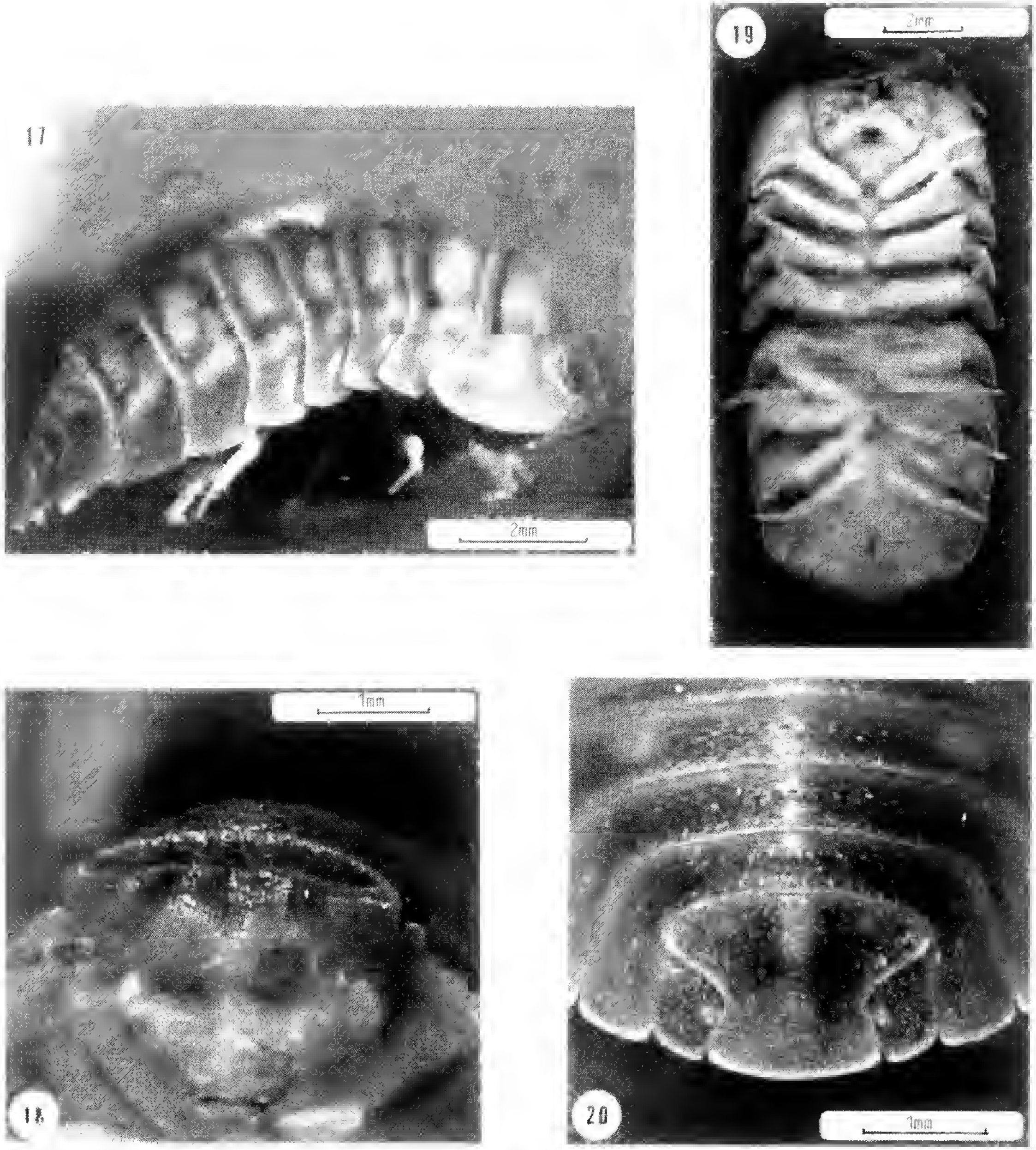
Light brown-coloured body with two clear spots on every peraeonite. Lateral sides of the body oblique. Frontal line and secondary frontal line uninterrupted. *Sulcus arcuatus* absent and external lobe of the schisma greater than internal. Interlocking system restricted to I and II peraeonites.

This species differs from *B. binotata* (B.-L., 1912) , *B. laevigata* (B.-L., 1912) and *B. sulcata* (B.-L., 1912) in many characters, particularly in that the *sulcus arcuatus* is absent in *B. humphreysi* and present in the three other species.

Description

Size of 13.4x6.5mm. for the holotype and 15.7x6.5mm. for the biggest female. Colour light brown, with two clear spots on every peraeon segment on both sides of uniformly coloured central part of body. Dark spot between uniformly coloured light grey brown (fig.17) tergite and epimeron. Pleon and telson uniformly coloured. Black eyespots with 18-19 ommatidia.

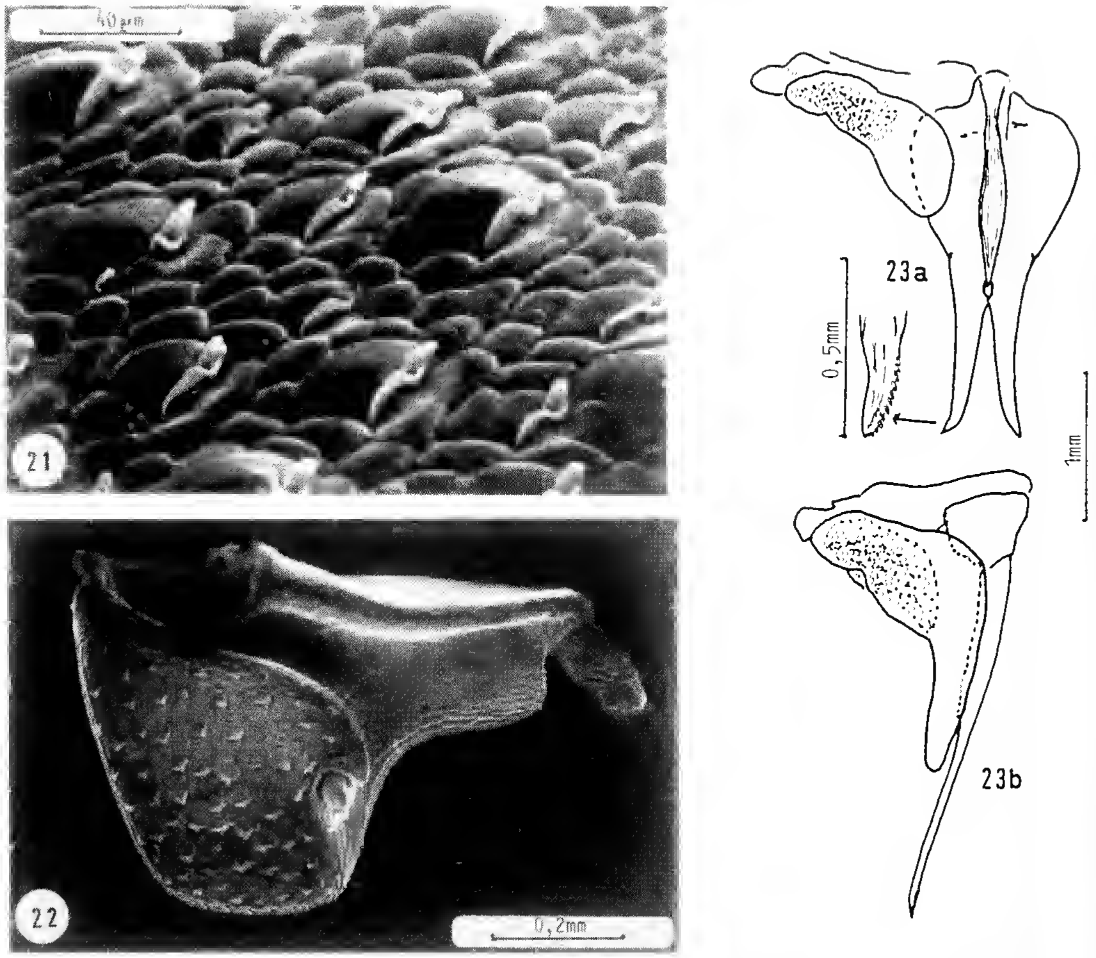
Conglobating species with lateral sides of body oblique. Cephalon (fig.18) with uninterrupted secondary frontal line not raised above level of vertex. Frontal line



Figures 17-20 *Buddelundia humphreysi* sp.nov. **17:** whole animal in lateral view; **18:** cephalon in frontal view; **19:** whole animal in ventral view; **20:** telson and uropods.

distinct and uninterrupted. Very small latero-ocular tubercles. Clypeal line divided and depressed medially; clypeal lobes subrectangular and horizontal.

First peraeon segment with posterior margin progressively sinuate. Lateral margins thin. No *sulcus arcuatus*. Schisma with external lobe greater than internal. Internal



Figures 21-23 *Buddelundia humphreysi* sp.nov. **21:** surface of the first peraeonite (S.E.M.); **22:** left uropod; **23:** first **(23a)** and second **(23b)** male pleopods.

process of the second peraeon segment moderately developed. Interlocking system restricted to first two peraeon segments (fig.19).

Pleura of fifth pleon segment parallel; telson hour-glass shaped with apex margin convex (fig.20).

Body smooth, without setae (fig.21). A1 with about 7 aesthetascs apically. A2 with two jointed flagellum; ratio distal joint/proximal joint = 1.2. Uropod with distal part of the protopodite slightly rounded, exopodite reduced (fig.22).

Distribution

This species is not troglobitic and is common outside caves.

Derivation of name

After Dr W.F. Humphreys who collected many of these new species.

Buddelundia zebricolor sp.nov.

Figures 24-32

Holotype

Outside of C-167, 16.IX.1988, WAM 977-88 1 female

Paratypes

Outside of cave C-18 (= Dry Swallet Cave), 21.IX.1988, WAM 983-88 1 female; outside of cave C-118, 14.X.1988, WAM 973-88 1 female; C-15, 25.VI.1989, WAM 76-91 1 female; C-102, 9.VII.1989, WAM 77-91 1 male; C-106 (= Shot Pot Cave), 21.VI.1989, WAM 78-91 2 males, DH 1 male; C-163 (= Wanderer's Delight Cave), 29.VI.1989, WAM 79-91 1 male; C-177, 7.VII.1989, WAM 80-91 1 male; C-207 (= Two Hundred Cave), 16.VII.1989, WAM 81-91 1 female; C-219, 30.VI.1989, WAM 82-91 1 male; C-222, 30.VI.1989, WAM 83-91 1 female; C-224, 30.VI.1989, WAM 84-91 1 female ; C-252, 22.VII.1989, WAM 85-91 1 female; C-254, 7.VIII.1989, WAM 86-91 1 female, DH 1 female.

Diagnosis

Lateral sides of the body oblique. Only the frontal line is present and uninterrupted. No *sulcus arcuatus* and external lobe of the schisma greater than internal. Interlocking system includes all the peraeon segments.

Buddelundia zebricolor belongs to the primitive group of *Buddelundia* which lack a secondary frontal line. Within this group it is closest to *B. albomarginata* Wahrberg, 1922 and *B. tomentosa* (B.-L., 1912).

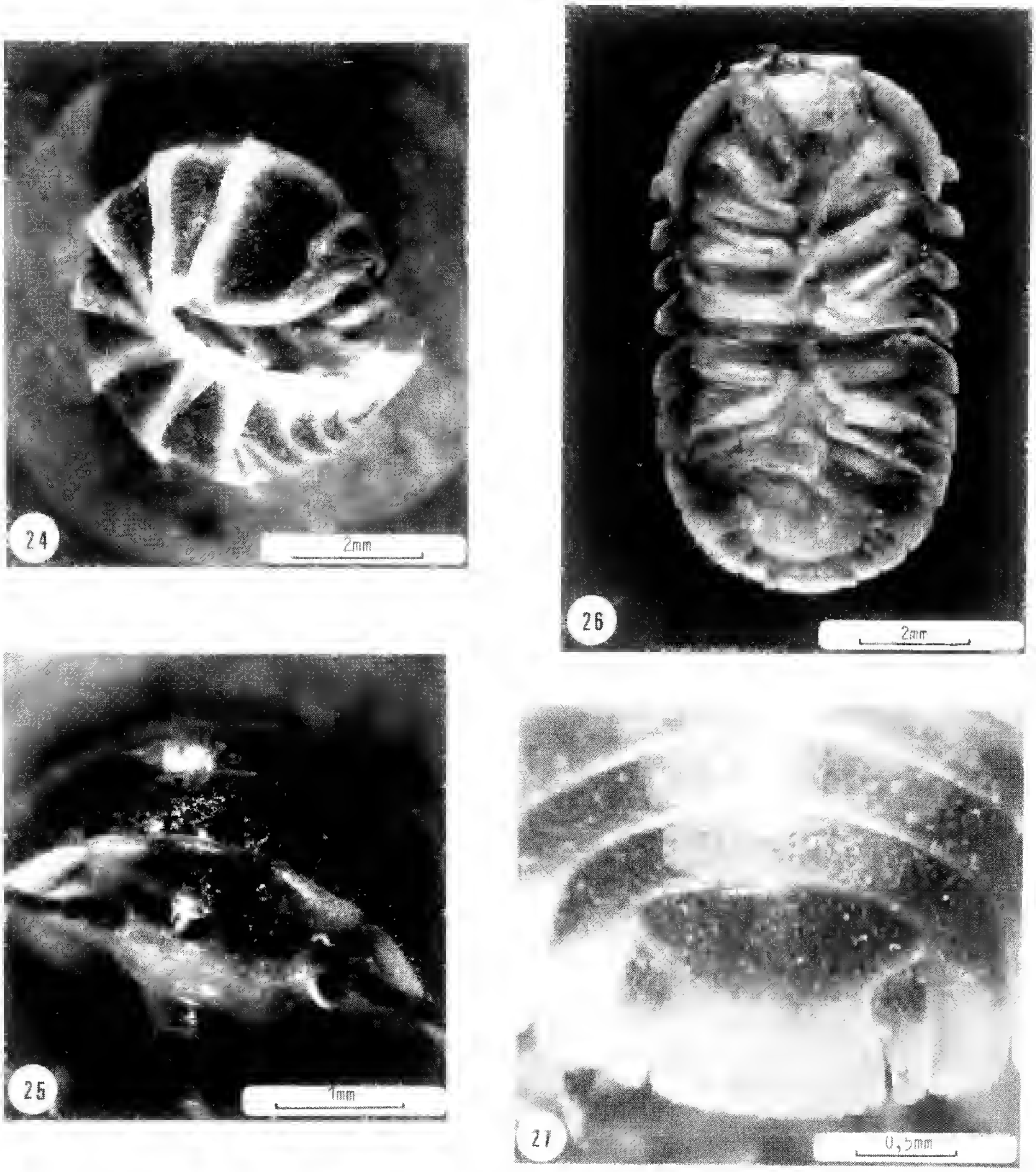
It differs from *B. albomarginata* by the tegumentary surface having setae which are absent in *B. albomarginata*. The shape of the schisma is also different and the external lobe, is greater in *B. albomarginata*, and smaller in *B. zebricolor*. The shape of the telson shows an apex wider in *B. zebricolor* than in *B. albomarginata*; while the protopodite of uropod is triangular in *B. zebricolor*, subquadrangular in *B. albomarginata*. The posterior margin of the first peraeon segment is barely or not sinuate in *B. zebricolor* and angularly sinuate in *B. albomarginata*.

It differs from *B. tomentosa* by the shape of the frontal line which is straight in *B. zebricolor* and curved backwards on the vertex in *B. tomentosa*. Moreover this line is higher on the vertex in *B. zebricolor* than in *B. tomentosa*. The tegumentary surface has erect setae in *B. tomentosa*; curved setae in *B. zebricolor*. The lateral margins of the first peraeon segment are thicker in *B. tomentosa*; the lateral sides of the peraeon segments are more vertical in that species and oblique in *B. zebricolor*.

Description

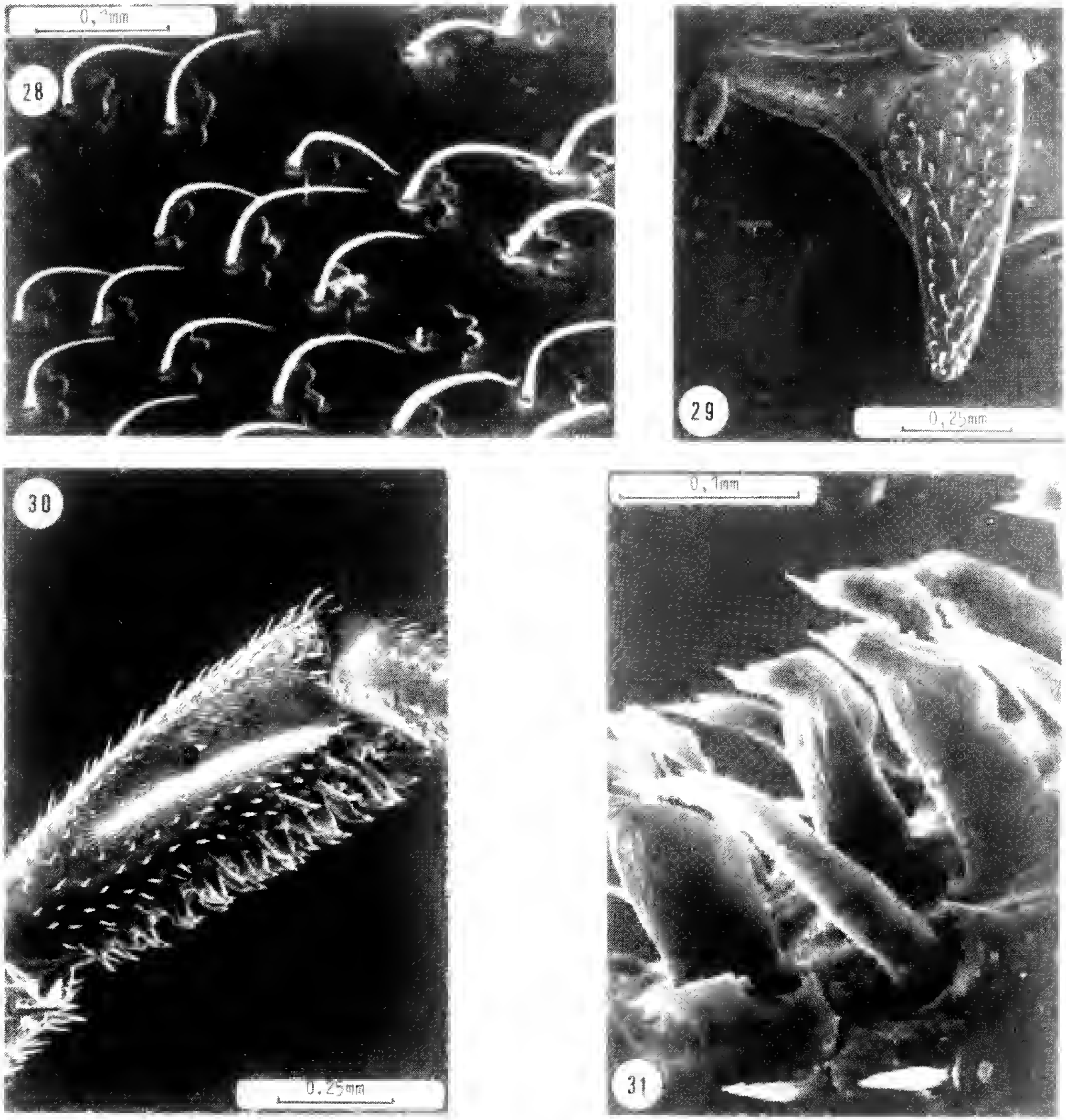
Size of holotype 10.2x5.3mm. Generally deep grey colour, posterior and lateral margins of peraeon segments, pleura of pleon segments and apex of uropod protopodite and of telson white, giving animal pale transverse stripes and white border (fig.24). Black eyes with 14-15 ommatidia.

Conglobating with lateral sides of body oblique, splayed out at anterior part of first epimera of peraeon. Cephalon (fig.25) with frontal line clear and uninterrupted. Secondary frontal line absent, as is lateral-ocular tubercle. Clypeal line uninterrupted and clypeal lobes horizontal and rounded.



Figures 24-27 *Buddelundia zebricolor* sp.nov. **24:** whole animal in lateral view; **25:** cephalon in frontal view; **26:** whole animal in vertical view; **27:** telson and uropods.

First peraeon segment with posterior margin not sinuate, lateral margins thin; no *sulcus arcuatus*. External schisma with external lobe protruding backwards compared to internal lobe (fig.26). Second peraeon segment with triangular process on ventral



Figures 28-31 *Buddelundia zebricolor* sp.nov. **28:** surface of the first peraeon (S.E.M.); **29:** right uropod (S.E.M.); **30:** carpus of first male peraeopod (S.E.M.); **31:** ventral setae of carpus of the first male peraeopod.

surface of epimera; fold on ventral face of third to seventh peraeon segment, progressively more prominent posteriorly.

Pleon with pleura of fifth segment parallel. Telson hour-glass shaped with apex slightly rounded (fig.27).

Body smooth, tergites covered with small setae curved backwards (fig.28). A1 with

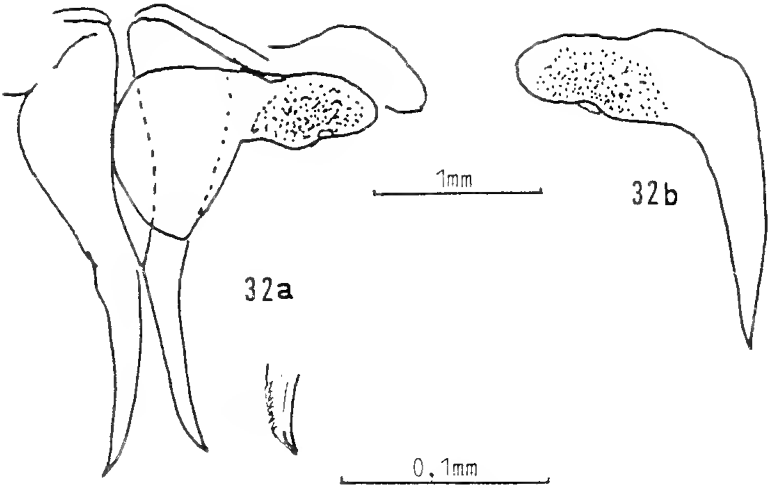


Figure 32 *Buddelundia zebricolor* sp.nov.; first (**32a**) and second (**32b**) male pleopods.

7-8 aesthetascs on apex of distal article. A2 two-jointed flagellum; ratio distal joint/proximal joint = 1.32. Uropod (fig.29) with distal part of protopodite convergent and with apex rounded; largest specimens and males with protopodite triangular with apex acute; exopodite and endopodite reduced.

Sexual dimorphism is obvious on peraeopods where some carpian brush setae are broad and short in males (figs 30 & 31).

Distribution

This species is not troglobitic and is common outside caves.

Derivation of name

In allusion to the regular succession of clear and dark stripes which make the animal stripy.

Buddelundia zebricolor fulva subsp.nov.

Figures 33-34

Holotype

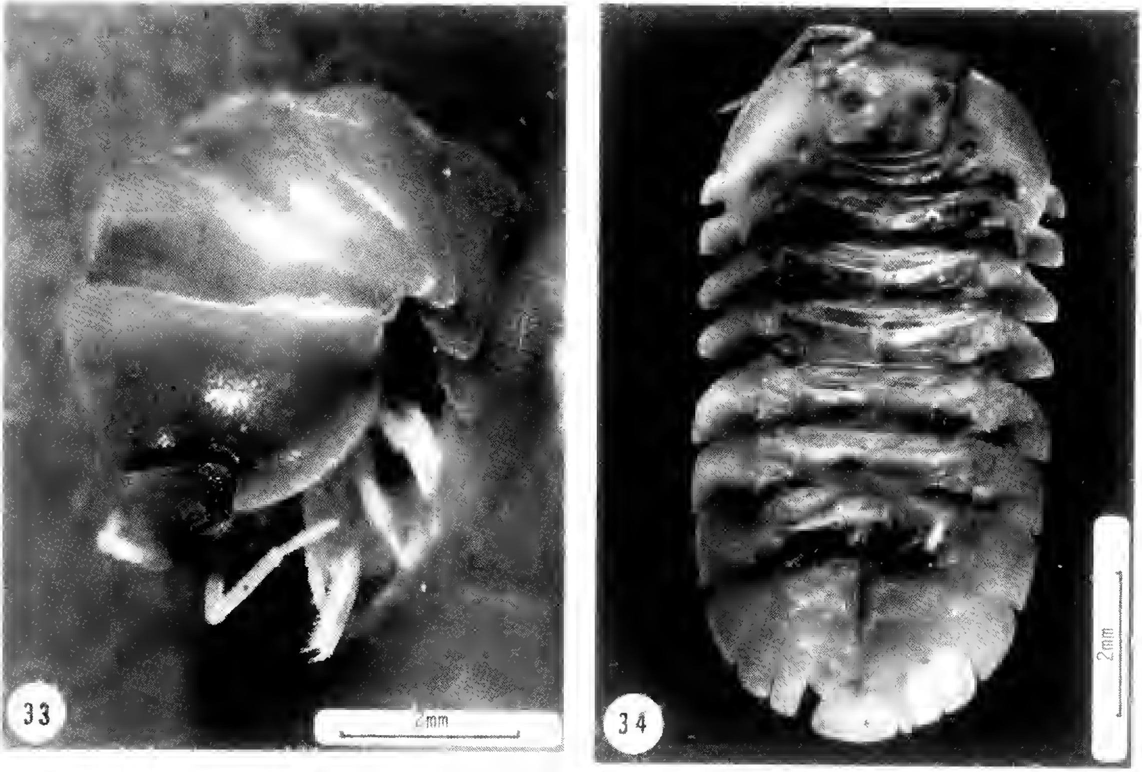
C- 94, 20.IX.1988, WAM 981-88 1 male.

Paratypes

C- 94, 20.IX.1988, WAM 87-91 2 males, DH 1 male.

Diagnosis

Similar to *B. z. zebricolor* except frontal line which is slightly more raised above vertex and colour which is uniformly fawn-coloured. For the moment, it seems advisible to consider *fulva* as a subspecies of *zebricolor* rather than a distinct species.



Figures 33-34 *Buddelundia zebricolor fulva* subsp.nov. **33:** whole animal in lateral view; **34:** whole animal in ventral view.

Description

Size 11.7x5.7mm. for holotype. Fawn colour in animals freshly preserved, changing to pale grey with time in alcohol. Black eyes with 14 ommatidia, the external row colourless, so animal appears microphthalmic.

The overall morphology is similar to *B. z. zebricolor* (fig.33-34). Differences concern the frontal line which is slightly more raised above the level of the vertex in *B. z. fulva* than in *B. zebricolor zebricolor*. The lateral margins of the first peraeon segment are more splayed in *B. z. fulva* than in *B. z. zebricolor* but they are not structurally different and the two subspecies are closely related.

Distribution

This subspecies has been collected only in a cave and seems the single *Buddelundia* found in Cape Range caves which shows inclinations to troglomorphic features.

Derivation of name

From the latin *fulvus* in allusion to its fawn colour.

Acknowledgements

I thank Dr W.F. Humphreys and Dr G. Morgan of the Western Australian Museum, Perth, for reading the manuscript and Miss A.J.A. Green for her pertinent comments.

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A new species of damselfish (*Chrysiptera*: Pomacentridae) from Irian Jaya, Indonesia

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Abstract

A new species of pomacentrid, *Chrysiptera pricei*, is described from 48 specimens collected during 1991 at Yapen Island, northern New Guinea (Indonesian province of Irian Jaya). It belongs to a complex of closely related species containing *C. hemicyanea* (Weber), *C. oxycephalus* (Bleeker), *C. parasema* (Fowler), *C. sinclairi* Allen, and *C. springeri* Allen. Colour pattern differences provide the best means of separation. *C. pricei* is the only member of this complex with a combination of blue upper body, whitish ventral parts, and a small black area around the vent and genital papilla.

Introduction

Damselfishes (Pomacentridae) are among the most speciose and conspicuous of all fish groups associated with tropical and subtropical reefs. The family was reviewed by Allen (1991), who recognized 322 species in 28 genera. The present paper describes a new species belonging to the genus *Chrysiptera* Swainson that was collected during a recent visit by G. Allen to Yapen (sometimes spelled Japen) Island on the north coast of New Guinea.

The methods of counting and measuring are the same as those described by Allen (1972) except the length of the dorsal and anal spines are measured proximally at the base of the spine rather than the point where the spine emerges from the scaly sheath. Counts and proportions appearing in parentheses apply to the paratypes. Proportional measurements expressed in thousandths of the standard length are provided in Table 1. A summary of counts for fin rays, lateral-line scales and gill rakers on the first arch appears in Table 2. Type specimens have been deposited at Pusat Penelitian dan Pengembangan Oseanologi, Jakarta, Indonesia (NCIP); and the Western Australian Museum, Perth (WAM).

Systematics

Chrysiptera pricei sp. nov.

Figure 1; Table 1

Holotype

NCIP 4025, 32.0 mm SL, coral reef on edge of Ampimoi Bay across from Warironi Village, near Arareni Point, Yapen Island, Irian Jaya, Indonesia (approximately 01°53'S, 136°32'E), 2-5 m, rotenone, G. Allen and D. Price, 26 May 1991.

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Paratypes (collected with holotype)

NCIP 4026, 42 specimens, 8.9-34.7 mm SL; WAM 30391-001, 5 specimens, 23.3-31.3 mm SL.

Diagnosis

A species of the pomacentrid genus *Chrysiptera* with the following combination of characters: dorsal rays usually XIII,10 (occasionally XII, 10 or XIII,9); anal rays usually II,12 (occasionally II,11); pectoral rays usually 14 (rarely 13 or 15); gill rakers on first branchial arch 7 + 14-16, total rakers 21 to 23; tubed lateral-line scales 11-14; colour in life bright blue above a line connecting upper pectoral-fin base and base of uppermost caudal rays, whitish below; a small black spot on upper opercular margin and at base of uppermost pectoral rays; a black area surrounding vent and genital papilla. The new species belongs to a complex containing *C. hemicyanea* (Weber), *C. oxycephalus* (Bleeker), *C. parasema* (Fowler), *C. sinclairi* Allen, and *C. springeri* Allen. Colour pattern differences provide the best means of separation (see remarks).

Description

Dorsal rays XII,10 (XII or XIII,9 or 10); anal rays II,11 (II,10-12); pectoral rays 14 (13 or 14); gill rakers on first branchial arch 7 + 16 (7 + 14-16), total rakers 23 (21-23); lateral-line scales with tubes 11 (12-14); vertical scale rows 27 (27 or 28); scales above lateral-line to base of middle dorsal spines 1 1/2; scales below lateral line to anus 9.

Body moderately deep for the genus, the depth 1.9 (1.9-2.2) in standard length, and compressed, the width 2.7 (2.7-3.0) in depth; head length contained 3.0 (2.8-3.1) in standard length; snout 3.8 (3.6-4.6), eye 2.6 (2.4-2.8), interorbital space 3.6 (3.6-4.4), least depth of caudal peduncle 2.3 (2.2-2.6), length of caudal peduncle 2.2 (1.9-2.4), all in head length.

Mouth oblique, terminally located, the maxillary reaching to a vertical through anterior edge of eye; teeth of jaws biserial anteriorly, those of outer row conical posteriorly, becoming incisiform with flattened or gently rounded tips towards front of jaws, upper and lower jaw each with about 40 teeth in outer row, the largest about one-fourth diameter of pupil in height; a secondary row of slender buttress teeth at front of jaws, behind those of outer row in the spaces between them; single nasal opening on each side of snout; nostril with a low fleshy rim; margin of preorbital and suborbital smooth; pre and suborbital relatively narrow, the greatest depth about one-third eye diameter; margin of preopercle smooth to weakly crenulate; opercular series smooth except a blunt, flattened spine present on upper portion near angle.

Scales of head and body finely ctenoid; preorbital, suborbital, snout tip, lips, chin, and isthmus naked; preopercle with 2 major scale rows and a supplementary row of small scales along lower margin, rear margin narrowly naked; dorsal and anal fins with a basal scaly sheath; caudal fin scaled about half distance to end of lobes; paired fins scaled only basally; axillary scale of pelvic fins slightly more than half length of pelvic spine.

Tubes of lateral line ending below posterior spines of dorsal fin; pored scales posterior to tubed scales 8 (4-8); a series of 6 (6-9) pored scales mid-laterally on caudal peduncle to caudal base.

Figure 1 *Chrysiptera pricei*, holotype, 32.0 mm SL.

Origin of dorsal fin at level of third tubed scale of lateral line; spines of dorsal fin gradually increasing in length to sixth or seventh spine, remaining spines slightly decreasing in length; membrane between spines deeply incised; first dorsal spine 1.9 (1.3-1.8) in second dorsal spine; second dorsal spine 1.3 (1.3-1.8) in sixth dorsal spine; sixth dorsal spine 1.8 (1.7-1.9) in head; longest soft dorsal ray 1.4 (1.3-1.4) in head; length of dorsal fin base 1.7 (1.7-1.8) in standard length; first anal spine 2.4 (2.3-2.6) in second anal spine; second anal spine 1.7 (1.7-2.2) in head; longest soft anal ray 1.4 (1.3-1.5) in head; base of anal fin 2.2 (2.2-2.4) in base of dorsal fin; caudal fin emarginate with pointed lobes, its length 1.1 (1.0-1.1) in head length; pectoral fin relatively short, just reaching a vertical through origin of anal fin in adults, the longest ray 1.1 (1.0-1.1) in head length; filamentous tips of pelvic fins of adults reaching origin of anal fin or slightly beyond, the longest ray 1.1 (1.0-1.1) in head length.

Colour of holotype in alcohol (after nine months preservation): brown on upper half of head and on body above a line connecting upper pectoral-fin base and base of uppermost caudal rays, pale yellowish tan on lower parts except small area around vent and genital papilla black; a vertical blue streak across basal portion of each scale on upper sides; each scale of cheek and opercular series with prominent blue spot or streak; a short blue stripe on side of snout from front of eye; faint bluish spots also evident on top of head; a small black "ear" spot on upper edge of operculum anterior to and slightly below lateral-line origin; spinous dorsal fin and basal scaly sheath of soft dorsal fin bluish

Table 1 Morphometric proportions of type specimens of *Chrysiptera pricei* (as percentage of the standard length)

Character	Holotype NCIP 4025	Paratypes WAM P.30391-001	WAM P.30391-001	WAM P.30391-001	WAM P.30391-001	NCIP 4026
Standard length (mm)	32.0	23.3	25.4	28.2	31.3	34.7
Body depth	51.3	46.8	46.1	52.1	48.6	48.4
Body width	17.8	15.5	15.4	18.8	18.2	18.2
Head length	32.8	35.6	33.9	34.0	31.3	32.9
Snout length	7.2	9.0	8.7	8.2	8.6	8.6
Eye diameter	12.5	15.0	12.2	13.1	12.8	12.7
Interorbital width	8.8	8.2	7.9	9.6	9.3	9.2
Least depth of caudal peduncle	14.7	15.0	14.2	13.1	14.4	14.1
Length of caudal peduncle	15.6	15.0	17.7	15.6	16.6	15.3
Snout to origin of dorsal fin	40.0	42.5	40.9	40.4	40.3	40.3
Snout to origin of anal fin	67.5	67.0	67.3	68.1	68.4	67.1
Snout to origin of pelvic fin	39.7	42.1	39.8	41.8	41.2	39.8
Length of dorsal fin base	57.5	59.7	54.3	60.3	59.4	58.5
Length of anal fin base	25.0	24.5	23.6	27.7	25.9	26.2
Length of pectoral fin	30.6	32.6	30.7	31.9	31.9	30.3
Length of pelvic fin	29.1	32.2	31.5	29.4	29.1	28.5
Length of pelvic spine	17.8	18.5	18.1	18.4	16.0	18.2
Length of 1st dorsal spine	7.5	8.2	8.7	6.0	8.6	7.8
Length of 2nd dorsal spine	14.4	11.6	12.2	10.6	11.2	12.4
Length of 6th dorsal spine	18.1	18.9	18.9	19.1	17.9	19.0
Length of longest dorsal ray	24.1	25.8	23.6	23.8	23.0	24.8
Length of 1st anal spine	8.1	7.7	7.1	7.4	7.3	8.4
Length of 2nd anal spine	19.4	18.0	15.7	19.5	17.6	19.6
Length of longest anal ray	24.1	25.8	24.0	23.8	20.8	24.5
Length of caudal fin	30.6	32.2	30.7	30.1	31.9	30.3

brown; remainder of fins pale; a small black spot at base of uppermost pectoral fin rays. The paratypes have a similar coloration.

Colour in life: mainly bright blue on upper half of head and on sides of body above a line connecting upper pectoral-fin base and base of uppermost caudal rays, whitish below; a dark charcoal streak on each scale of upper sides, but overall impression is bright blue; metallic blue spots and streaks on cheek, gill cover, and top of head. The blue coloration dorsally on the caudal peduncle is particularly evident underwater.

Remarks

Chrysiptera Swainson is a diverse group containing 25 species, all from the Indo-West and Central Pacific region. Allen (1975 and 1991) characterised the genus (formerly known as *Glyphidodontops* Bleeker) as small damselfishes, usually with a relatively elongate body (2.1-2.7 in SL for most species), with smooth preopercular and suborbital margins, and biserial dentition in most species. The group is in need of revision, and may ultimately be split into several genera. The new species belongs to a complex containing *C. hemicyanea* (Weber), *C. oxycephalus* (Bleeker), *C. parasema* (Fowler), *C. sinclairi* Allen, and *C. springeri* Allen. This group is mainly restricted to the area that includes Indonesia, Philippines, New Guinea, and Solomon Islands. The various species have allopatric distributions except for *C. oxycephalus*, which is widespread through the region and generally sympatric with each of the other species. These fishes have a distinctive shape that is relatively deep-bodied for the genus (1.9-2.2 in SL), a deeply incised spinous dorsal fin, and bright coloration consisting largely of blue or a combination of blue and yellow. Colour pattern differences provide the best means of separation. *C. hemicyanea* is mainly bright blue with yellow ventrally. *C. parasema* is bright blue except for a yellow caudal peduncle and yellow pelvic, soft dorsal, and anal fins. *C. oxycephalus* is overall pale yellow with numerous small blue spots covering the head and body. *C. sinclairi* and *C. springeri* are entirely blue without any yellow and the latter species differs from the other members of the complex in having 12 dorsal spines instead of 13. *C. pricei* also differs from C. *oxycephalus* and *C. sinclairi* in having a lower gill raker count (21-23 versus usual counts of 30-34). *C. pricei* is the only member of this complex that has a whitish colour ventrally and a small black spot covering the vent and genital papilla. Illustrations and a brief diagnosis of each member of the complex and all other species of *Chrysiptera* were provided by Allen (1991).

The species is thus far known only from the type locality, but collections of reef fishes from northern Irian Jaya are generally lacking. The habitat of the type locality consists of a fringing reef in a sheltered bay with a high percentage of live coral cover (both soft and stony)and heavy silt deposition from nearby rivers. The depth range extends from about two to 10 m. Fish are seen solitarily or in groups of up to 20-30 individuals that hover a short distance above the bottom. Presumably they feed primarily on plankton.

It is named *pricei* in honour of Mr. David Price who assisted with the collection of type specimens.

Acknowledgements

Special thanks are due David and Tammy Price for providing accommodation and logistic assistance to G. Allen during the visit to Irian Jaya. Funds for this trip were generously donated by T.F.H. Publications, Inc., under the auspices of Dr. Herbert R. Axelrod.

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The gastric nematodes of *Varanus caudolineatus* (Reptilia: Varanidae) in Western Australia.

Hugh I. Jones*

Abstract

Adult *Abbreviata levicauda* (Nematoda: Physalopteroidea) occurred in low numbers (1-10) in 4.3% of 139 *Varanus caudolineatus* examined. The caudal morphology of male nematodes conformed to that in specimens recovered from *V. tristis*. Both these lizards are predominantly arboreal.

Introduction

Varanus caudolineatus is a small arboreal lizard confined to the desert areas of Western Australia, where it is an inhabitant of healthy mulga (*Acacia aneura*), and eucalypt hollows and rocky crevices (Pianka 1969). In studies on the diet of this lizard Pianka (1969) and King (unpublished) collected worms from the stomachs of 139 specimens, now preserved in the Western Australian Museum. This paper records the examination of these nematodes.

Materials and Methods

Specimens had been fixed in formalin and stored in 70% alcohol. They were cleaned, cleared in chlorolactophenol, and examined using an Olympus BA microscope. The drawing was made by means of a drawing tube. All specimens have been deposited in the Western Australian Museum.

Specimens examined.

Four males, five females and three immature worms, WAM 25-91, ex. R87661, collected 13 k SW Mt. Phillip HS, 24°31'S, 116°14'E, 09.07.1984; one female, one immature, WAM 26-91, ex. R13362, collected Jigalong, 23°22'S, 120°47'E, June 1959; three males, six females, WAM 27-91, ex. R26320, collected Eastern Goldfields, 30°45'S, 121°30'E, no date; three males (incomplete), WAM 28-91, ex. R47793, collected 30 k. SE Bulloo Downs HS, 27.08.1974; four males, six females, WAM 29-91, ex. R87637, collected 12 k. SW Yinnietharra HS, 24°45'S, 116°96'E, 07.07.1984; two adult and two immature males, three females (incomplete), WAM 30-91, ex. R87770, same data as for R87637. The following four hosts contained immature worms only: five, WAM 31-91, ex. R70895, collected 3.5 k. N. of Yowie Rockhole, 30°26'S,

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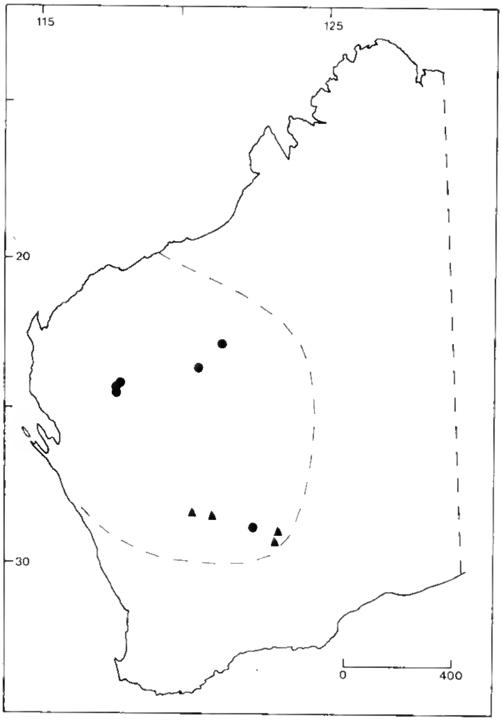

Figure 1 Distribution of *Abbreviata levicauda* infections in *Varanus caudolineatus*. ● adult worms; ▲ immature worms only. Interrupted line indicates limits of host's range. (Adapted from Storr *et al.*, 1983).

122°21'E, 09.08.1980; five, WAM 32-91, ex. R73223, 2 k. N. of Yowie Rockhole, 30°27'S, 122°21'E, 18.10.1979; one, WAM 33-91, ex. R73433, 9 k. 190° Mt. Elvire HS, 29°26'S, 119°35'E, 17.09.1980; three, WAM 34-91, ex. R84443, 14 k. S. Dromedary Hill, 29°11'S, 118°24'E, 01.10.1983.

Results

Nematodes were recovered from the stomachs of ten lizards (figure 1). Adult *Abbreviata levicauda* Jones, 1983 were identified from six lizards (4.3%), in numbers ranging from one to ten (mean, 6.5). Four lizards contained immature nematodes only, and these have been assigned to the same species. No other nematode species were present.

No cysts containing larval worms had been observed in or on the stomach walls during dissection (King, personal communication), though they have been recorded in this lizard (Jones, unpublished).

Measurements and morphology were similar to those of *A. levicauda* described from *V. gouldii* (Jones 1983), except in respect of the two following characteristics: the copulatory spicules were shorter in specimens from *V. caudolineatus*, the right measuring 220-240 um and the left 380-480 um. Secondly, the morphology of the male tail differed; in all specimens examined in this study, the tubercles on the male tail extend

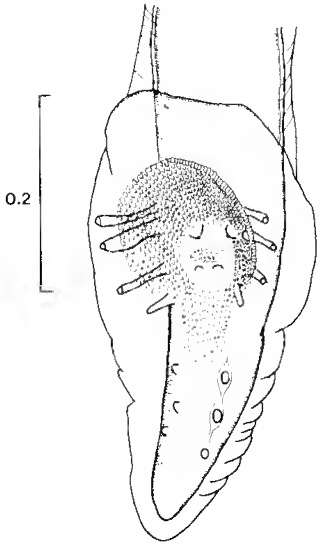

Figure 2 *Abbreviata levicauda.* Ventral surface of male tail of specimen from *V. caudolineatus.* Measurement in mm.

a short distance posterior to the cloaca, and the ventral surface of the tail is smooth and free of tubercles posterior to the level of the anteriormost pair of ventrolateral caudal papillae. The three pairs of these sessile or short pedunculate postcloacal papillae on the lateral ventral surface of the tail are evenly-spaced (figure 2).

Discussion

The configuration of the male tail in these specimens of *A. levicauda* from *V. caudolineatus* is identical to that described from specimens of this nematode from *V. tristis* (Jones 1986). I suggested in that paper that when this species of nematode occurs concurrently with closely similar related taxa, character displacement occurs. In *V. gouldii*, in which three species of *Abbreviata* may be present in high numbers in the same host, the male tail in *A. levicauda* has reduced tubercles posterior to the cloaca, and the penultimate pair of caudal papillae are situated close to the posteriormost pair, thus accentuating the difference from other species. The similarity in structure of *A. levicauda* from *V. caudolineatus* (in which no other nematode species were found) to those from sympatric *V. tristis*, in which there was a low prevalence and intensity of congeners, supports this suggestion.

Nematodes in the genus *Abbreviata* occur in the larger species of *Varanus* lizards throughout Australia, especially in the arid inland and the North. Specificity appears to be related principally to the ecology rather than to the phylogeny of these lizards (Jones 1988). It is noteworthy that both *V. caudolineatus* and *V. tristis* are largely arboreal, and although *V. caudolineatus* is a smaller lizard than *V. tristis*, there is likely to be considerable niche overlap.

Compared with larger tropical and desert varanids, which may support hundreds of *Abbreviata* at high prevalence, both intensity and prevalence of *A. levicauda* in *V. caudolineatus* were low. In Australia, species of *Abbreviata* are known to mature only in the larger species in each snake and lizard Family, the smaller species acting as paratenic hosts to the larvae which are often encysted in the stomach wall (Jones 1978 and unpublished). It is therefore interesting that *Abbreviata* occur as adults in the small *V. caudolineatus*, whereas they are unable to mature in the larger lizard-eating *V. eremius*, in the stomachs of which encysted larvae are found in large numbers (Jones unpublished). Many species of *Abbreviata* appear to have a low host specificity in reptiles, and the ability of A. *levicauda* to mature in one of these two closely-related small varanids and not in the other is perplexing; the explanation is probably to be sought in the evolutionary ecology of these lizards. Studies on other small Australian varanids would be rewarding.

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A new species of damselfish (Pomacentridae: *Stegastes*) from Ascension Island, Atlantic Ocean

Gerald R. Allen* and Kevin N. Smith*

Abstract

Stegastes lubbocki is described from 40 specimens collected at Ascension Island in the Middle Atlantic Ocean during 1977. It is primarily separable from the other 13 Atlantic members of the genus on the basis of its distinctive colour pattern consisting of dark brown (blue in life) on most of the body and fins with an abruptly pale (yellow in life) caudal peduncle and caudal fin. The largest known specimen is a mature female 50 mm SL, thus it is possibly the smallest *Stegastes*; other species range from 70 to 140 mm SL.

Introduction

The pomacentrid genus *Stegastes* Jenyns occurs worldwide in tropical and subtropical seas. The species of this genus are bottom-dwelling, territorial damselfishes, generally not exceeding a total length of 14 cm. They inhabitat coral or rocky reefs, from tidepool depths to at least 45 m, although most occur in less than 10 m. They are omnivorous, but the diet consists largely of various algae.

The genus contains 33 species including 13 each from the Indo-West Pacific and Atlantic regions, and seven species from the Eastern Pacific. These fishes were included by most previous authors in either *Pomacentrus* Lacepède or *Eupomacentrus* Bleeker, but Emery and Allen (1980) presented evidence for their separate generic status and resurrected *Stegastes* as the oldest available name.

The present paper describes a new species of Stegastes collected in 1977 by the late Roger Lubbock at tiny Ascension Island in the middle Atlantic. Two other island endemics (*S. sanctaehelenae* and *S. sanctipauli*) occur in the mid-Atlantic at St Helena Island and St Paul's Rocks, and a third, *S. rocasensis*, is endemic to Atol das Rocas, off northern Brazil.

Methods of counting and measuring follow those of Allen (1972) and Randall and Allen (1977). The counts and proportions which appear in parentheses are those of the paratype if differing from the holotype. A summary of proportional measurements and meristic data is presented in Tables 1 and 2. Type specimens are deposited at The Natural History Museum [formerly the British Museum (Natural History), London (BMNH)]; National Museum of Natural History, Washington, D.C. (USNM); and the Western Australian Museum, Perth (WAM).

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Figure 1 *Stegastes lubbocki*, holotype, 49.4 mm SL.

Systematics

Stegastes *lubbocki* sp. nov.

Figure 1

Holotype

WAM P. 30283-001, 49.4 m SL; Pratt Point, Ascension Island (07°57′S, 14°22′W); rock pools; R. Lubbock; 29 December 1977.

Paratypes

BMNH 1992.4.6:1-8, 8: 26.4-42 mm SL, Pan Am Beach, S.W. Bay, Ascension Island, 12 m, R. Lubbock, 20 December 1977; USNM 320806, 4: 25.2-43.6 mm SL, same data as holotype; WAM P30279-001, 7: 15.2-24.8 mm SL, English Bay, Ascension Island, 15 m, R. Lubbock, 7 January 1978; WAM P30280-001, 26.7 mm SL, Pyramid Point, Ascension Island, 25 m, R. Lubbock, 10 January 1978; WAM P30281-001, 19.3 mm SL, Catherine's Point, Ascension Island, rockpool, R. Lubbock, 30 December 1977; WAM P30282-001, 2: 15.3-16.4 mm SL, English Bay, Ascension Island, 12 m, R. Lubbock, 18 December 1977; WAM P30284-001, 16: 22-50.5 mm SL, English Bay, Ascension Island, 15 m, R. Lubboek, 21 December, 1977.

Diagnosis

A species of the pomacentrid genus *Stegastes* with the following combination of features: dorsal rays XII,14-17; anal rays II, 13-14; pectoral rays 19-21; tubed lateral-line scales 18-21; total gill rakers on first arch 18-21; colour mainly dark brown (to blackish on vertical fins) with abruptly pale (yellow in life) area covering peduncle, caudal fin, and posterior portion of dorsal fin.

Description

Dorsal rays XII,16 (14-17); anal rays II,14 (13-14) (II,15); pectoral rays 19 (19-21),

Table 1 Frequency distribution of fin-rays and lateral-line scales for type specimens of *Stegastes lubbocki.*

Soft dorsal rays				Anal rays	
14	15	16	17	13	14
1	6	32	1	2	38

Pectoral rays			Lateral-line scales			
19	20	21	18	19	20	21
21	18	1	4	5	30	1

branched caudal rays 13, gill rakers on first branchial arch 9 + 11 (7-9 + 11-14); lateral-line scales with tubes 20 (18-21); vertical scale rows 28; scales above lateral-line to base of middle dorsal spines 1 1/2; scales below lateral-line to anus 9.

Body ovate, the depth 2.1 (2.1-2.5) in standard length, and compressed, the width 2.2 (2.2-2.6) in depth; head length contained 3.3 (3.1-3.3) in standard length; snout 4.3 (4.0-4.9); eye 2.8 (2.6-2.9); interorbital width 3.6 (3.5-4.2), least depth of caudal peduncle 2.1 (2.1-2.4) length of caudal peduncle 1.9 (1.9-2.3), all in length of head.

Mouth slightly oblique, jaws equal, the maxilla reaching level of anterior part of pupil; teeth of jaws uniserial, relatively long and close-set, with flattened or slightly notched tips; about 32-36 teeth in each jaw; the longest teeth exceeding width of nostril opening; single nasal opening on each side of snout; nostril with a low fleshy rim; margin of preorbital smooth; margin of suborbital finely serrate; preorbital and suborbital bones relatively narrow, the greatest depth about 1/2 eye diameter, the lower margin free; vertical limb of preopercle distinctly serrate; opercle series entire except a pair of flattened spines present on upper edge of gill cover, the largest near angle. Scales of head and body finely ctenoid; predorsal scales extending forward to level of nostrils; anterior part of preorbital, snout tip, lips, chin, and isthmus scaleless; preopercle with 2 major scale rows and an additional row of smaller scales along lower margin; dorsal and anal fins with a basal scaly sheath; caudal fin scaled nearly two-thirds distance to end of lobes; pectoral fins scaled on basal one-fourth; axillary scale of pelvic fins slightly more than half length of pelvic spine.

Tubes of lateral-line ending below middle rays of soft portion of dorsal fin; a series of 8-10 pored scales midlaterally on caudal peduncle to caudal base.

Origin of dorsal fin at level of second tubed scale of lateral line; spines of dorsal fin gradually increasing in length to last spine, membrane between spines moderately incised; last dorsal spine 1.9 (1.6-2.2) in head; first dorsal spine 1.8 (1.7-2.2) in last spine; sixth dorsal spine 1.1 (0.9-1.1) in last dorsal spine; longest soft dorsal ray 1.9 (1.6-2.2) in head; length of base of dorsal fin 1.7 (1.6-1.8) in standard length; first anal spine slightly shorter than first dorsal spine, its length 2.5 (2.3-2.8) in second spine; second anal spine 1.8 (1.6-1.8) in head; longest soft anal ray 1.3 (1.0-1.3) in head; base of anal fin 2.5 (2.2-2.9) in base of dorsal fin; caudal fin emarginate with pointed lobes, its length 1.0 (1.0-1.2) in head length; pectoral fins relatively short, reaching to about level of anus or

Table 2 Morphometric proportions of selected type specimens of *Stegastes lubbocki* n. sp. Expressed in percentage of the standard length.

Character	Holotype WAM P30283-001	USNM 320806	WAM P30284-001	WAM P30284-001	USNM 320806	USNM 320806	USNM 320806
Standard length (mm)	49.4	43.7	50.0	41.6	42.1	33.6	37.8
Body depth	46.3	40.5	43.9	41.2	47.4	47.9	39.7
Body width	20.8	17.3	18.7	18.5	18.1	19.0	16.3
Head length	30.6	30.5	31.7	32.0	31.3	32.6	32.7
Snout length	7.2	6.7	8.1	7.7	7.1	6.9	6.5
Eye diameter	11.1	11.4	10.9	11.4	11.4	12.6	11.9
Interorbital width	8.4	8.1	8.6	9.1	7.9	7.6	8.4
Least depth caudal peduncle	4.4	3.7	3.5	3.8	4.0	2.2	2.9
Length caudal peduncle	14.4	13.9	13.5	13.9	14.4	13.8	13.9
Snout to origin dorsal fin	16.4	15.5	15.2	15.5	16.0	16.5	16.2
Snout to origin anal fin	37.3	37.9	36.9	35.3	36.2	40.0	38.6
Snout to origin pelvic fin	69.8	69.7	69.7	72.6	70.8	68.5	70.7
Length dorsal-fin base	38.7	38.9	42.8	44.1	45.0	42.3	36.8
Length anal-fin base	60.4	60.1	59.9	57.7	57.8	58.2	54.2
Length pectoral fin	23.9	24.1	24.3	25.9	21.2	23.4	24.5
Length pelvic fin	25.0	27.0	26.7	27.0	28.7	28.6	26.0
Length pelvic spine	37.5	41.6	40.9	39.3	36.6	38.0	39.0
Length 1st dorsal spine	11.8	11.2	10.1	10.6	9.4	10.7	10.7
Length 6th dorsal spine	8.8	8.8	11.3	7.4	9.3	8.2	7.4
Length 12th dorsal spine	1.51	15.8	16.3	16.6	15.8	17.2	16.1
Length longest soft dorsal ray	16.1	17.5	15.9	16.1	16.0	15.4	15.1
Length 1st anal spine	21.5	25.7	23.5	20.8	26.0	23.4	23.0
Length 2nd anal spine	6.6	6.6	6.5	6.8	5.8	4.9	7.9
Length longest soft anal ray	16.7	18.4	17.6	18.4	18.8	18.3	17.9
Length caudal fin	29.7	28.5	29.0	28.8	29.0	29.3	29.4

just short of this point, the longest ray 1.2 (1.1-1.3) in head length; filamentous tips of pelvic fins reaching to origin of anal fin or slightly beyond, the longest ray 0.9 in head length.

Colour in life

Lubbock (pers. comm., 1978) described the living colours as follows: head and most of body bluish; caudal peduncle and caudal fin bright yellow.

Colour in alcohol

The holotype is mainly dark brown with many dark vertical lines on side following each transverse scale row; caudal peduncle, posterior part of dorsal fin, and caudal fin pale yellowish; most of dorsal fin, anal fin, and pelvic fins blackish; pectoral fin pale with brown blotch at base of uppermost rays. Most of the paratypes are paler; the dark ground colour evidently has faded in preservative. Juveniles under about 25 mm SL have a small (about pupil size or smaller) dark spot at the base of the first few soft dorsal rays.

Remarks

The 13 previously known species of *Stegastes* from the Atlantic Ocean were summarised by Allen (1991). Most of these have very similar morphometric and meristic features. Colour pattern differences are generally useful for separating them except for several species that are relatively drab brown. *Stegastes lubbocki* does not have any obvious close relative and is easily distinguished by its highly contrasted dark body and pale tail. The only Atlantic species that approaches this coloration is *S. partitus* (Poey) which in life is sometimes very dark brown on its anterior two-thirds and abruptly white posteriorly (see illustration on page 180 in Allen, 1991). In addition, *S. lubbocki* is more slender than most species in the genus. It's greatest body depth ranges from 2.1 to 2.5 in the standard length compared with 1.9-2.2 for most other species. The only other slender-bodied species in the Atlantic region is *S. leucostictus* (Müller and Troschel) with a depth ranging from 2.1 to 2.4. However, this species is very different in colour, either plain drab brown or bicoloured (dark dorsally and yellow ventrally). It is also possible that *S. lubbocki* attains a much smaller size than other members of the genus. Our largest specimen measures only 50 mm SL compared with maximum standard lengths of 70-140 mm for the other species. The holotype and largest paratypes have mature gonads, indicating that sexual maturity is attained at a standard length between 40 and 50 mm.

The species is named *lubbocki* in memory of Dr Roger Lubbock, the collector of the type material. An unfortunate traffic accident in Brazil prematurely ended his career in ichthyology. Although his professional life spanned relatively few years, Dr Lubbock made numerous valuable contributions to the knowledge of reef fish taxonomy.

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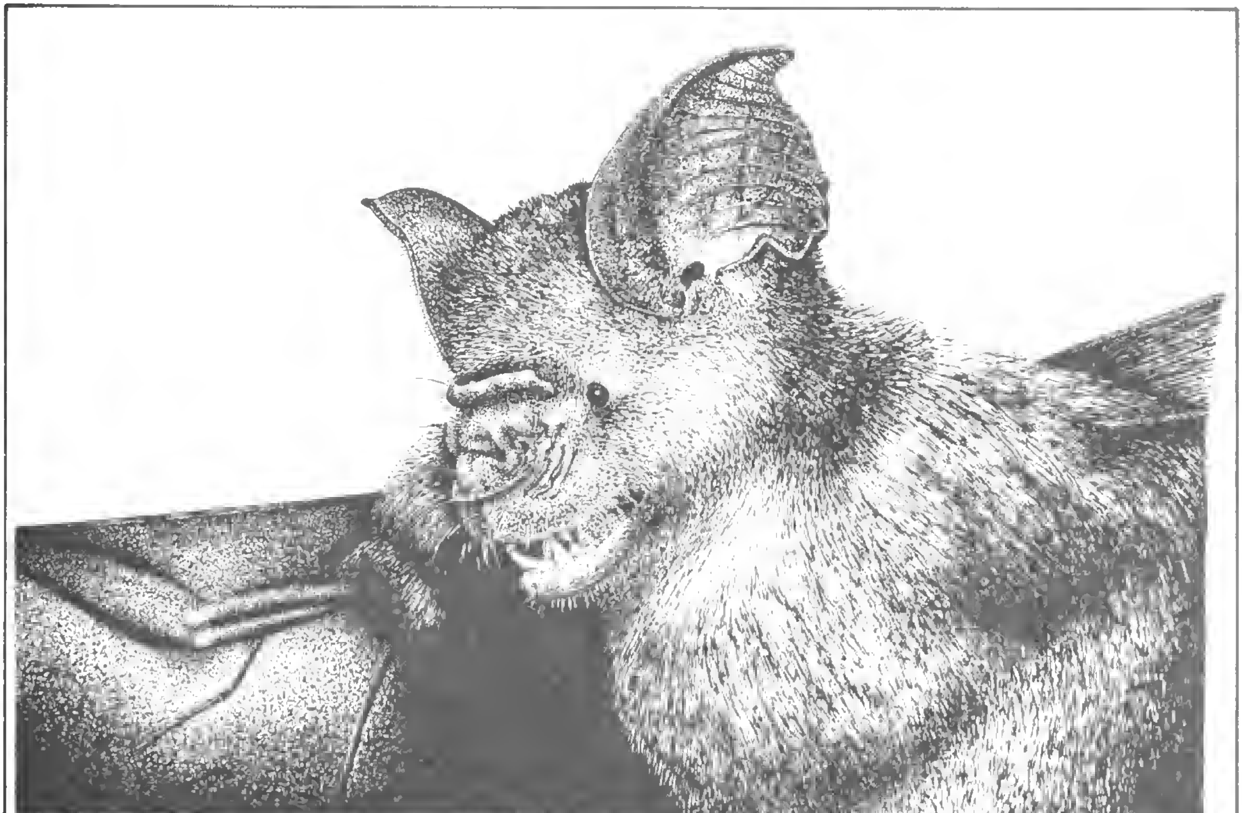

RECORDS of the Western Australian Museum

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P.F. Berry
K. McNamara
M. Harvey

Cover: *Hipposideros Sumbae* from Sumba Island, Nusa Tenggara, Indonesia.
Illustration by Jill Ruse.

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Taxonomic reappraisal of the *Hipposideros larvatus* species complex (Chiroptera: Hipposideridae) in the Greater and Lesser Sunda Islands, Indonesia

D.J. Kitchener* and I. Maryanto**

Abstract

A total of 173 adult specimens of *Hipposideros* previously allocated to *H. larvatus* (*sensu lato*) was examined morphologically. Univariate and multivariate statistical analyses based on 31 skull and 16 external measurement were utilised and morphology of glans penis and baculum examined. These specimens came from islands in Nusa Tenggara (Sumbawa; Flores; Sumba; Savu; Roti; Semau and Timor) and a Western group (Madura; Java; Pulau Laut; Krakatau; Sumatra and Nias — with a few specimens from Peninsular Malaysia, Sarawak and Thailand).

Analysis of variance revealed that almost all skull and external characters differed significantly between locality groups; differences between locality groups greatly outweighed those due to adult age or sex effects.

The sharpest morphological boundary was between the Nusa Tenggara and Western Groups. The Nusa Tenggara specimens represent *Hipposideros sumbae* Oei, 1960. Most Nusa Tenggara islands examined had populations with a distinctive morphology; those from Sumbawa and Roti were subspecifically distinct from the nominate subspecies on Sumba. The subspecific status of populations on Savu and Semau was indeterminate.

The Western group comprised three distinct taxa: *H. madurae* sp. nov. (two subspecies), *H. sorenseni* sp. nov. and *H. larvatus* (Horsfield, 1823). There was considerable variation in the latter species requiring considerably more study. A fourth taxon was recognised on West Java based on the distinctive shape of its baculum; its specific status will be determined following collection of additional specimens. Specimens from Peninsular Malaysia, and Sarawak were tentatively considered consubspecific with *H. l. larvatus* from W. Java, Sumatra, Pulau Laut, Krakatau and Nias. The single specimen from Thailand was smaller with a distinctive glans penis and baculum. It probably represents *Hipposideros grandis* G.M. Allen, 1936.

Introduction

Tate (1941) provided the first taxonomic appraisal of the forms of *Hipposideros larvatus* (Horsfield, 1823), a species he placed in the *H. speoris* group and diagnosed in some detail (Tate 1941: 377). Tate (op. cit.) stated that *H. larvatus* is easily distinguished from similar forms by the following combination of characters: anterior nasal horseshoe leaf with median cleft; forearm length 57 to 63 mm (but Tate 1941: 383 & 385 lists the forearm length of the *H. larvatus, H. deformis* and *H. vulgaris* holotypes as 53, 53 and 56 mm, respectively); tibia length 21-24 mm; ear emarginate; three lateral facial leaflets; transverse

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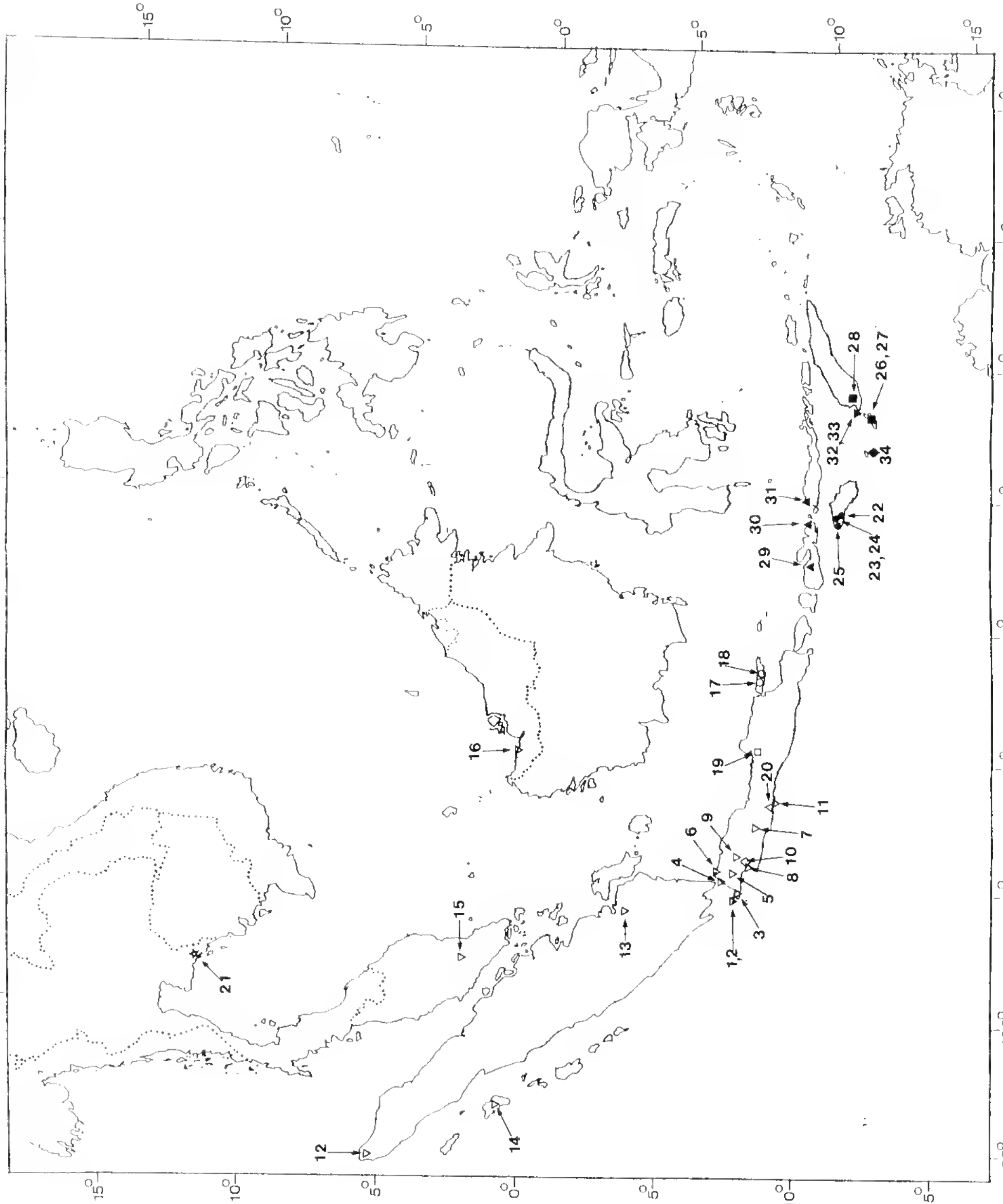


Figure 1 Map showing locality of specimens examined in this study.

noseleaf with three septa and four cells; and frontal sac present in both sexes. This diagnosis is further amplified slightly by Oey and van der Feen (1958) and Hill (1963).

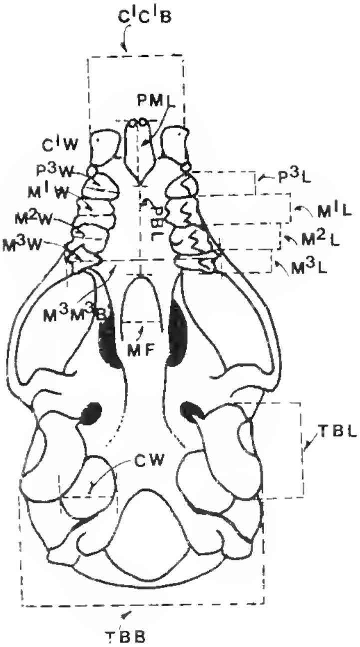
Tate (1941) lists the following subspecies or synonyms of *H. larvatus: H. insignis* (Horsfield, 1823) (Java); *H. deformis* (Horsfield, 1823) (Java); *H. vulgaris* (Horsfield, 1823) (Java); *H. leptophyllus* (Dobson, 1874) (Khasia Hills, Assam); *H. grandis* G.M. Allen, 1936 (Chindwin, Burma); *H. neglectus* Sody, 1936 (C. Borneo); *H. barbensis* Miller, 1900 (St Barbe I.) and *H. poutensis* J.A. Allen, 1906 (Hainan I., China). He studied a number of specimens of *H. larvatus* from Java, Borneo, Sumatra, Malay Peninsular, Thailand, Vietnam, Hainan and islands in the South China Sea. He concluded that throughout this range *H. larvatus* commonly showed a variation of from 3 to 4 mm in forearm length. He could not, however, detect differences in M^3 which was the basis of the original diagnosis of *H.l. grandis*. He also expressed doubts that *H. l. neglectus* was subspecifically distinct from the nominate subspecies. He thought it probable, though, that the Javanese forms *insignis, deformis* and *vulgaris* were probable synonyms of *H. larvatus.*

According to Oey and van der Feen (1958), Temminck (1835: 15) considered that Horsfield's form *vulgaris* was the female of *insignis* and that he could find no important differences between *insignis* and *H. larvatus.*

Hill (1963), in his classical revision of the genus *Hipposideros*, disagreed with Tate's (1941) comments in that he considered *neglectus* a valid subspecies and included in this subspecies specimens from Nias I. that Miller (1942: 116) thought may be separable from both *H. l. larvatus* and *H. l. neglectus.* He also agreed with Shamel (1942: 322) that *grandis* was subspecifically distinct from *neglectus.* Hill's (1963) classification of *H. larvatus* included the more recently described forms (*H. l. alongensis* Bourret, 1942 and *H. l. sumbae* Oei, 1960) and is as follows (distributions include additions by van Strien 1986):

H. l. larvatus (includes *vulgaris, deformis* and *insignis*) — Java, Kangean I.; Oey and van der Feen (1958) also list it on Bali I. but this is not confirmed.
H. l. leptophyllus — Khasi Hills, Assam.
H. l. barbensis — St Barbe I., S. China Sea.
H. l. poutensis — Pouten, Hainan I.
H. l. grandis — Akanti, upper Chindwin, Burma.
H. l. neglectus — Borneo; Karimata I., N. Pagai, Serasan I., S. Natuna I., Sumatra; Nias I., Simeulue I., Butang I., Malay Peninsular and Tioman I.
H. l. alongensis — Bay d'Along, Indochina.
H. l. sumbae — Sumba I. and Timor I.

Previous studies on the intraspecific taxonomy of *Hipposideros larvatus* have been superficial. Recognition of subspecies of *H. larvatus* has largely depended on a single character only, namely the length of the forearm (e.g., Sody 1936, Tate 1941) — although Oei (1960) and Shamel (1942) also briefly refer to larger or smaller cranial measurements when they diagnosed the forms *grandis* and *sumbae* and Hill (1963) provides cranial measurements for a number of subspecies of *H. larvatus.*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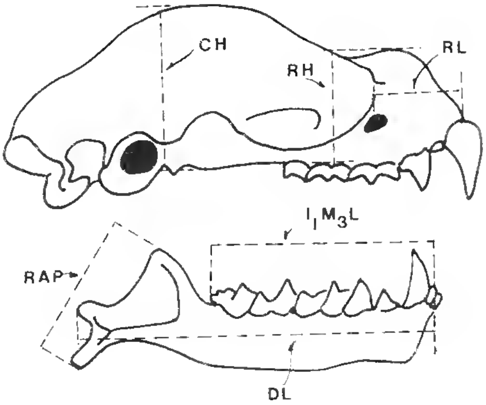
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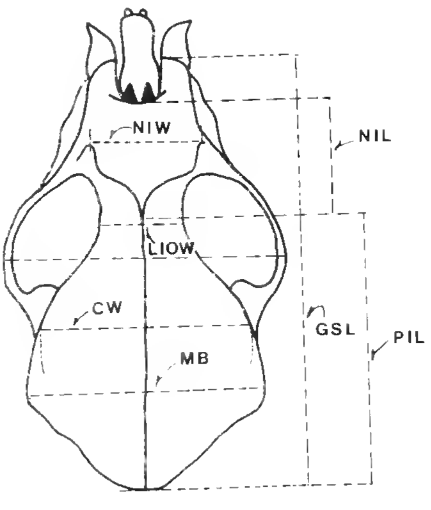
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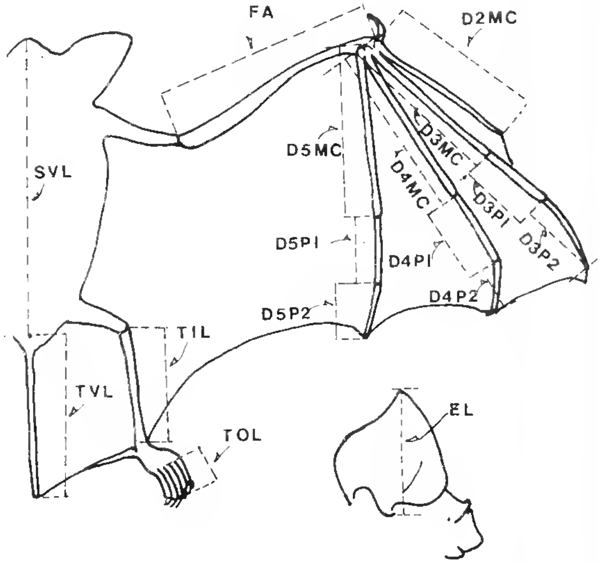
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◀ **Figure 2** Measurement points of the skull and external characters of *Hipposideros* spp. recorded in this study. The description of the measurement codes are: GSL, greatest skull length; BW, braincase width; ZB, zygomatic breadth; MB, mastoid breadth; CH, cranial height-measured by placing lower arm of callipers against basisphenoid and basioccipital and upper arm to highest point on cranium, excluding sagittal crest; RH, rostrum height from base of M^2 to highest point of nasal inflation; RL, rostrum length; LIOW, least interorbital width; PIL, cranial length; NIL, nasal inflation length; PBL, palatal bridge length; PML, premaxilla length; MF, mesopterygoid fossa width; TBL, tympanic bulla length; TBB, tympanic bulla breadth; NIW, nasal inflation width; CW, cochlea width; M^3M^3B, breadth across M^3 to M^3 from outer basal face; C^1C^1B, breadth across C^1C^1 from outer basal face; C^1W, P^3W, and $M^{1-3}W$ and P^3L, $M^{1-3}L$, maxillary teeth widths and lengths; I_1M_3L, lower tooth row length; DL, dentary length; RAP, distance from ramus to angular tip; SVL, snout to vent length; TVL, tail to vent length; EL, ear length; TIL, tibia length; TOL, toe (metatarsal and phalanges, exluding claw) length; FA, forearm length; D2MC, digit 2 metacarpal length; D3MC, digit 3 metacarpal length; D3P1, digit 3 phalanx 1 length; D3P2, digit 3 phalanx 2 length; D4MC, digit 4 metacarpal length; D4P1, digit 4 phalanx 1 length; D4P2, digit 4 phalanx 2 length; D5MC, digit 5 metacarpal length; D5P1, digit 5 phalanx 1 length; and D5P2, digit 5 phalanx 2 length.

We have available to us specimens previously allocated to *H. larvatus* (s. l.) from Java and Nusa Tenggara collected by us during the combined Western Australian Museum — Museum Zoologicum Bogoriense (MZB) expeditions of 1987-1991, as well as specimens in MZB that have not been previously reported upon. These are from islands in Nusa Tenggara (Sumbawa, Sumba, Roti, Savu, Semau, Timor) and Madura I., Pulau Laut I., Krakatau Is, Sumatra and Nias I., (as well as a few specimens from Peninsular Malaysia, Thailand and Borneo).

This paper presents the results and taxonomic conclusions of our examination of morphological variation of individuals within and between the above island populations.

Methods

A total of 173 adult specimens was examined in this morphometric comparison. The numbers of males and females from each locality (see Figure 1 for locality of specimens) is presented in Table 1. They are listed in the "Specimens Examined" section. All these specimens are currently lodged in the Western Australian Museum (WAM) or the Museum Zoologicum Bogoriense, Bogor (MZB). At the completion of this series of surveys half of all the WAM specimens, including the holotypes, will be lodged in MZB, Bogor.

Thirty one measurements of skull characters and 16 of external characters (all in mm), were recorded from adult specimens (see Figure 2, caption). In the graphical presentations in this paper, where a value represents more than one specimen the number of specimens is indicated.

Terminology used in the description of skull, dentary and dental (skull) characters and external characters follows Hill and Smith (1984). Pelage descriptions, when following the colour terminology of Smithe (1975), are capitalised.

Adults were diagnosed as those specimens with basioccipital and sphenoid bones completely fused and epiphyseal swellings absent from metacarpal joints. Additionally, three adult age classes were established based on extent of wear on the upper molar teeth: class 1, no wear or barely perceptible wear on M^{1-2} protocone; class 2, moderate wear on M^{1-2} protocone; class 3 heavy wear on M^{1-3} protocone (see Figure 3).

Sexual dimorphism of skull and external characters was investigated by multiple regressions on sex, age and locality group. Only specimens with a complete data set were included in these analyses. Consequently when the specimens from Semarang (Central Java) were included in the analysis the data set for external measurements was reduced to 13 characters. Snout to vent, tail to vent and ear lengths were excluded because these measurements were not recorded from the Semarang specimens and some of those from W. Java and Sumatra because they were 'cabinet' skins only.

Taxonomic considerations

In evaluating whether or not forms of *Hipposideros* examined in this study warranted recognition as distinct taxa, particular attention was given to the distinctness of skull, glans penis and baculum morphology. The latter was considered particularly important because Zubaid and Davison (1987) found that the morphology of the baculum was species-specific in all 10 species of *Hipposideros* they studied from Peninsular Malaysia. Pelage and overall body, wing and leg morphology were considered of secondary importance.

In this paper the canonical (discriminant) analyses (DFA) are presented after the systematic section. However, results of these analyses, particularly the relationships between specimens from different localities in discriminant function space, were important in recognising taxonomic groupings.

Systematics

Hipposideros larvatus larvatus (Horsfield, 1823)

Tables 1; Figures 1,4,5a,6a,7,8 and 9

Rhinolophus larvatus larvatus. Horsfield, T., 1823, Zoological Researches in Java and the neighbouring islands. No. 6.

Rhinolophus vulgaris Horsfield, T., 1823 Zool. Res. Java, No. 6, Java

Rhinolophus deformis Horsfield, T., 1823 Zool. Res. Java, No. 6, Java

Rhinolophus insignis Horsfield, T., 1823 Zool. Res. Java, No. 6, Java

Hipposideros larvatus neglectus Sody, 1936, Seventeen new generic, specific and subspecific names for Dutch East Indian mammals, Natuurk. Tijdschr. Ned-Ind. 96: 42-55. C. Borneo.

Holotype

British Museum (Natural History) number BM 79.11.21.93.

Type locality

Java.

Specimens examined

Listed in section "Specimens Examined".

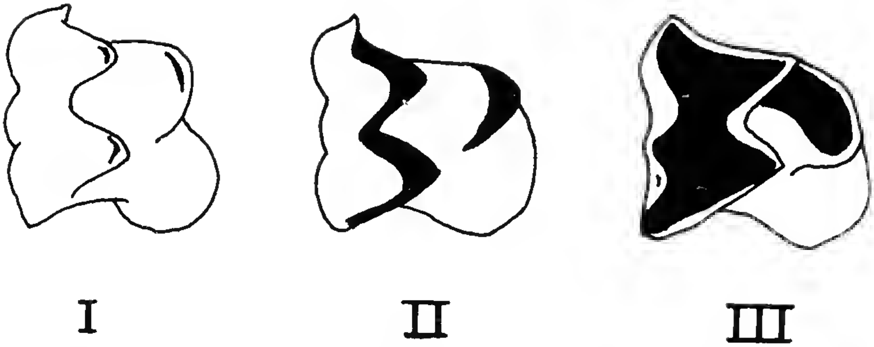

Figure 3 Adult tooth wear categories. Class I, no wear or barely perceptible wear on M^1 protocone; class II, moderate wear on M^1 protocone; class III heavy wear on M^1 protocone.

Diagnosis

Hipposideros larvatus differs from *H. madurae* sp. nov. in averaging larger in most skull measurements. For example: greatest skull length 21.49 v. 20.84; zygomatic breadth 12.87 v. 12.23; C^1C^1 breadth 5.45 v. 5.11; mastoid breadth larger relative to both rostrum height (2.202 v. 2.120) and least interorbital width (with exception of two Pulau Laut specimens (Figure 7); C^1C^1 breadth averages larger relative to both nasal inflation length (0.945 v. 0.856) and I_1M_3 length (0.547 v. 0.523); cranial length longer relative to nasal inflation length (2.456 v. 2.263); tibia length averages larger (22.15 v. 19.32). Glans penis more laterally compressed distally with central distal fleshy lobe attached to baculum more elongate (Figure 6a). Baculum elongate and thin in dorsal profile, bifurcating distal arms long and thin rather than short and deep, basal area much smaller (Figure 5a).

It differs from *H. sorenseni* sp. nov., from which its skull is generally similar in size, in larger average C^1C^1 breadth (5.45 v. 5.34) and dentary angular to condyle length (5.87 v. 5.53). Glans penis distally more laterally compressed with distal fleshy lobe attached to baculum more elongate. Baculum less robust, in dorsal profile long and thin with broad basal pedestal, rather than basal half suboval, bifurcating distal arms much longer and thinner.

It differs from *Hipposideros sumbae* sp. nov. in averaging larger in most skull measurements (Table 1). For example: greatest skull length (21.49 v. 20.24); palatal bridge length (3.78 v. 3.41); nasal inflation length (5.77 v. 5.18); nasal inflation width (6.53 v. 6.24); and dentary length (15.20 v. 13.91); M^3M^3 breadth (8.70 v. 8.01); I_1M_3 length (9.96 v. 9.23). Palatal width relatively broader as indicated by M^3M^3 breadth relative to nasal inflation width (Figure 8); nasal inflation length larger relative to nasal inflation width (0.883 v. 0.830); cranial length shorter relative to nasal inflation length (2.456 v. 2.608); dentary length larger relative to rostrum length (Figure 9); Digit 5 phalanx 2 longer (10.88 v. 9.53-9.92); glans penis with distal end more laterally compressed and lateral profile square rather than gently rounded (Figure 6a). Baculum longer (1.07 v. 0.75-0.84) dorsal profile long and thin, with broad basal pedestal rather than basal half suboval, with long narrow rather than short broad bifurcated distal arms (Figure 5a).

Table 1 Measurements (in mm) for skull and external characters for male and female adults combined of *Hipposideros larvatus* (Indonesia); *H. madurae; H.m. madurae; H.m. jenningsi; H. sorenseni. H. larvatus* (Sarawak); *H. larvatus* (Malaya); *H.* sp. indet. (Sukabumi, W. Java); *H.* sp. *cf. grandis; H. sumbae* (total); *H. s. sumbae; H. s. rotiensis; H. s. sumbawae; H. sumbae* subsp. indet. A (Semau); *H. sumbae* subsp. indet. B (Savu) and *H. sumbae* cf. subsp. *rotiensis* (Timor). Explanation of measurement codes presented in Figure 2 caption.

CHARACTER TAXON		GSL	BW	ZB	MB	CH	RH	RL	LIOW	PIL	NIL	PBI
Hipposideros l. larvatus (W. Java, Pulau Laut, Krakatau, Sumatra, Nias I)	N	60	60	60	60	60	60	60	60	60	60	60
	X	21.49	10.05	12.87	10.99	6.88	4.99	5.24	3.28	14.17	5.77	3.78
	SD	0.51	0.30	0.29	0.20	0.21	0.24	0.27	0.19	0.44	0.35	0.25
	MIN	20.38	9.33	11.83	10.42	6.46	4.51	4.76	2.90	13.01	5.02	3.32
	MAX	22.76	10.66	13.48	11.32	7.34	5.68	5.95	3.66	15.13	6.58	4.34
Hipposideros madurae (total)	N	15	15	15	15	15	15	15	15	15	15	15
	X	20.84	9.50	12.23	10.52	6.61	4.97	5.27	3.17	13.51	5.97	3.71
	SD	0.36	0.21	0.26	0.23	0.16	0.37	0.20	0.16	0.24	0.28	0.15
	MIN	20.25	9.19	11.75	10.18	6.30	4.40	4.96	2.92	13.05	5.49	3.42
	MAX	21.62	9.91	12.78	10.91	6.89	5.43	5.59	3.44	13.92	6.45	3.98
Hipposideros madurae madurae (Madura I.)	N	8	8	8	8	8	8	8	8	8	8	8
	X	20.77	9.45	12.18	10.43	6.52	4.67	5.35	3.07	13.48	5.99	3.75
	SD	0.43	0.26	0.31	0.25	0.14	0.20	0.20	0.14	0.21	0.30	0.16
	MIN	20.25	9.19	11.75	10.18	6.30	4.40	5.09	2.92	13.29	5.49	3.48
	MAX	21.62	9.91	12.78	10.91	6.68	5.04	5.59	3.28	13.77	6.45	3.98
Hipposideros madurae jenningsi (Semarang-C. Java)	N	7	7	7	7	7	7	7	7	7	7	7
	X	20.92	9.56	12.29	10.63	6.72	5.32	5.18	3.27	13.55	5.94	3.67
	SD	0.27	0.14	0.20	0.16	0.11	0.13	0.16	0.11	0.28	0.27	0.13
	MIN	20.56	9.43	11.92	10.40	6.61	5.07	4.96	3.13	13.05	5.49	3.42
	MAX	21.39	9.79	12.50	10.88	6.89	5.43	5.47	3.44	13.92	6.21	3.82
Hipposideros sorenseni (Pangandaran-C/W Java)	N	7	7	7	7	7	7	7	7	7	7	7
	X	21.63	10.00	12.49	10.94	6.83	5.04	5.41	3.19	14.43	5.68	3.82
	SD	0.33	0.13	0.17	0.19	0.23	0.27	0.21	0.10	0.43	0.40	0.14
	MIN	21.15	9.83	12.34	10.58	6.62	4.75	5.06	3.00	13.65	4.83	3.56
	MAX	22.11	10.17	12.81	11.15	7.27	5.43	5.63	3.29	14.86	6.00	3.96
Hipposideros l. larvatus (Sarawak)	Value N = 1	22.04	9.90	13.67	11.20	6.85	4.85	5.32	3.70	14.27	6.32	3.99
Hipposideros l. larvatus (P. Malaysia)	Value	22.36	10.58	13.32	11.29	7.07	5.04	5.45	3.53	13.79	6.45	3.86
	N = 2	20.88	9.60	12.67	10.89	6.52	4.77	5.19	3.35	13.62	6.04	3.59
Hipposideros sp. indet (Sukabumi-W. Java)	Value	21.08	9.88	12.10	10.80	6.60	4.98	5.37	3.14	13.82	5.56	3.74
	N = 2	21.34	9.90	12.45	11.03	6.55	4.96	5.60	3.45	14.72	5.44	3.67
Hipposideros sp. cf. *H. grandis* (Thailand)	Value N = 1	21.07	9.74	12.14	10.67	6.74	4.63	5.48	3.47	13.45	6.30	3.68
Hipposideros sumbae	N	86	86	86	86	86	86	86	86	86	86	86
	X	20.24	9.44	11.89	10.29	6.52	4.79	5.17	3.14	13.51	5.18	3.41
	SD	0.45	0.26	0.32	0.20	0.16	0.24	0.24	0.18	0.30	0.27	0.18
	MIN	19.28	8.71	11.19	9.82	6.17	4.24	4.63	2.78	12.97	4.56	3.03
	MAX	21.26	10.01	12.79	10.76	6.91	5.49	5.78	3.64	14.69	5.88	3.93
Hipposideros sumbae sumbae	N	15	15	15	15	15	15	15	15	15	15	15
	X	20.57	9.68	12.12	10.49	6.51	4.75	5.39	3.08	13.46	5.30	3.45
	SD	0.30	0.20	0.20	0.15	0.12	0.24	0.17	0.09	0.23	0.28	0.21
	MIN	20.05	9.31	11.72	10.27	6.25	4.38	5.18	2.89	13.20	4.86	3.10
	MAX	20.99	10.01	12.48	10.76	6.73	5.33	5.60	3.20	13.88	5.87	3.93
Hipposideros sumbae rotiensis	N	9	9	9	9	9	9	9	9	9	9	9
	X	20.76	9.59	11.96	10.39	6.57	4.99	5.39	2.99	13.65	5.30	3.57
	SD	0.22	0.15	0.23	0.09	0.15	0.19	0.19	0.19	0.19	0.29	0.16
	MIN	20.55	9.35	11.80	10.26	6.33	4.70	5.17	2.78	13.38	4.88	3.36
	MAX	21.15	9.86	12.55	10.51	6.71	5.20	5.78	3.17	13.91	5.88	3.80
Hipposideros sumbae sumbawae	N	54	54	54	54	54	54	54	54	54	54	54
	X	20.01	9.34	11.80	10.20	6.51	4.76	5.04	3.20	13.48	5.11	3.36
	SD	0.35	0.21	0.29	0.18	0.16	0.23	0.19	0.18	0.32	0.25	0.16
	MIN	19.28	8.82	11.19	9.82	6.23	4.24	4.63	2.80	12.97	4.56	3.03
	MAX	20.84	9.89	12.38	10.60	6.91	5.29	5.48	3.64	14.69	5.63	3.83
Hipposideros sumbae subsp. indet. A (Semau)	N	4	4	4	4	4	4	4	4	4	4	4
	X	20.78	9.72	12.15	10.42	6.72	4.71	5.25	2.96	13.86	5.36	3.37
	SD	0.15	0.19	0.24	0.06	0.12	0.13	0.04	0.11	0.21	0.23	0.16
	MIN	20.60	9.52	11.80	10.36	6.60	4.58	5.20	2.80	13.65	5.12	3.13
	MAX	20.97	9.89	12.32	10.49	6.83	4.88	5.30	3.07	14.05	5.65	3.46
Hipposideros sumbae subsp. indet. B (Savu)	N	3	3	3	3	3	3	3	3	3	3	3
	X	20.08	9.05	11.57	10.20	6.39	4.80	5.24	3.08	13.33	5.19	3.44
	SD	0.08	0.30	0.30	0.12	0.21	0.14	0.12	0.07	0.20	0.10	0.18
	MIN	20.01	8.71	11.34	10.10	6.17	4.64	5.11	3.03	13.15	5.13	3.28
	MAX	20.17	9.30	11.91	10.33	6.59	4.90	5.32	3.16	13.55	5.30	3.63
Hipposideros sumbae (Timor)	N	1	1	1	1	1	1	1	1	1	1	1
	VALUE	21.26	9.70	12.79	10.62	6.50	5.49	5.46	2.87	14.18	5.42	3.56

PML	MF	TBL	TBB	NIW	CW	M^3M^3B	C^1C^1B	C^1W	P^3L	P^3W	M^1L	M^1W	M^2L
60	60	60	60	60	60	60	60	60	60	60	60	60	60
4.18	2.19	2.90	10.46	6.53	2.56	8.70	5.45	1.54	1.41	1.63	2.03	2.12	1.98
0.19	0.10	0.17	0.23	0.15	0.17	0.20	0.22	0.12	0.08	0.08	0.08	0.12	0.09
3.49	1.99	2.48	9.92	6.07	2.21	8.32	5.05	1.28	1.26	1.40	1.78	1.78	1.74
4.63	2.43	3.21	10.96	6.76	2.96	9.09	5.98	1.79	1.64	1.82	2.24	2.30	2.23
15	15	15	15	15	15	15	15	15	15	15	15	15	15
4.11	2.08	2.82	9.92	6.22	2.55	8.56	5.11	1.49	1.33	1.53	2.01	2.11	1.96
0.14	0.08	0.16	0.30	0.14	0.15	0.12	0.17	0.08	0.09	0.06	0.11	0.15	0.08
3.93	1.97	2.54	9.50	5.97	2.22	8.19	4.76	1.35	1.21	1.42	1.82	1.80	1.81
4.38	2.21	3.03	10.43	6.52	2.78	8.74	5.42	1.61	1.52	1.68	2.16	2.31	2.07
8	8	8	8	8	8	8	8	8	8	8	8	8	8
4.13	2.10	2.76	9.82	6.26	2.49	8.52	5.05	1.48	1.32	1.55	2.01	2.21	1.94
0.14	0.08	0.15	0.21	0.16	0.16	0.16	0.21	0.09	0.07	0.04	0.11	0.07	0.06
3.96	1.97	2.54	9.54	6.03	2.22	8.19	4.76	1.35	1.21	1.47	1.82	2.15	1.83
4.38	2.20	2.97	10.20	6.52	2.65	8.74	5.42	1.58	1.43	1.60	2.16	2.31	2.03
7	7	7	7	7	7	7	7	7	7	7	7	7	7
4.10	2.05	2.89	10.04	6.18	2.62	8.60	5.18	1.50	1.35	1.52	2.01	1.98	1.98
0.14	0.08	0.14	0.36	0.11	0.12	0.06	0.09	0.07	0.12	0.08	0.12	0.13	0.10
3.93	1.98	2.69	9.50	5.97	2.47	8.50	5.05	1.41	1.21	1.42	1.84	1.80	1.81
4.34	2.21	3.03	10.43	6.29	2.78	8.67	5.32	1.61	1.52	1.68	2.15	2.21	2.07
7	7	7	7	7	7	7	7	7	7	7	7	7	7
4.16	2.21	2.98	10.34	6.48	2.51	8.66	5.34	1.51	1.30	1.68	2.00	2.20	1.96
0.20	0.08	0.14	0.16	0.08	0.09	0.15	0.19	0.07	0.04	0.06	0.09	0.11	0.13
3.90	2.11	2.79	10.09	6.32	2.40	8.46	5.08	1.43	1.25	1.58	1.87	2.06	1.68
4.36	2.30	3.20	10.53	6.57	2.65	8.86	5.60	1.64	1.35	1.78	2.09	2.39	2.06
4.50	2.37	2.85	10.59	6.77	2.65	9.12	5.51	1.56	1.43	1.78	2.01	2.15	2.16
4.45	2.09	2.83	10.85	6.51	2.55	9.22	5.67	1.54	1.35	1.85	2.06	2.32	2.05
4.35	2.00	2.63	10.41	6.35	2.65	8.24	5.03	1.61	1.32	1.61	2.05	2.05	2.06
4.20	2.10	3.04	10.30	6.60	2.70	8.36	5.32	1.66	1.35	1.55	1.96	2.05	1.77
3.76	2.23	3.01	10.59	6.32	2.29	8.48	5.20	1.51	1.36	1.59	2.06	2.13	1.98
4.05	2.27	3.03	10.37	6.60	2.61	8.52	5.26	1.35	1.35	1.58	1.76	2.07	1.80
86	86	86	86	86	86	86	86	86	86	86	86	86	86
3.98	2.10	2.83	9.77	6.24	2.49	8.01	4.93	1.41	1.28	1.50	1.93	1.97	1.88
0.20	0.14	0.13	0.24	0.16	0.17	0.17	0.19	0.07	0.10	0.07	0.08	0.13	0.08
3.53	1.76	2.56	9.29	5.92	2.13	7.63	4.50	1.24	1.10	1.34	1.72	1.60	1.73
4.41	2.92	3.17	10.34	6.78	2.85	8.50	5.44	1.61	1.56	1.69	2.14	2.21	2.06
15	15	15	15	15	15	15	15	15	15	15	15	15	15
3.88	2.17	2.78	9.93	6.35	2.32	8.19	4.95	1.42	1.30	1.49	1.96	2.06	1.89
0.15	0.09	0.15	0.20	0.14	0.14	0.16	0.17	0.07	0.12	0.06	0.06	0.08	0.07
3.53	2.01	2.56	9.59	6.09	2.15	7.90	4.70	1.32	1.11	1.40	1.87	1.93	1.77
4.08	2.35	3.04	10.25	6.59	2.58	8.50	5.32	1.61	1.56	1.61	2.07	2.21	2.04
9	9	9	9	9	9	9	9	9	9	9	9	9	9
4.19	2.11	2.93	9.83	6.40	2.56	7.95	4.92	1.43	1.28	1.47	1.96	1.94	1.88
0.06	0.08	0.14	0.27	0.20	0.12	0.16	0.19	0.10	0.13	0.09	0.11	0.14	0.05
4.11	1.94	2.70	9.36	6.13	2.37	7.76	4.64	1.24	1.10	1.38	1.84	1.76	1.81
4.31	2.21	3.16	10.34	6.78	2.70	8.29	5.25	1.52	1.54	1.69	2.14	2.12	1.96
54	54	54	54	54	54	54	54	54	54	54	54	54	54
3.94	2.06	2.82	9.68	6.18	2.54	7.97	4.91	1.41	1.29	1.49	1.92	1.95	1.86
0.19	0.16	0.12	0.20	0.11	0.14	0.14	0.18	0.07	0.10	0.07	0.08	0.13	0.08
3.55	1.76	2.57	9.29	5.92	2.21	7.63	4.50	1.26	1.13	1.34	1.72	1.60	1.73
4.39	2.92	3.03	10.07	6.38	2.82	8.26	5.25	1.53	1.51	1.68	2.09	2.15	2.06
4	4	4	4	4	4	4	4	4	4	4	4	4	4
4.18	2.21	2.83	10.09	6.37	2.51	8.08	5.18	1.42	1.25	1.57	1.96	2.08	1.94
0.12	0.05	0.13	0.14	0.17	0.24	0.09	0.20	0.06	0.08	0.07	0.02	0.11	0.07
4.02	2.14	2.64	9.97	6.23	2.33	8.00	4.96	1.36	1.16	1.51	1.93	1.93	1.84
4.31	2.25	2.93	10.30	6.61	2.85	8.21	5.44	1.49	1.33	1.68	1.98	2.20	2.00
3	3	3	3	3	3	3	3	3	3	3	3	3	3
4.05	2.06	2.77	9.76	6.21	2.24	7.88	4.76	1.36	1.23	1.57	1.92	1.88	1.90
0.23	0.09	0.08	0.17	0.19	0.12	0.23	0.12	0.06	0.05	0.09	0.01	0.05	0.16
3.78	1.96	2.68	9.57	6.03	2.13	7.69	4.67	1.31	1.18	1.47	1.91	1.84	1.74
4.20	2.12	2.84	9.91	6.41	2.37	8.13	4.89	1.42	1.27	1.64	1.93	1.93	2.05
1	1	1	1	1	1	1	1	1	1	1	1	1	1
4.41	2.27	3.17	10.32	6.43	2.72	8.16	5.40	1.40	1.37	1.41	2.05	1.76	2.02

CHARACTER TAXON		M^2W	M^3L	M^3W	I_1M_3L	DL	RAP	SVL	TVL
Hipposideros l. larvatus (W. Java, Pulau Laut, Krakatau, Sumatra, Nias I)	N	60	60	60	60	60	60	43	43
	X	2.35	1.28	1.89	9.96	15.20	5.87	55.68	30.46
	SD	0.14	0.05	0.08	0.23	0.32	0.25	2.50	2.42
	MIN	2.02	1.17	1.71	9.39	14.07	5.25	50.30	26.14
	MAX	2.58	1.45	2.07	10.44	16.07	6.66	61.23	35.43
Hipposideros madurae (total)	N	15	15	15	15	15	15	8	8
	X	2.30	1.28	1.92	9.78	14.65	5.65	56.11	27.69
	SD	0.18	0.05	0.07	0.30	0.29	0.29	2.14	2.74
	MIN	2.00	1.21	1.78	9.09	14.20	5.13	52.19	23.55
	MAX	2.56	1.40	2.05	10.21	15.15	6.09	58.90	30.91
Hipposideros madurae madurae (Madura I.)	N	8	8	8	8	8	8	8	8
	X	2.43	1.27	1.92	9.70	14 52	5.56	56.11	27.69
	SD	0.12	0.05	0.07	0.34	0.33	0.29	2.14	2.74
	MIN	2.24	1.21	1.78	9.09	14.20	5.13	52.19	23.55
	MAX	7.56	1.36	2.00	10.11	15.15	6.01	58.90	30.91
Hipposideros madurae jenningsi (Semarang-C. Java)	N	7	7	7	7	7	7	-	-
	X	2.16	1.30	1.92	9.88	14.80	5.74	-	-
	SD	0.11	0.06	0.08	0.22	0.17	0.27	-	-
	MIN	2.00	1.23	1.82	9.50	14.61	5.20	-	-
	MAX	2.31	1.40	2.05	10.21	15.02	6.09	-	-
Hipposideros sorenseni (Pangandaran-C/W Java)	N	7	7	7	7	7	7	6	6
	X	2.42	1.31	1.93	10.03	14.92	5.53	53.89	32.78
	SD	0.11	0.07	0.08	0.17	0.24	0.39	4.01	2.49
	MIN	2.18	1.22	1.82	9.77	14.42	5.00	50.16	30.07
	MAX	2.50	1.39	2.02	10.23	15.16	6.10	60.00	36.20
Hipposideros l. larvatus (Sarawak)	Value N = 1	2.38	1.37	1.96	10.79	15.45	6.33	56.73	29.93
Hipposideros l. larvatus (P. Malaysia)	Value	2.51	1.33	1.84	10.63	15.64	5.90	60.09	33.10
	N = 2	2.31	1.31	1.93	10.01	15.21	5.97	57.99	34.62
Hipposideros sp. indet. (Sukabumi-W. Java)	Value	2.37	1.25	1.84	10.00	14.88	5.73	51.78	28.79
	N = 2	2.19	1 24	1.86	9.89	14.96	5.80	56.73	30.79
Hipposideros sp. cf. *H. grandis* (Thailand)	Value N = 1	2.39	1.30	1.84	9.52	14.27	5.61	57.23	31.77
Hipposideros sumbae	N	86	86	86	86	86	86	72	71
	X	2.19	1.22	1.78	9.23	13.91	5.50	52.34	28.26
	SD	0.11	0.05	0.09	0.24	0.37	0.30	2.20	2.03
	MIN	1.84	1.10	1.52	8.48	13.09	4.60	47.67	24.05
	MAX	2.48	1.32	1.95	9.76	14.81	6.08	58.97	32.55
Hipposideros sumbae sumbae	N	15	15	15	15	15	15	15	15
	X	2.26	1.24	1.84	9.40	14.17	5.49	52.43	28.73
	SD	0.07	0.05	0.05	0.20	0.34	0.28	1.71	2.16
	MIN	2.11	1.16	1.75	9.08	13.54	4.82	49.80	24.78
	MAX	2.40	1.32	1.95	9.76	14.81	5.92	56.04	32.55
Hipposideros sumbae rotiensis	N	9	9	9	9	9	9	9	8
	X	2.17	1.20	1.73	9.27	14.10	5.63	51.60	30.23
	SD	0.05	0.06	0.05	0.23	0.21	0.43	2.72	1.44
	MIN	2.09	1.10	1.66	9.00	13.77	4.86	47.80	27.53
	MAX	2.24	1.28	1.83	9.69	14.43	5.96	55.20	32.14
Hipposideros sumbae sumbawae	N	54	54	54	54	54	54	41	41
	X	2.17	1.22	1.78	9.16	13.77	5.45	52.68	27.88
	SD	0.12	0.04	0.09	0.22	0.34	0.26	2.14	1.93
	MIN	1.84	1.12	1.52	8.48	13.09	4.60	48.65	24.05
	MAX	2.48	1.32	1.94	9.58	14.28	5.96	58.97	31.60
Hipposideros sumbae subsp. indet. A (Semau)	N	4	4	4	4	4	4	4	4
	X	2.28	1.22	1.81	9.36	14.24	5.81	49.52	27.65
	SD	0.14	0.06	0.08	0.09	0.15	0.32	2.22	1.70
	MIN	2.10	1.15	1.72	9.25	14.09	5.41	47.67	26.16
	MAX	2.40	1.28	1.87	9.44	14.40	6.08	52.27	30.09
Hipposideros sumbae subsp. indet. B (Savu)	N	3	3	3	3	3	3	3	3
	X	2.20	1.18	1.69	9.19	13.79	5.43	53.17	26.56
	SD	0.04	0.02	0.08	0.42	0.19	0.33	0.60	0.63
	MIN	2.15	1.16	1.61	8.72	13.64	5.11	52.79	25.86
	MAX	2.23	1.20	1.77	9.52	14.00	5.77	53.87	27.08
Hipposideros sumbae (Timor)	N	1	1	1	1	1	1		
	VALUE	2.00	1.26	1.76	9.25	14.73	6.08		

EL	TIL	TOL	FA	D2MC	D3MC	D3P1	D3P2	D4MC	D4P1	D4P2	D5MC	D5P1	D5P2
43	59	60	60	60	60	60	60	60	60	60	60	60	60
20.94	22.15	5.05	57.47	45.70	42.89	19.13	19.61	42.01	13.54	10.11	38.03	14.79	10.88
1.14	1.42	0.41	2.00	1.75	1.59	0.87	1.29	1.49	0.68	0.61	1.32	0.69	0.65
18.56	18.37	3.99	53.19	42.48	39.20	16.44	16.84	39.04	12.22	8.68	35.28	12.77	9.82
23.31	24.83	5.78	62.05	49.84	46.15	20.90	22.39	45.33	15.64	12.07	41.21	16.37	15.52
8	15	15	15	15	15	15	15	15	15	15	15	15	15
20.13	19.32	4.55	54.96	43.79	41.27	18.81	18.12	39.89	13.24	9.85	36.00	14.37	10.44
0.57	1.03	0.40	1.39	1.48	1.20	0.94	1.17	1.20	0.93	0.68	1.25	0.68	0.42
19.61	17.58	3.96	53.13	40.56	38.85	17.41	14.84	37.60	12.01	8.71	33.60	12.90	9.98
21.23	20.81	5.14	57.93	46.35	43.28	20.45	19.88	42.28	15.74	11.04	38.69	15.87	11.33
8	8	8	8	8	8	8	8	8	8	8	8	8	8
20.13	19.66	4.85	54.91	43.43	40.88	18.52	18.41	39.41	12.66	9.48	35.77	14.06	10.44
0.57	0.77	0.22	1.03	1.66	1.32	0.75	0.71	1.21	0.44	0.63	1.30	0.49	0.38
19.61	18.34	4.58	53.58	40.56	38.85	17.41	17.39	37.60	12.01	8.71	33.60	12.90	10.04
21.23	20.59	5.14	56.09	45.71	42.05	19.83	19.88	40.99	13.44	10.51	37.20	14.46	11.05
-	7	7	7	7	7	7	7	7	7	7	7	7	7
-	18.94	4.19	55.01	44.20	41.72	19.13	17.79	40.45	13.91	10.28	36.27	14.74	10.45
-	1.21	0.23	1.81	1.24	0.93	1.08	1.50	0.99	0.90	0.46	1.23	0.71	0.50
-	17.58	3.96	53.13	42.64	40.52	17.72	14.84	39.25	12.87	9.64	34.95	13.77	9.98
-	20.81	4.66	57.93	46.35	43.28	20.45	19.44	42.28	15.74	11.04	38.69	15.87	11.33
6	7	7	7	7	7	7	7	7	7	7	7	7	7
21.20	21.97	4.59	57.52	46.23	43.41	18.99	19.80	41.69	13.67	10.08	35.51	14.83	10.91
1.09	0.75	0.33	1.55	0.86	0.43	0.42	0.76	1.37	0.61	0.83	1.49	0.44	0.70
20.16	21.38	4.19	55.41	44.79	42.58	18.45	18.78	39.18	12.96	9.13	35.81	14.14	10.05
22.78	23.31	5.11	60.22	47.65	43.95	19.68	20.70	43.19	14.83	11.37	39.84	15.45	12.06
20.21	21.98	5.40	56.89	47.03	44.00	18.58	19.02	41.61	13.35	10.74	38.50	14.75	10.64
20.46	22.65	5.08	57.82	46.82	43.80	19.94	20.34	42.32	14.25	11.06	38.26	15.36	12.17
20.18	22.49	5.18	59.24	47.24	44.53	18.70	20.04	43.11	13.18	10.63	39.08	15.47	10.79
22.46	22.17	5.04	56.47	45.20	42.71	18.59	19.09	42.22	13.27	10.31	37.34	13.96	10.50
22.38	22.51	4.99	58.65	45.03	42.70	20.13	20.36	42.26	12.79	10.45	38.49	14.26	11.05
23.23	21.48	5.22	54.01	43.58	40 76	17.30	18.10	40.51	13.89	9.62	36.55	14.86	9.82
72	86	86	86	86	86	86	86	86	86	86	86	86	86
21.14	19.59	4.96	54.00	42.97	40.48	17.62	17.95	39.01	39.01	12.98	8.99	35.44	9.74
1.06	0.75	0.37	1.44	1.25	1.05	0.72	1.01	0.97	0.97	0.53	0.53	0.84	0.53
19.11	17.38	3.90	49.86	39.57	38.17	15.20	14.97	36.39	36.39	11.62	7.39	33.34	8.46
23.77	21.24	5.59	57.02	45.59	43.44	19.07	20.54	40.98	40.98	14 73	10.05	37.30	11.11
15	15	15	15	15	15	15	15	15	15	15	15	15	15
21.81	19.83	5.15	54.34	43.26	40.78	17.53	17.77	39.39	39.39	12.99	8.82	35.62	9.55
0.91	0.67	0.12	0.96	1.25	1.02	0.52	0.51	0 80	0.80	0.43	0.36	0.75	0.32
20.37	19.03	4.94	52.34	40.68	38.82	16.69	17.17	37.79	37.79	12.15	8.29	34.43	9.03
23.04	21.24	5.37	55.55	45.07	43.08	18.64	19.08	40.46	40.46	13.57	9.54	37.30	9.99
9	9	9	9	9	9	9	9	9	9	9	9	9	9
22.46	20.23	5.21	53.83	43.31	40.50	18.36	18.84	39.44	39.44	13.50	8.99	35.78	9.92
0.86	0.49	0.16	1.61	0.74	0.43	0.37	0.71	0.36	0.36	0.30	0.17	0.42	0.44
21.12	19.29	5.02	51.89	42.21	40.01	17.98	17.89	38.80	38.80	13.06	8.78	35.11	9.43
23.77	21.03	5.43	55.84	44.48	41.46	18.98	20.15	39.85	39.85	14.00	9.28	36.40	10.61
41	54	54	54	54	54	54	54	54	54	54	54	54	54
20.51	19.41	4.85	53.92	42.90	40.44	17.43	17 85	38.87	12.87	9.03	35.35	14.28	9.76
0.61	0.77	0.42	1.52	1.29	1.09	0.71	1.10	0.98	0.53	0.61	0.86	0.56	0.54
19.11	17.38	3.90	49.86	39.57	38.17	15.20	14.97	36.39	11.62	7.39	33.34	12.45	8.59
21.61	20.88	5.59	57.05	45.59	43.44	18.96	20.54	40.97	14.73	10.05	37.14	15.31	11.11
4	4	4	4	4	4	4	4	4	4	4	4	4	4
22.06	19.76	5.08	54.17	42.36	40.32	18.47	17.93	39.27	13.26	8.96	35.61	14.08	9.53
1.13	0.79	0.22	1.99	1.79	1.28	0.53	0.66	1.59	0.82	0.67	1.18	0.85	0.82
20.84	18.84	4.81	52.03	40.11	38.69	17.80	17.03	37.31	12.23	8.35	34.14	13.09	8.46
23.29	20.58	5.30	56.13	44.31	41.68	19.07	18.57	40.98	14.05	9.76	36.84	14.85	10.41
3	3	3	3	3	3	3	3	3	3	3	3	3	3
21.14	19.69	5.02	54.12	42.09	39.48	17.84	17.71	37.67	12.84	9.01	34.66	13.97	9.65
0.89	0.27	0.12	1.50	0.73	1.26	0.56	1.48	0.44	0.23	0.42	1.12	0.67	0.39
20.11	19.52	4.89	52.79	41 59	38.23	17.20	16.00	37.23	12.58	8.54	33.81	13.23	9.22
21.75	20.00	5.12	55.79	42.93	40.74	18.23	18.60	38.11	13.03	9.35	35.93	14.53	9.99

Description

Skull (Table 1, Figures 4, 7-9)

Cranium long relative to nasal length (2.456), lateral profile gently sloping to posteriormost point but a little more sharply sloping approaching junction of sagittal and lambdoidal crests; premaxilla-maxilla ventral junction U or V shaped; sagittal crest well developed but posterior one-quarter weak and barely reaching lambdoidal crest; supraorbital ridges moderately well developed and diverge sharply from junction with sagittal crest; nasal inflation with curved posterolateral edges; nasal inflation moderate; frontal depression shallow; rostral eminences moderately inflated, separated by shallow groove; nasal inflation lateral profile subrounded to only slightly arched; anteorbital foramen elongate and separated from orbit by moderately wide bar; maxilla generally encloses slightly elongate palatal foramen but occasionally do not enclose this foramen or do so only partially; posterior palatal margin usually U shaped, occasionally slightly more sharply angled; vomer projects posterior of palatal shelf; sphenoid bridge parallel sided or very slightly expanded posteriorly, from ventral aspect almost conceals sphenorbital sinus above, moderately deep median groove; C^1 with low anterior cusp, posterior cusp absent; PM^2 slightly extruded from toothrow, compressed tightly between C^1 and PM^4 (which are in contact or nearly so); PM_2 moderately large usually three-quarters length of PM_4.

Externals

Anterior noseleaf with small but distinct median emargination; occasionally this emargination supported by small tongue like protrusion beyond margin of leaf; three accessory lateral leaflets; internarial septum only very slightly inflated but its width not exceeding *c.* 0.7 mm; narial lappets well developed height above surface of anterior noseleaf *c.* 0.6 mm; nostril slightly pocketed; intermediate leaf width only slightly less than that of anterior noseleaf, with moderate median swelling and weaker lateral swellings; posterior leaf moderate with three well defined septa, upper edge semicircular; frontal sac in both sexes, but in females reduced to a depression, often shallow with a tuft of hair; ear with small process at antitragal fold.

Pelage

Dorsal surface with basal two-thirds of hairs Cream Color to Straw Yellow tipped with Fawn Color to Russet. This tipping dominates colour of back and forehead but is only very light on shoulders, neck and face such that under colour emerges as a pale cape of hair in these parts. Throat and chin hairs Cinnamon to Straw Yellow, while venter a darker Drab to Smoke Gray. Wing membranes and ears Burnt Umber.

Glans penis (Figure 6a)

The glans penis was examined from specimens from Ciampea, Ujong Kulon, Carita (W. Java), Krakatau Is, Aceh (N. Sumatra) and Nias I. The glans distal part laterally compressed such that the distal lobe covering cranial arms of baculum elongate. In lateral profile, distal end of glans slightly flared with the anterodorsal part projected slightly more so than the corresponding ventral part dorsal slit about 1.2 mm long, such that when lateral distal flanges widened it exposed large urethral vestible.

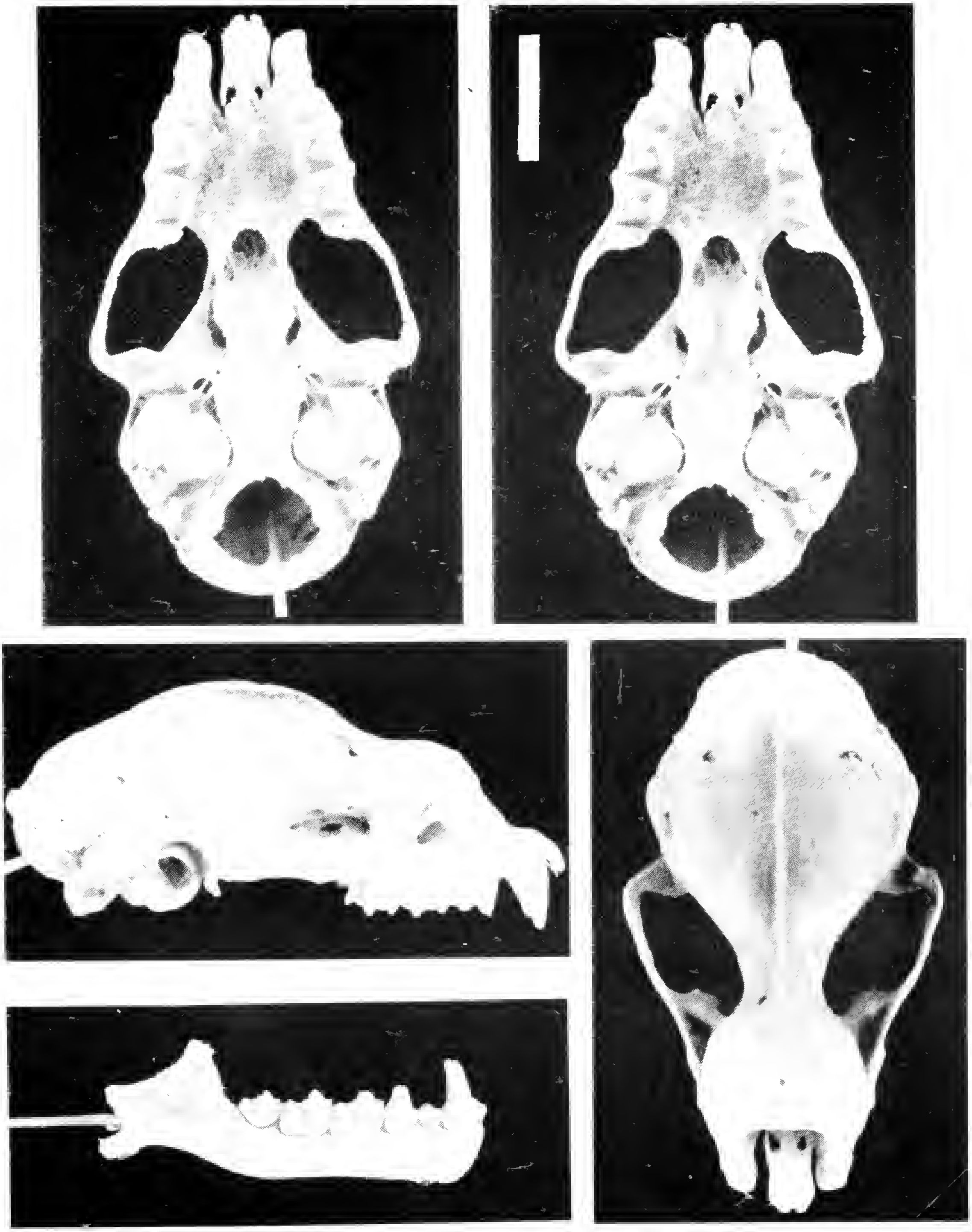

Figure 4 Photograph of skull and dentary of *Hipposideros l. larvatus*, MZB 1415, Krakatau Is; ventral view as stereopair. Scale line 5 mm.

Baculum (Figure 5a)

Short, base 0.51 ± 0.048 (N = 8) wide, total length 1.07 ± 0.068(8). Almost three quarters of length baculum comprises bifurcating arms from base, distal one quarter of arms inflected sharply cranially to a height above the base of 0.51 ± 0.078(8).

Distribution

W. Java, Palau Laut, Krakatau Is, Sumatra, Nias I., probably Peninsular Malaysia and Borneo (Figure 1).

Referred specimens

Two specimens from Pahang, Peninsular Malaysia and one from Sarawak were examined and measured. They had a glans penis and baculum that were very similar to *H. l. larvatus*. Further, when these three specimens were included in the DFA they clustered with the *H. l. larvatus* group.

Hipposideros madurae sp. nov.

Table 1; Figures 1,5b,c,6b,7-9,17,20-21

Diagnosis

Hipposideros madurae differs from *Hipposideros larvatus* in having a generally smaller skull (Table 1). For example greatest skull length (20.84 v. 21.49); zygomatic breadth (12.23 v. 12.87); C^1C^1 breadth (5.11 v. 5.45); mastoid breadth shorter relative to rostrum height (2.120 v. 2.202) and least interorbital width (with exception of two Pulau Laut specimens (Figure 7); C^1C^1 breadth averages shorter relative to nasal inflation length (0.856 v. 0.945) and I_1-M_3 length (0.523 v. 0.547); cranial length shorter relative to nasal inflation length (2.263 v. 2.456). Tibia length averages smaller (19.32 v. 22.15). Glans penis less laterally compressed distally with central distal fleshy lobe attached to baculum more elongate (Figure 6a & b). Baculum oval in dorsal outline rather than elongate, bifurcating distal arms short and deep rather than long and thin, basal area much larger (Figures 5a,b,c,6a,b).

It differs from *Hipposideros sorenseni* in having a generally smaller skull (Table 1). For example: greatest skull length (20.84 v. 21.63); braincase width (9.50 v. 10.00); zygomatic breadth (12.23 v. 12.49); cranial length (13.51 v. 14.43); greatest skull length averages shorter relative to nasal inflation length (3.491 v. 3.808); mastoid breadth narrower relative to least interorbital width (Figure 7); cranial length shorter relative to nasal inflation length (2.263 v. 2.541). Digit 5 metacarpal length smaller relative to toe length (Figure 17); tibia length smaller relative to toe length (Figure 18). Baculum shorter (0.75-0.93 v. 1.15-1.20), distal bifurcating arms relatively longer with concomitant shorter solid basal part (Figure 5b,c and d).

It differs from *H. sumbae* by averaging larger in most skull measurements (see Table 1). For example, greatest skull length (20.84 v. 20.24); palatal bridge length (3.71 v. 3.41); nasal inflation length (5.97 v. 5.18); dentary length (14.65 v. 13.91); M^3-M^3 breadth (8.56 v. 8.01); I_1-M_3 length (9.78 v. 9.23). Palatal width relatively broader as indicated by outside M^3M^3 breadth relative to nasal inflation width (Figure 8). Nasal inflation length relative to nasal inflation width averages much larger (0.960 v. 0.830); cranial length relatively shorter relative to nasal inflation length (2.263 v. 2.608); dentary length larger relative to rostrum length (Figure 9). Digit 5 phalanx 2 longer (10.45-10.91 v. 9.53-9.92). Glans penis with distal outline squarer in lateral profile, central distal lobe more vertical (Figure 6b and c). Baculum more robust, distal bifurcating arms longer with concomitant shorter base, cranial projection of arms taller with distal edge more vertical (Figure 5b,c and e).

Hipposideros madurae madurae subsp. nov.

Table 1; Figures 1,5b,6b,10,18,20

Holotype

Museum Zoologicum Bogoriense, MZB 10613B, adult male, carcase in alcohol, penis intact, skull separate.

Type locality

Sampang, Pulau Madura (Madura I.) nr NE Java (7° 13′S; 113° 15′E); altitude 0-30 m..

Paratypes

Listed in section "Specimens Examined".

Diagnosis

Hipposideros m. madurae differs from *H. m. jenningsi* sp. nov. in having a generally slightly smaller skull (Table 1). Rostrum height shorter relative to both nasal inflation length (0.780 v. 0.896) and mastoid breadth (Figure 10); cranial height smaller relative to nasal inflation length (1.089 v. 1.131); least interorbital width smaller relative to nasal inflation length (0.513 v. 0.551); toe length longer relative to tibia length (Figure 18).

Description

Skull (Table 1; Figure 20)

Skull as for *H. l. larvatus* but skull smaller; zygomatic breadth narrower; C^1C^1 breadth narrower; supraorbital ridges tend to be weaker and diverge less sharply from junction with sagittal crest; frontal depression very shallow; rostrum tends to be flatter; mesopterygoid fossa tends to be narrower with palation squarer and occasionally (MZB 10613F and MZB 10615B) with a tiny postpalatal projection; sphenoidal bridge parallel sided and conceals considerably less of sphenorbital sinus.

Externals (Table 1)

As for *H. l. larvatus.*

Glans Penis (Figure 6b)

Distal view suboval with central fleshy lobe attached to baculum subrectangular; this distal lobe with moderately large basal oval eminences projecting anterior of lobe; distal tip in lateral view only very slightly flared with anterior margin almost vertical; dorsal slit *c.* 1.1 mm long, such that when lateral distal flanges widened urethral vestible large.

Baculum (Figure 5b)

Baculum short (greatest length 0.75-0.82, N = 2); with wide (0.59 - 0.60) robust basal part; bifurcating distal arms short, a little more than half basal length, with cranial projecting part robust and 0.75-0.82 above basal part. Anterior edge of cranial arms almost vertical.

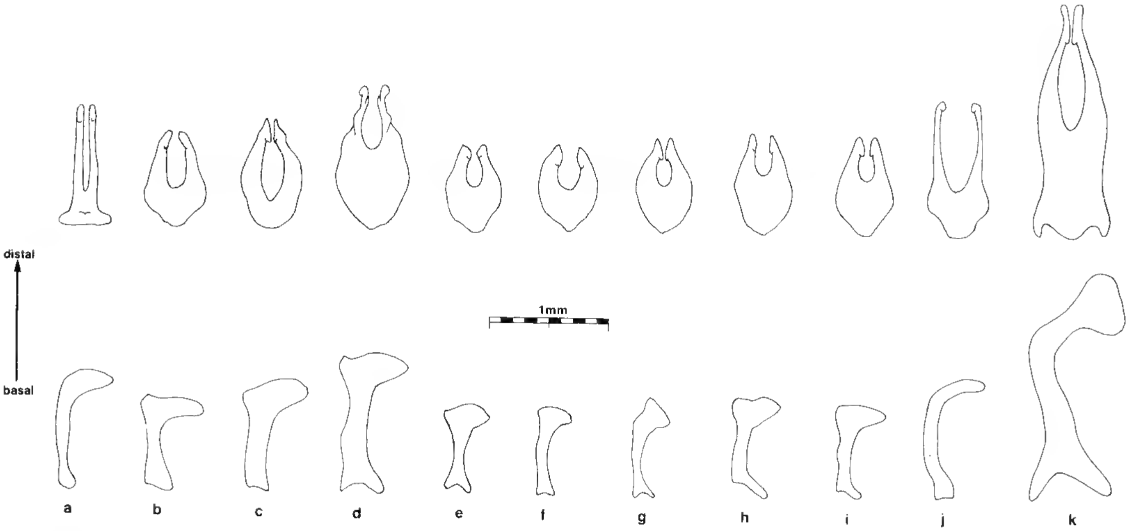

Figure 5 Baculum of forms of *Hipposideros* studied (top, dorsal view; bottom, lateral view). (a) *H. l. larvatus* (WAM M23305); (b) *H. m. madurae* (MZB 10613c); (c) *H. m. jenningsi* (MZB 14855); (d) *H. sorenseni* (MZB 10612A); (e) *H. s. sumbae* (WAM M30338); (f) *H. s. rotiensis* (WAM M35369); (g) *H. s. sumbawae* (WAM M31553); (h) *H. sumbae* subsp. indet. A (WAM M38017) (Semau I.); (i) *H. sumbae* subsp. indet. B (WAM M35259) (Savu I.); (j) *H.* sp. indet. (WAM M30009) (Sukabumi, W. Java); and (k) *Hipposideros* sp. cf. *H. grandis* (WAM M26828) (Thailand).

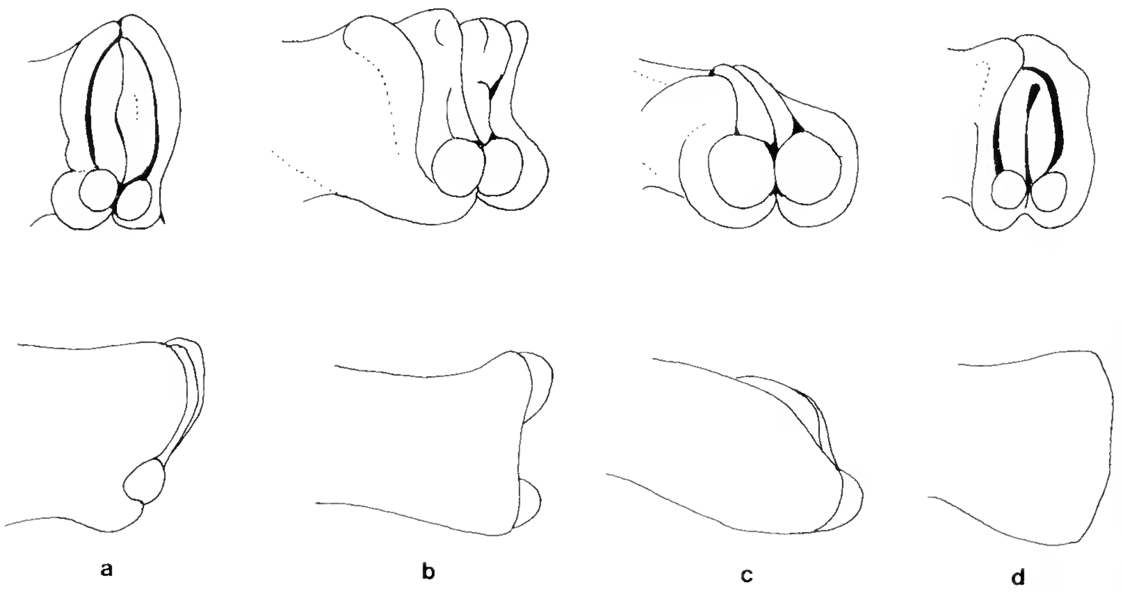

Figure 6 Glans penis of (a) *Hipposideros l. larvatus*; (b) *H. madurae*; (c) *H. sumbae*; and (d) *H.* sp. cf. *H. grandis* (Thailand). (Top row, oblique view; bottom row, lateral view).

Distribution

Madura I., Indonesia.

Etymology

Named after Madura I.

Hipposideros madurae jenningsi subsp. nov.

Table 1; Figures 1,5c,6b,10,18 and 21

Holotype

Museum Zoologicum Bogoriense, MZB14883 (collection number 103/40), adult female, 'puppet skin', skull separate, collected 29 February 1940 by A. V. Von Bemmel.

Type locality

Goa (≡ cave) Landak, near Desa (village), Karang Sagung, Semarang district, C. Java (*c.* 6° 58′S, 110° 29′E).

Paratypes

Listed in section "Specimens Examined".

Diagnosis

Hipposideros m. jenningsi differs from *H. m. madurae* in the characters indicated above in the diagnosis of that subspecies.

Description

Skull (Table 1, Figure 21)

As for *H. l. larvatus* but skull smaller, particularly nasal length relative to cranial length; zygomatic breadth narrower; C^1C^1 breadth narrower; supraorbital ridges tend to be weaker; frontal depression very shallow; rostrum tends to be flatter; mesopterygoid fossa tends to be a sharper U shape, occasionally (MZB 14862) with a tiny postpalatal projection; sphenoidal bridge parallel sided and conceals considerably less of sphenorbital sinus.

Externals (Table 1)

As for *H. l. larvatus.*

Glans penis

Similar to *H. m. madurae* (see Figure 6b).

Baculum (Figure 5c)

Similar to *H. m. madurae* but a little larger (0.93 v. 0.75-0.82) and with distal bifurcating arms a little longer relative to basal part.

Distribution

Near Semarang, C. Java, Indonesia (Figure 1).

Etymology

Named after Dr Gerald B. Jennings, Head Division of Virology, U.S. Naval Medical Research Unit No. 2, Jakarta Detachment, in recognition of his many kindnesses in assisting staff of the Western Australian Museum/ Museum Zoologicum Bogoriense with their research programme in Indonesia.

Figures 7-19 Univariate plots of skull and external characters of *H. larvatus* (▽); *H. m. madurae* (○); *H. m. jenningsi* (□); *H. sorenseni* (△); *H.* sp. indet. (Sukabumi) (◇); *H. s. sumbae* (●); *H. s. rotiensis* (■); *H. s. sumbawae* (▲); *H. sumbae* subsp. indet A (Semau) (▼); *H. sumbae* subsp. indet. B (Savu) (◆) and Timor (ø).

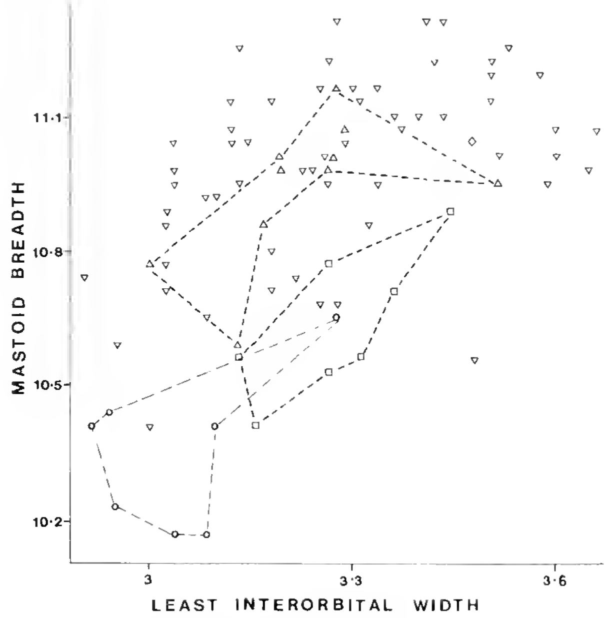

Figure 7 Mastoid breadth *versus* least interorbital width.

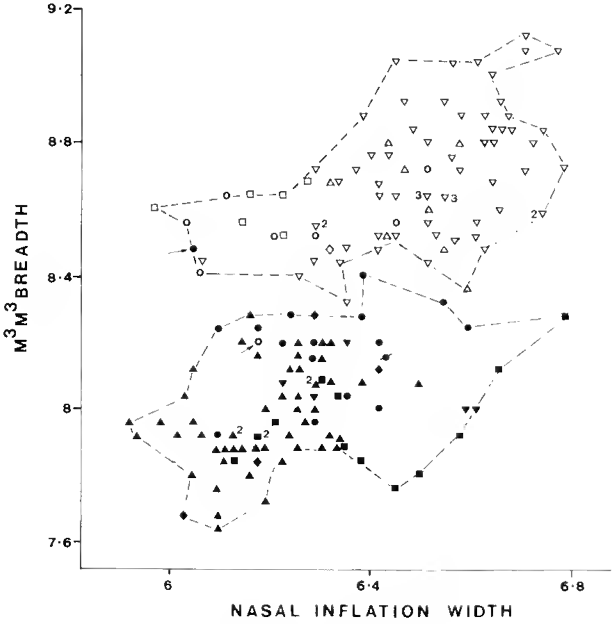

Figure 8 M^3M^3 breadth *versus* nasal inflation width.

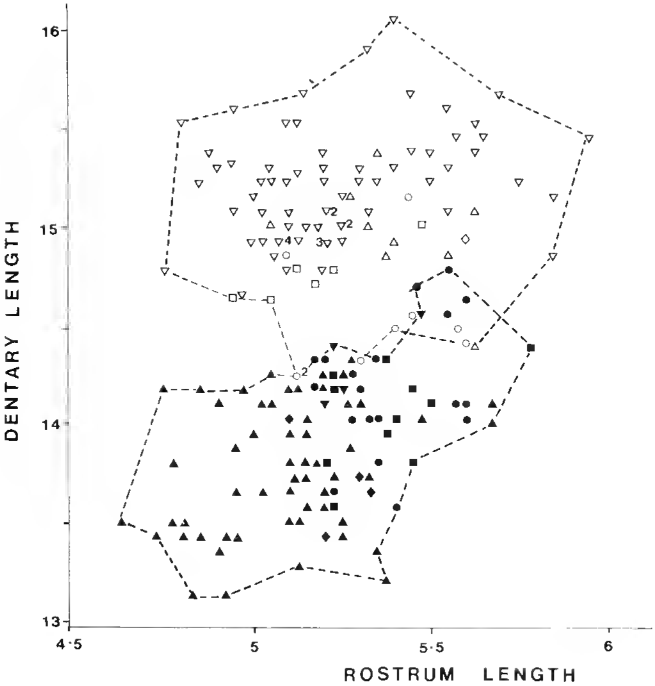

Figure 9 Dentary length *versus* rostrum length.

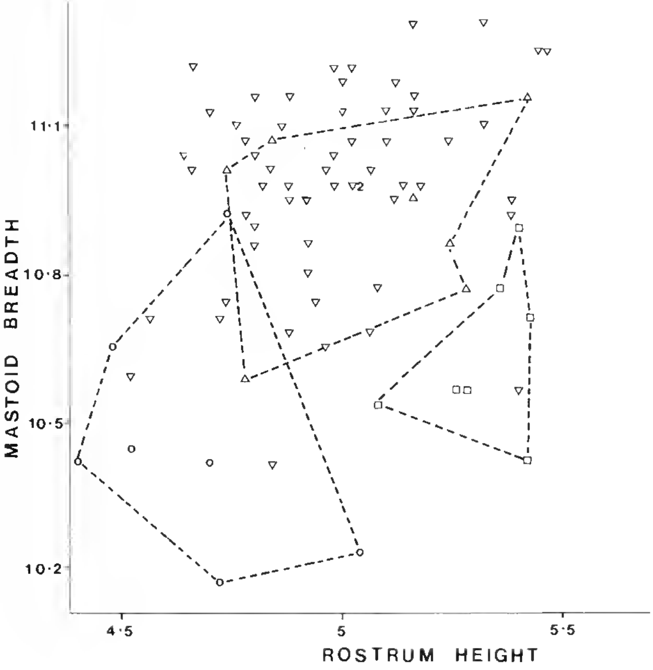

Figure 10 Rostrum height *versus* mastoid breadth.

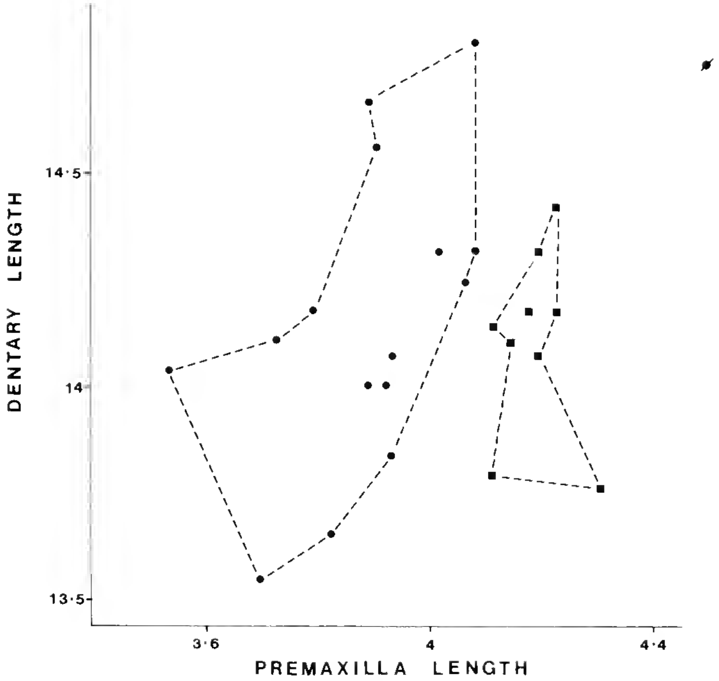

Figure 11 Dentary length *versus* mesopterygoid fossa width.

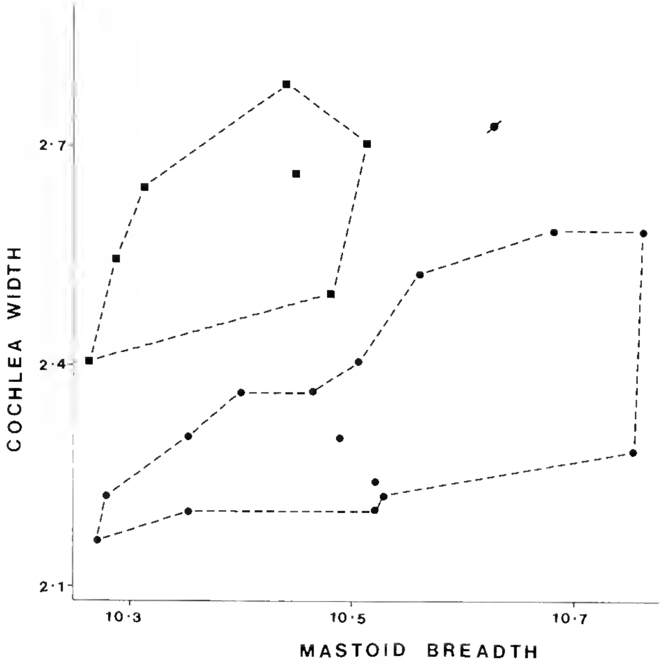

Figure 12 Cochlea width *versus* mastoid breadth.

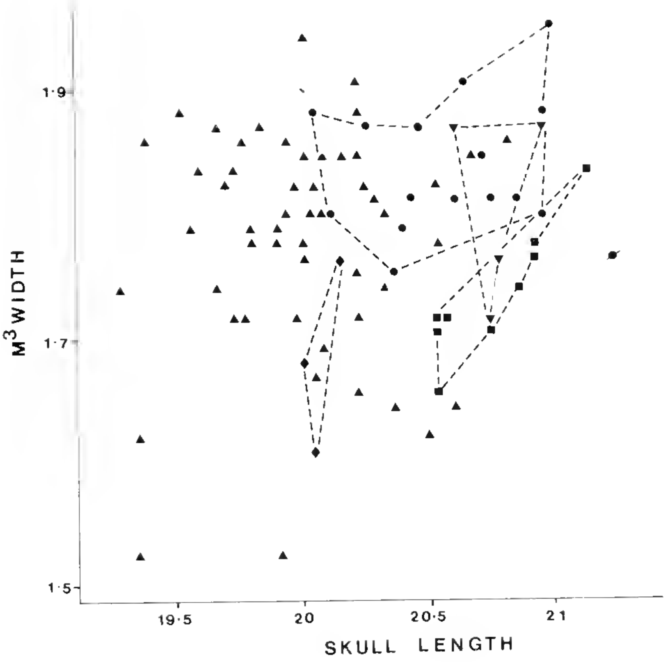

Figure 13 M^3 width *versus* greatest skull length.

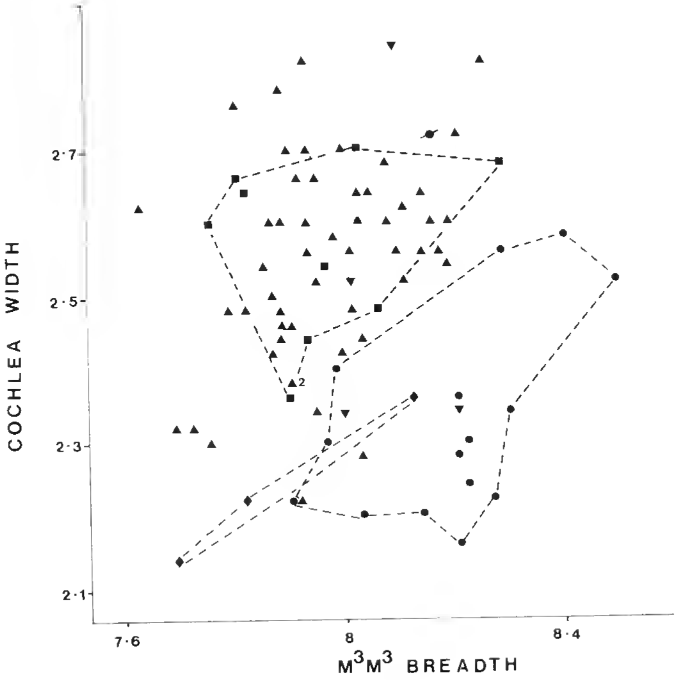

Figure 14 Cochlea width *versus* M^{3}M^3 breadth.

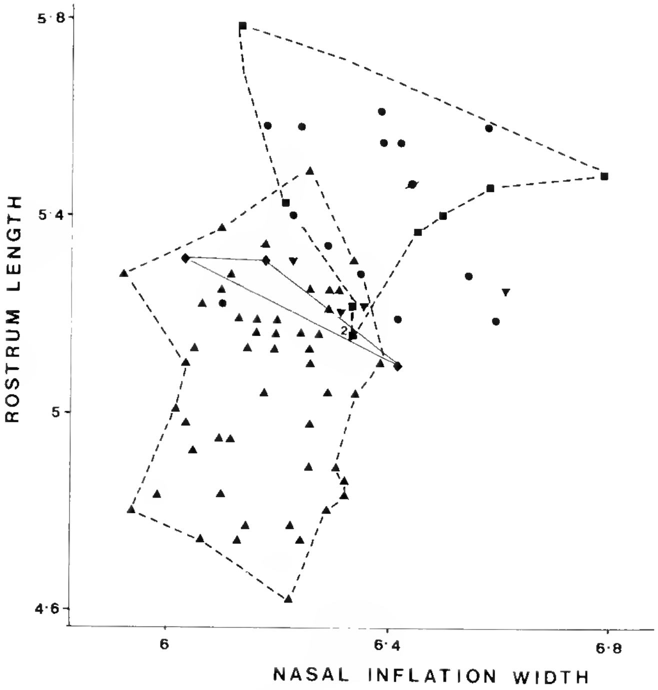

Figure 15 Rostrum length *versus* nasal inflation width.

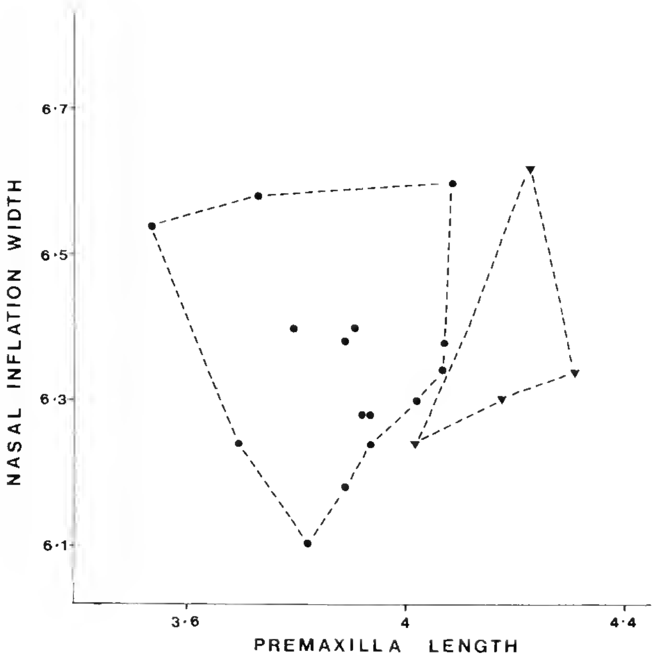

Figure 16 Nasal inflation width *versus* premaxilla length.

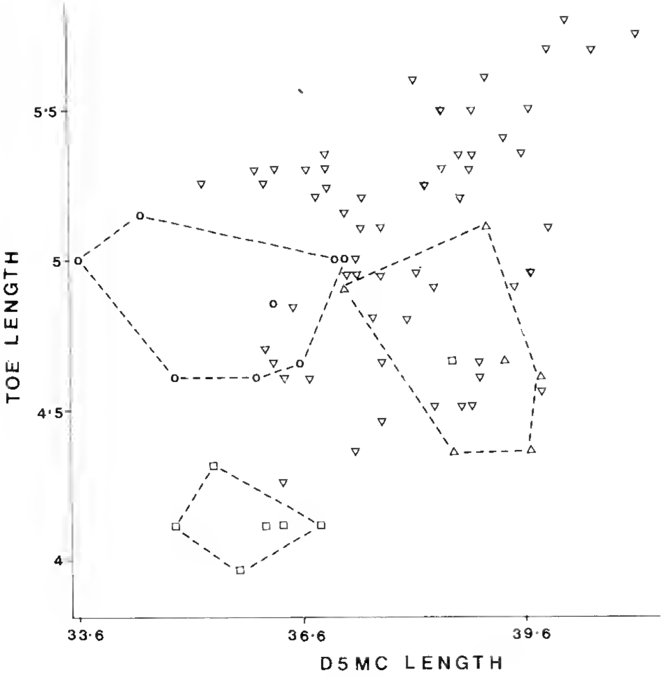

Figure 17 Toe length *versus* digit 5 metacarpal length.

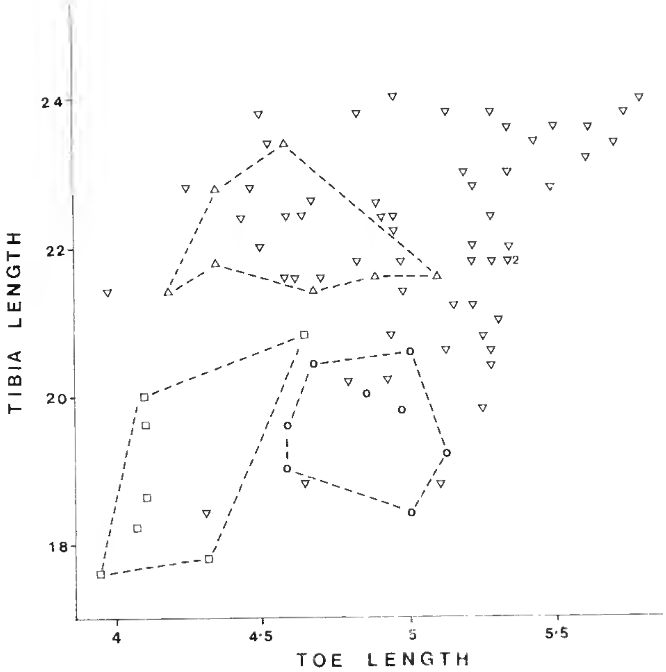

Figure 18 Tibia length *versus* toe length.

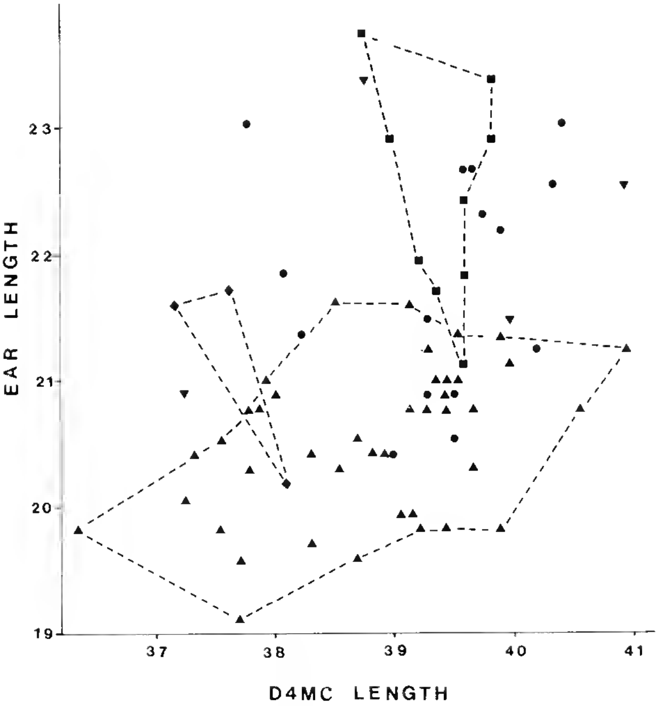

Figure 19 Ear length *versus* digit 4 metacarpal length.

Hipposideros sorenseni sp. nov.

Table 1; Figures 1,5d,7-9,17-18 and 22

Holotype

Museum Zoologicum Bogoriensis MZB 11333, skull separate, scientific 'cabinet' skin, collected by Bapak Sudarmanu on 15 January 1976.

Type locality

Gua Kramat (≡ holy cave), Pangandaran, W. Java (*c.* 7°41'S, 108°40'E).

Specimens examined

Listed in section "Specimens Examined".

Diagnosis

Hipposideros sorenseni skull generally similar in size to *H. larvatus*, but differs from that species in averaging smaller in both C^1C^1 breadth (5.34 v. 5.45) and dentary angle to condyle length (5.53 v. 5.87). Glans penis distally less laterally compressed and distal fleshy lobe attached to baculum more oval. Baculum more robust; dorsal profile suboval rather than long and thin with broad basal pedestal; bifurcating distal arms much shorter and robust.

It differs from *H. madurae* in having a generally larger skull. For example: greatest skull length (21.63 v. 20.84); braincase width (10.00 v. 9.50); zygomatic breadth (12.49 v. 12.23) and cranial length (14.43 v. 13.51); greatest skull length averages larger relative to nasal inflation length (3.808 v. 3.491); cranial length longer relative to nasal inflation length (2.541 v. 2.263); mastoid breadth wider relative to least interorbital width (Figure 7). Digit 5 metacarpal length longer relative to toe length (Figure 17); tibia length longer relative to toe length (Figure 18). Baculum longer (1.15-1.20 v. 0.75-0.93); distal bifurcating arms relative shorter with concomitant broader solid basal part.

It differs from *H. sumbae* in averaging larger in most skull measurements (Table 1). For example; greatest skull length (21.63 v. 20.24); palatal bridge length (3.82 v. 3.41); nasal inflation length (5.68 v. 5.18); nasal inflation width (6.48 v. 6.24); dentary length (14.92 v. 13.91); M^3M^3 breadth (8.66 v. 8.01); I_1M_3 length (10.03 v. 9.23); palatal width relatively broader as indicated by M^3M^3 breadth relative to nasal inflation width (Figure 8); nasal inflation length relative to nasal inflation width larger (0.877 v. 0.830) dentary length larger relative to rostrum length (Figure 9). Digit 5 phalanx 2 longer (10.91 v. 9.53-9.92). Glans penis with distal end lateral profile squarer. Baculum longer (1.15-1.20 v. 0.75-0.84), more robust, cranial projection of bifurcating arms with distal edge more vertical.

Description

Skull (Table 1, Figure 22)

Generally similar in size and description to that of *H. l. larvatus* but differs in both C^1C^1 breadth and dentary angle to condyle averaging smaller; supraorbital ridges slightly weaker; frontal depression very shallow; sphenorbital bridge slightly constricted posteriorly and only partially conceals sphenorbital sinus.

Externals

As for *H. l. larvatus.*

Glans penis

As for *H. m. madurae.*

Baculum (Figure 5d)

Large robust baculum with greatest length 1.15-1.20 (N= 2); base large, comprises approximately two-thirds length of baculum, width 0.64-0.65; bifurcating distal arms short with cranial height from base 0.59-0.65.

Distribution

Pangandaran, southern border of C. and W. Java (Figure 1).

Etymology

Named after Dr Kurt Sorensen, Officer in Charge, U.S. Naval Medical Research Unit No. 2, Jakarta Detachment, in recognition of his support and encouragement of staff of the Western Australian Museum/Museum Zoologicum Bogoriense with their research programme in Indonesia.

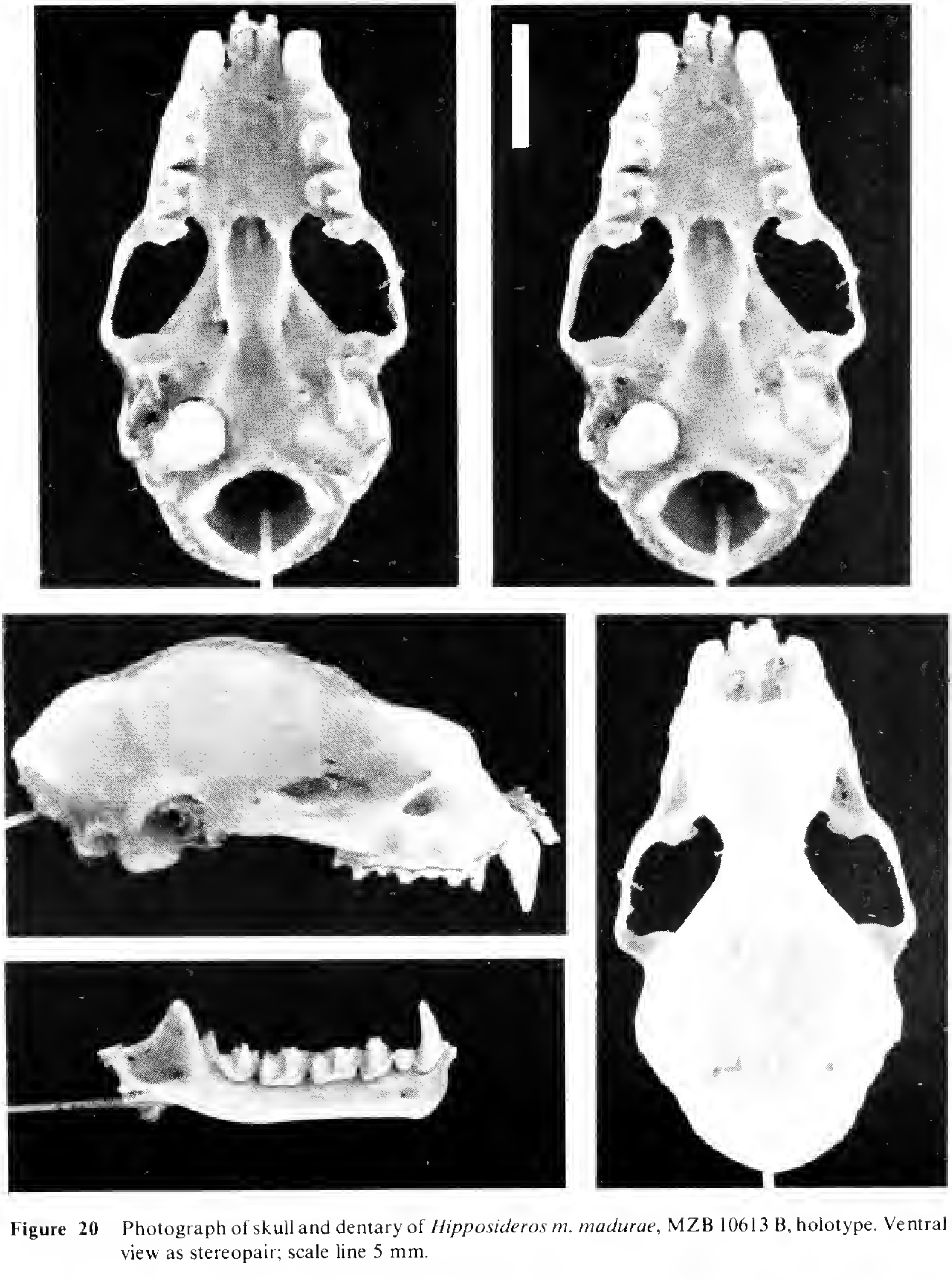

Figure 20 Photograph of skull and dentary of *Hipposideros m. madurae*, MZB 10613 B, holotype. Ventral view as stereopair; scale line 5 mm.

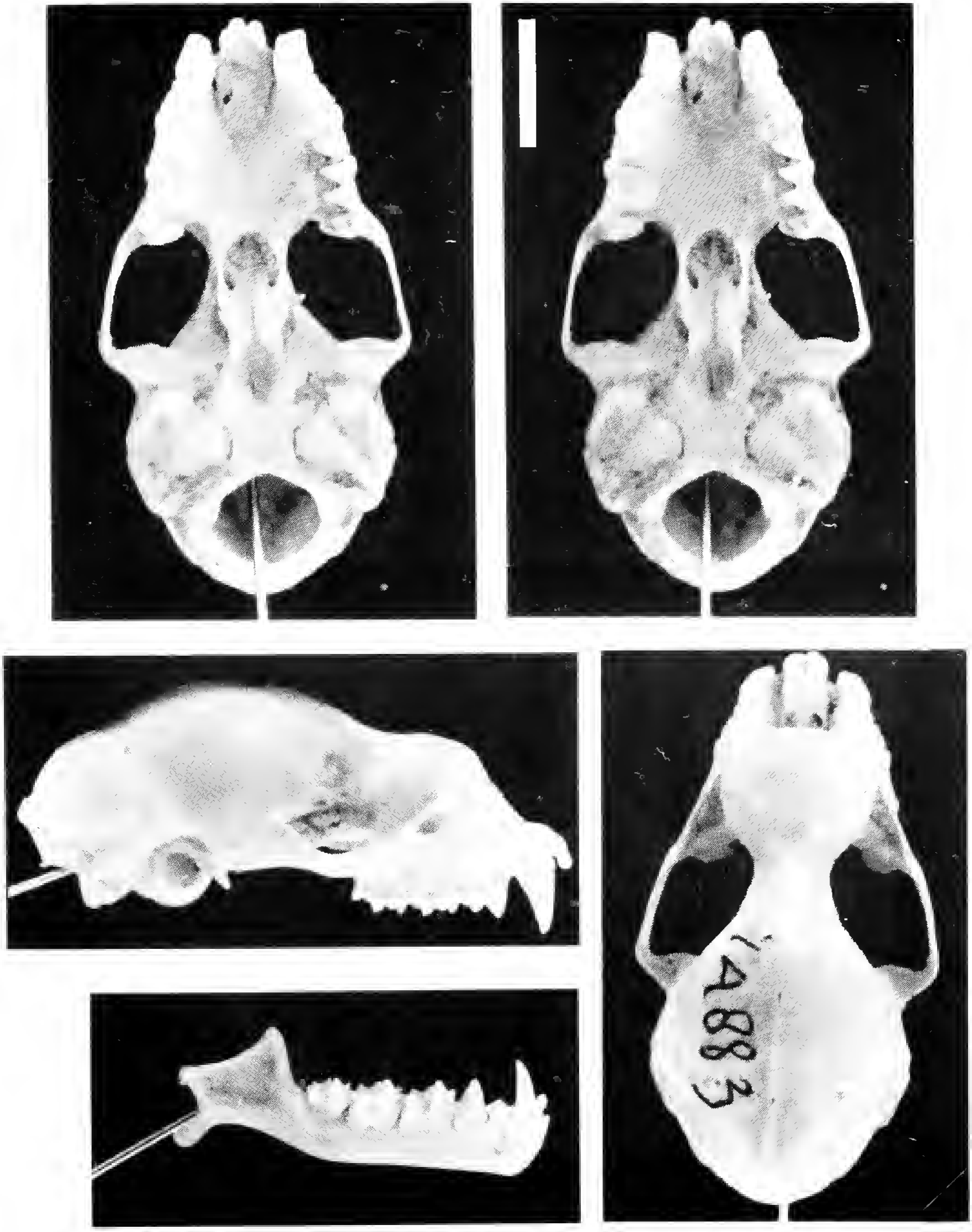

Figure 21 Photograph of skull and dentary of *Hipposideros m. jenningsi*, MZB 14883, holotype. Ventral view as stereopair; scale line 5 mm.

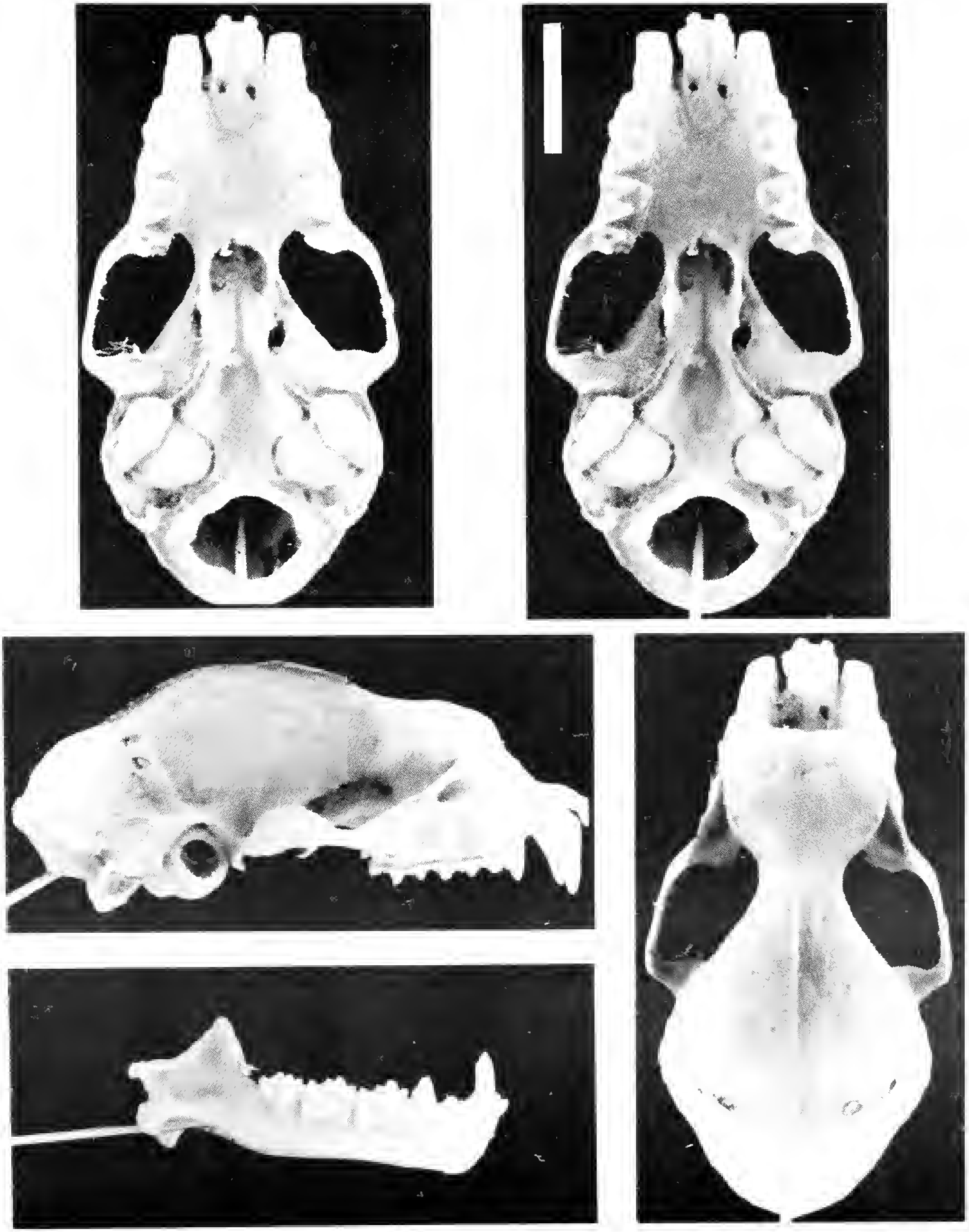

Figure 22 Photograph of skull and dentary of *Hipposideros sorenseni* MZB 11333, holotype. Ventral view as stereopairs; scale line 5 mm.

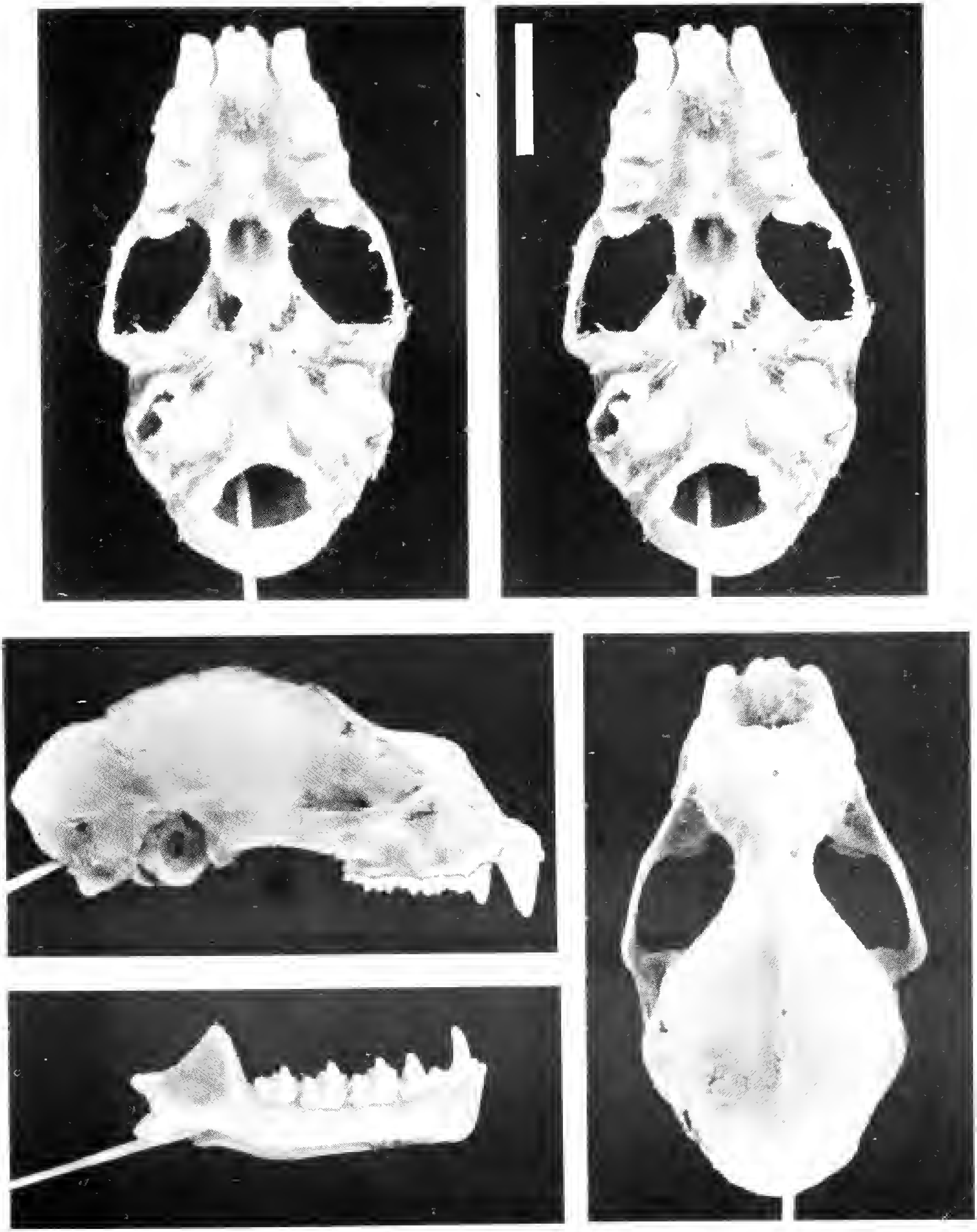

Figure 23 Photograph of skull and dentary of *Hipposideros s. sumbae* (WAM M30493) from Sumba I. Ventral view as stereopairs; scale line 5 mm.

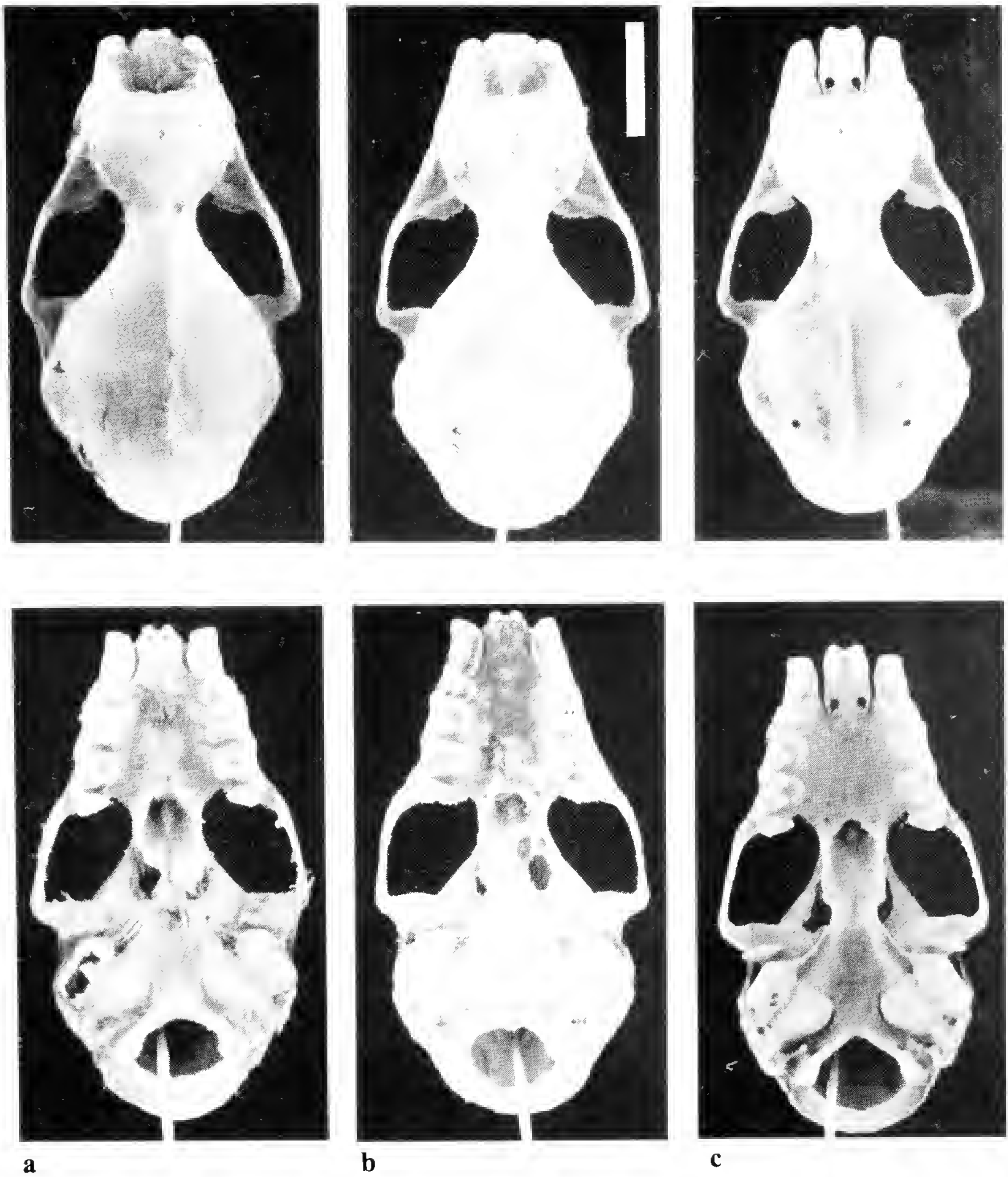

Figure 24 Photograph of skull of (**a**) *Hipposideros s. sumbae* (WAM M30493); (**b**) *H. s. rotiensis* (WAM M35436) and (**c**) *H. s. sumbawae* (WAM M31494); scale line 5 mm.

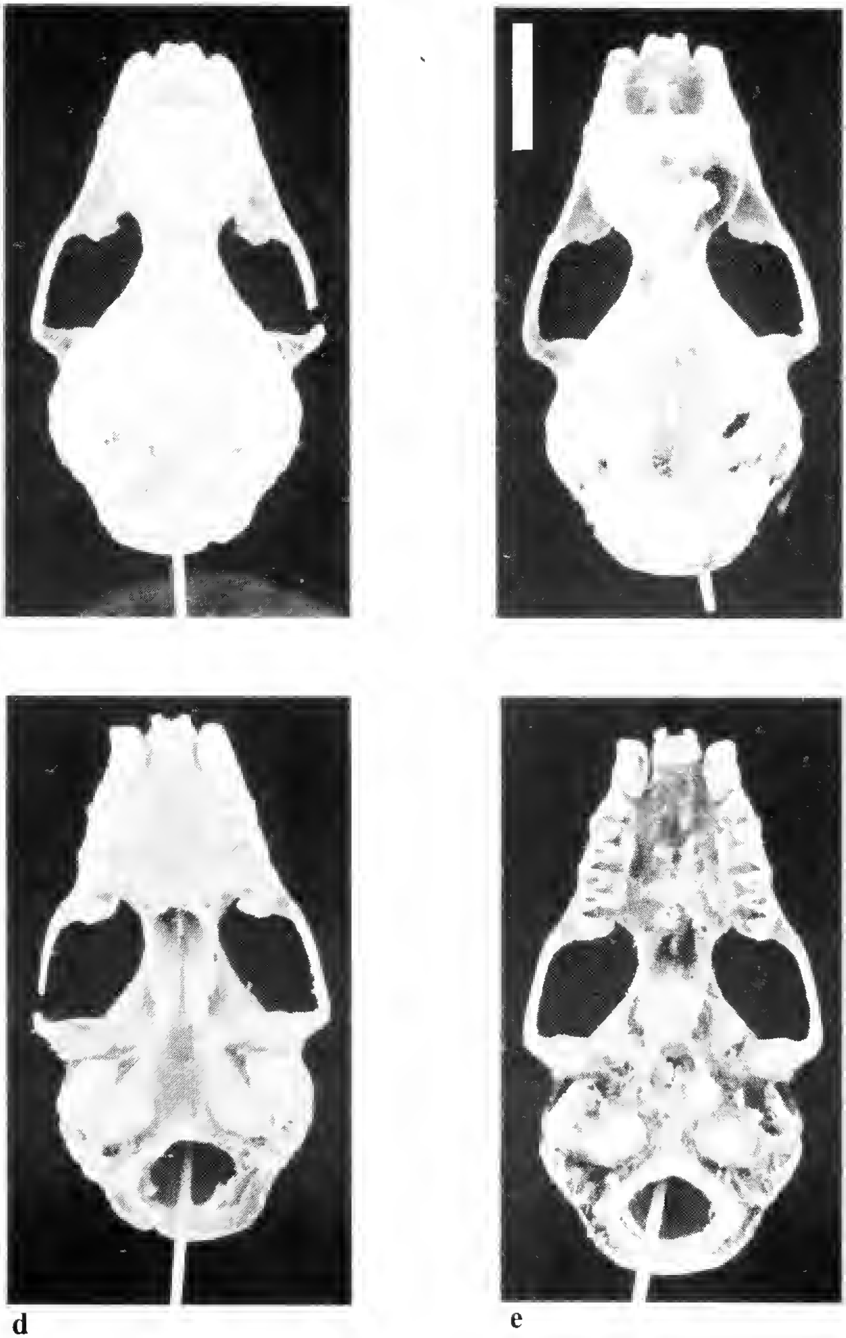

Figure 24 (cont). Photograph of skull of (**d**) *Hipposideros s.* subsp. indet. A (WAM M38016); and (**e**) *H. s.* subsp. indet. B (WAM M35213); scale line 5 mm.

Hipposideros sumbae Oei, 1960

Diagnosis

Hipposideros sumbae differs from *H. larvatus, H. madurae* and *H. sorenseni* in averaging smaller in most skull measurements (Table 1). Posterior palatal width relatively narrower as indicated by M^3M^3 breadth relative to nasal inflation width (Figure 8); nasal inflation length relative to nasal inflation width smaller (0.830 v. 0.877-0.960); dentary length smaller relative to rostrum length (Figure 9). Digit 5 phalanx 2 shorter (9.53-9.92 v. 10.44-10.91). Glans penis with distal end lateral profile more pointed.

Hipposideros sumbae sumbae Oei, 1960

Table 1, Figures 1,5e,6c,8-9,11-15 and 24a

Hipposideros larvatus sumbae Oei, H.P., 1960, Notes on bats from Bali, Lombok and Sumba. Hemera Zoa. 67: 28-31.

Lectotype

Naturhistorisches Museum Basel number 5651/10157, adult male, collected by the Sumba-Expedition Bühler-Sutter 1949. Lectotype designated by van Bree (1961). Lectotype skull illustrated in Oey and van der Feen (1958).

Type locality

E. Sumba, Nusa Tenggara, from cave (*c*. 9°55′S, 120°41′E).

Specimens examined

Listed in section "Specimens Examined".

Diagnosis

Hipposideros s. sumbae differs from *Hipposideros s. rotiensis* subsp. nov. in having a skull with premaxilla length absolutely narrower and also narrower relative to dentary length (Figure 11); cochlea width shorter relative to mastoid breadth (Figure 12) and M^3M^3 breadth (Figure 14). M^3 width larger relative to greatest skull length (Figure 13). Digit 3 phalanges 1 and 2 generally smaller (17.53 v. 18.36 and 17.77 v. 18.84, respectively).

It differs from *Hipposideros s. sumbawae* subsp. nov. in averaging larger in many skull characters (Table 1). For example, greatest skull length (20.57 v. 20.01), braincase width (9.68 v. 9.34), zygomatic breadth (12.12 v. 11.80), I_1M_3 length (9.40 v. 9.16); greatest skull length averages longer relative to cranial height (3.160 v. 3.074); cochlea width shorter relative to M^3M^3 breadth (Figure 14); rostrum generally shorter and nasal inflation generally narrower (Figure 15); and ear length averages larger (21.81 v. 20.51).

Description

Skull (Figure 24a)

Similar to *H. l. larvatus* except for the following: most skull measurements average smaller; posterior palatal width relatively narrower as indicated by M^3M^3 breadth relative to nasal inflation width (Figure 8); nasal inflation length relative to nasal inflation width smaller (0.830 v. 0.884); dentary length smaller relative to rostrum length (Figure 9); sagittal crest occasionally reaches lambdoidal crest; supraorbital ridges very weak; nasal inflation only slightly arched in lateral profile; posterior palatal emargination usually u shaped, occasionally with tiny median posterior projection; PM_2 length small, usually less than three-quarters PM_4 length.

Externals

As for *H.l. larvatus* but colour of pelage on lower back a darker Fuscous to Burnt Umber; shoulder and neck cape generally a larger area of paler fur than in *H. l. larvatus* and extends often to middle of back.

Glans penis (Figure 6c)

Distal outline of glans suboval, in lateral profile rod shaped with dorsolateral edge of distal end gently sloping and not projecting anteriorly as in other species considered; apical fleshy lobe attached to baculum suboval, elongate and sloping sharply into dorsal urethral groove, this lobe with two large suboval basal eminences.

Baculum (Figure 5e)

Short, greatest length 0.75-0.84 (2), suboval in dorsal outline; solid base greatest width 0.51 (2); distal bifurcating arms robust approximately half greatest length and with cranial height 0.41-0.42 (2) above base; distal arm cranial part subvertical.

Distribution

Sumba I., Nusa Tenggara, Indonesia.

Etymology

Named after Sumba I.

Hipposideros sumbae rotiensis subsp. nov.

Table 1, Figures 1,5f,11-15,19 and 24b

Holotype

Western Australian Museum number (WAM) M35436, adult male, carcase fixed in 10% formalin and preserved in 70% ethanol; liver in WAM ultrafreezer, skull separate. Capture in cave by D.J. Kitchener on 10 October 1990. Weight 13.0 gm.

Type locality

Sangoen, Roti I. (*c.* 10°43′S, 123°09′E), altitude 10 m, in deep narrow limestone cave, area vegetated with partly cleared very open mixed woodland.

Paratypes

See section "Specimens Examined".

Diagnosis

Hipposideros s. rotiensis differs from *Hipposideros s. sumbae* in the characters indicated above in the diagnosis of that subspecies.

It differs from *Hipposideros s. sumbawae* subsp. nov. in having a generally larger skull (Table 1). For example: greatest skull length (20.76 v. 20.01), braincase width (9.59 v. 9.34), nasal inflation width (6.40 v. 6.18), dentary length (14.10 v. 13.77); nasal inflation width and rostrum length larger (Figure 15); and ear larger (Figure 19).

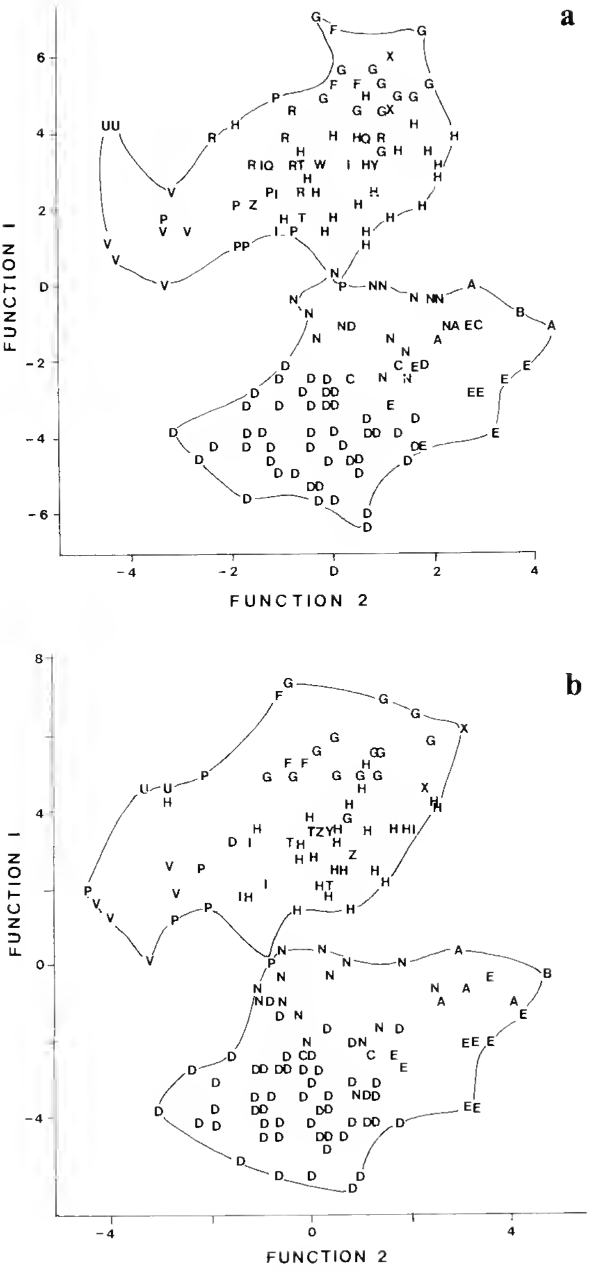

Figure 25 Canonical variate (discriminant) analysis plots of functions 1 and 2 for *Hipposideros* spp. considered in this study **grouped by localities** based on (a) skull and (b) external characters. Specimens group into two broad clusters: Nusa Tenggara (A, Semau I.; B, Timor I.; C, Savu I; D, Sumbawa I.; E, Roti I.; and N, Sumba I.) and 'Western' (F, Nias I.; G, Carita — W. Java; H, Krakatau Is; I, Ciampea — W. Java; P, Madura I.; Q, Pulau Laut — SC Java; R, Pangandaran — W/C Java; T, Aceh, N. Sumatra; U, Palembang — C. Sumatra; V, Semarang, C. Java; W, Sukabumi — W. Java; X, Cikajang — W. Java; Y, Ujong Kulon; Z, Candi — W. Java.

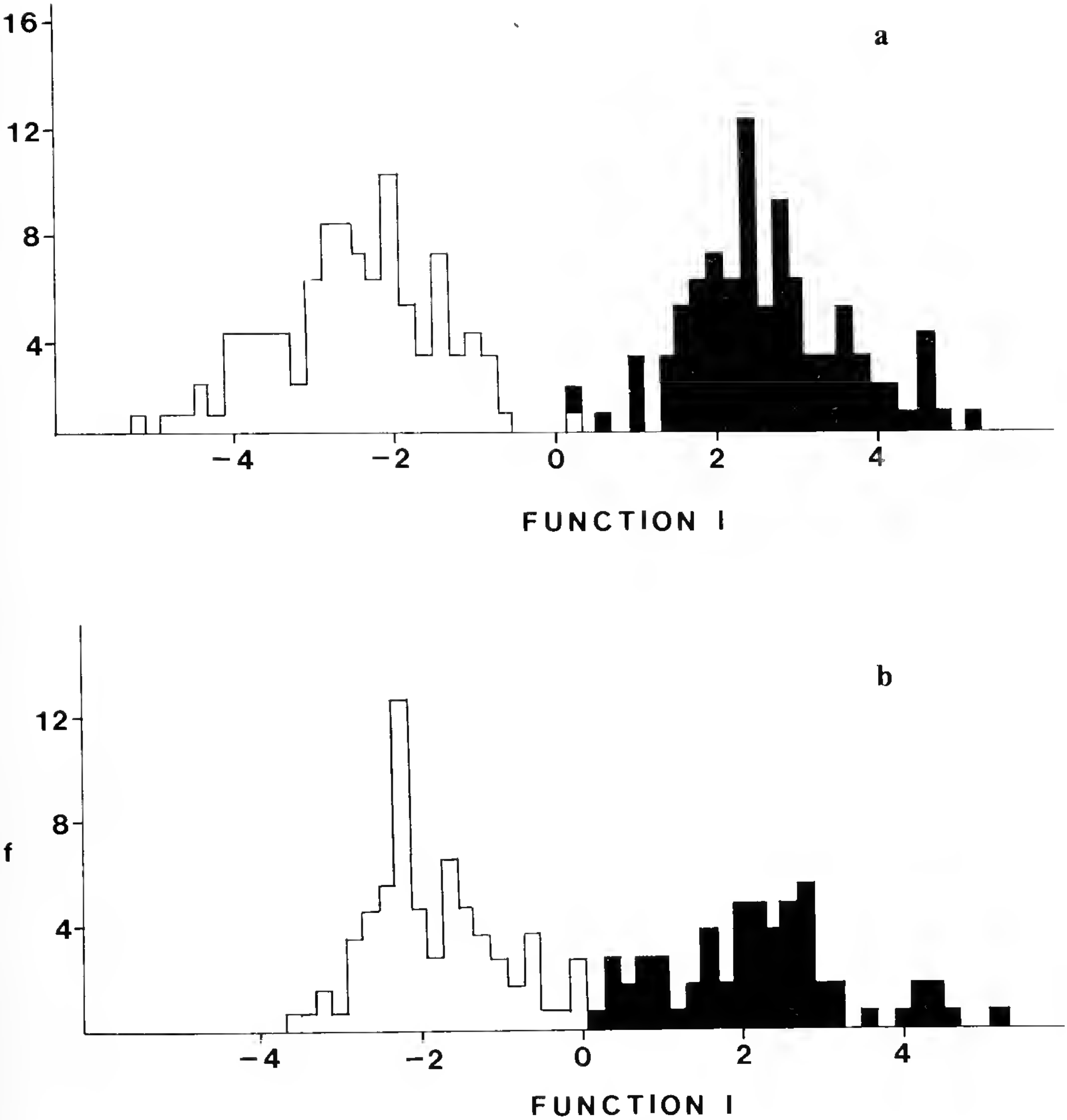

Figure 26 Canonical variate analysis of all specimens of *Hipposideros* spp examined but grouped into the Nusa Tenggara group and the Western group of Figure 25. Histogram of function 1 for (a) skull and (b) external characters □, Nusa Tenggara group and ■ Western group.

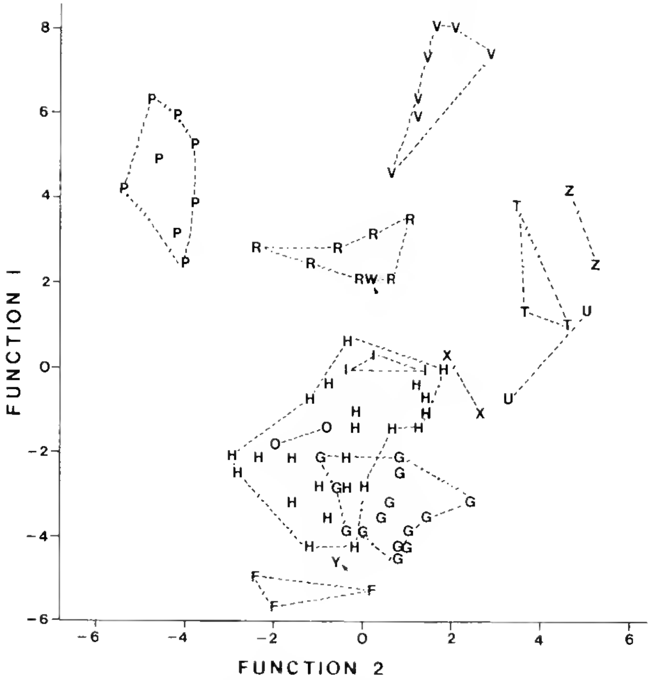

Figure 27 Canonical variate analysis based on skull characters of specimens of *Hipposideros* spp studied from the Western group of Figure 25, **grouped by collection locality**. Collection localities code as for Figure 25.

Description

Skull (Table 1, Figure 24b).

Externals, glans penis and baculum (Figure 5f) similar to *H. s. sumbae* but skull with cochlea longer (2.56 v. 2.32) and M^3 width smaller (1.73 v. 1.84); baculum similar in size and shape but with bifurcating distal arms tending to be wider apart, dimensions of baculum (N = 2): greatest length 0.76, basal width 0.55 and height above base of cranial part 0.32.

Distribution

Roti I., Nusa Tenggara, Indonesia (Figure 1).

Etymology

Named after Roti I.

Referred specimens

MZB 14852, adult male, puppet skin, skull separate, collected at Camplong, W. Timor on 6 January 1932. This specimen is referred to *H. sumbae rotiensis*. It exceeds the Rotinese specimens in some measurements. For example: mastoid breadth, rostrum height, cranial length, mesopterygoid foramen breadth, C^1C^1 breadth dentary length) but it lies closest to the Rotinese cluster in DFA (Figure 29). In particular it is placed in the Rotinese population in Figure 29c. This is a plot of functions 2 and 3 and would appear to be more influenced by shape rather than size differences.

Hipposideros sumbae sumbawae subsp., nov.

Table 1, Figures 1,5g,14,15,19 and 24c

Holotype

Western Australian Museum number (WAM) M31494, field number S383; adult male; weight 13.5 gm; carcase fixed in 10% formalin and preserved in 70% ethanol; liver in WAM ultrafreezer; skull separate; collected on 26 May 1988 in bat trap by D.J. Kitchener, R.A. How and Maharadatunkamsi.

Type locality

Gua (≡ cave) Batu Tering, 3 km S. Desa Batu Tering, W. Sumbawa, (*c*. 8°48'S, 117°22'E); from side adit of enormous limestone cavern; altitude *c*. 200 m. Stream passes within a few metres of cave, vegetation surrounding a dense gallery forest.

Paratypes

See section "Specimens Examined".

Diagnosis

Hipposideros s. sumbawae differs from both *H. s. sumbae* and *H. s. rotiensis* in the characters indicated above in the diagnoses of those subspecies.

Description

Skull (Table 1, Figure 24c), externals, glans penis and baculum (Figure 5g) similar to *H. s. sumbae* but skull with generally larger cochlea width (2.54 v. 2.32), rostrum length smaller (5.04 v. 5.39) and nasal inflation length smaller (5.11 v. 5.30). Baculum similar in size and shape: greatest length 0.83 ± 0.020 (3), basal width 0.49 ± 0.012 (3) and height above base of cranial part 0.33 ± 0.043 (3), slope of anterior edge of cranial projecting part of distal arms varies from near vertical to sharply sloping posteriorly (Figure 5g).

Distribution

Sumbawa I. and Flores I., Nusa Tenggara.

Etymology

Named after Sumbawa I.

Referred specimen

MZB 14243, ♂, skin and skull, from Gua Cermin near Labuan Bajo, W. Flores. This specimen had an injury to its right dentary which has repaired but left considerable bone damage and ossification. Its skull development is also likely to have been impaired as a consequence of this injury. For this reason it was not included in the analyses. However, inclusion of this specimen in the DFA placed it as an outlier of the Sumbawa population. The senior author visited this large cave in April 1990; no *Hipposideros* were present.

Hipposideros sumbae subsp. indet. A.

Table 1, Figures 1,5h,16,24d

Skull (Figure 24d)

The four specimens from **Semau I.** (see "Specimens Examined") appear to represent a distinct form. They have a distinct skull shape as shown by the plot of DFA functions 2 and 3 (Figure 29b). These specimens when unallocated in the DFA, classified into the

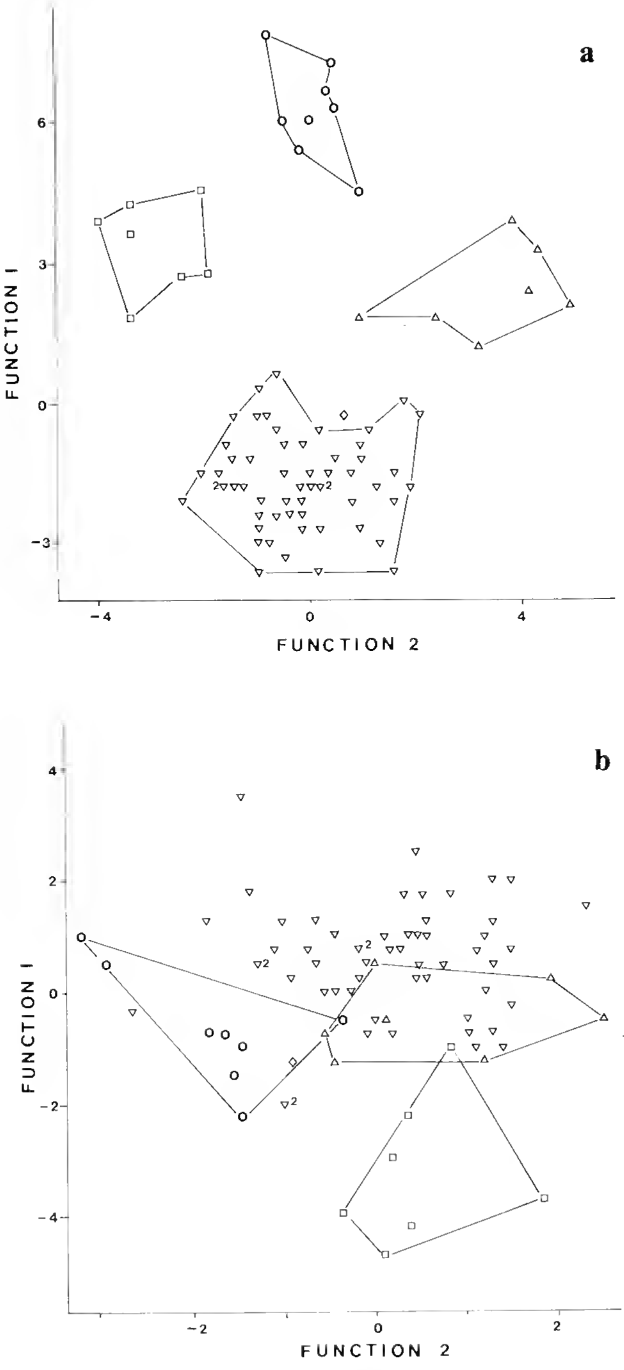

Figure 28 Canonical variate analysis based on skull characters of specimens of *Hipposideros* spp from the Western Group of Figure 25 **grouped by taxa** (*H. l. larvatus; H. m. madurae; H. m. jenningsi; H. sorenseni* and *H.* sp. indet. (Sukabumi — unallocated) (**a**) skull and (**b**) external characters.

Roti, Sumba and Sumbawa groups (see earlier). Most of their measurements overlap with those of other *H. sumbae* forms. This form can be distinguished from *H. s. sumbae* by having a larger premaxillae length relative to its nasal inflation width (Figure 16) and longer premaxillary length relative to nasal inflation width (0.656 v. 0.611) and digit 3 phalanx 1 averages larger (18.47 v. 17.85). Compared to *H. s. rotiensis* it has a wider M^3 width relative to rostrum length (0.434 v. 0.403) and rostrum length narrower relative to greatest skull length (0.253 v. 0.260). Compared to *H. s. sumbawae* its skull is generally larger (Table 1). For example, greatest skull length (20.78 v. 20.01), braincase width (12.15 v. 11.80), dentary length (14.24 v. 13.77) and greatest skull length generally longer relative to cranial height (3.142 v. 3.074); ear generally longer (22.06 v. 20.51); *H. sumbae* subsp. indet. A is distinct from *H. sumbae* subsp. indet. B (from Savu Island) in having skull generally larger (Table 1). For example, greatest skull length (20.78 v. 20.08); braincase width (9.72 v. 9.05). Least interorbital width relative to greatest skull length smaller (0.142 v. 0.153).

Externals

Glans penis and baculum

The glans penis and baculum (Figure 5h) are very similar to the other forms of *H. sumbae*. The baculum examined had the dimension: greatest length 0.86; greatest width 0.52; and height of cranial part of distal arm above base 0.41. The anterior face of this cranial part almost vertical.

Hipposideros sumbae subsp. indet. B

(Table 1, Figures 1,5c,13,14 and 24e)

Skull (Figure 24e)

The three specimens from **Savu I.** (see "Specimens Examined") cluster separately in discriminant function space from the other forms of *H. sumbae* (Figure 29a,b). They appear to represent a distinct form from these other subspecies from which they may be distinguished as follows:

It differs from *H. s. sumbae* by having a smaller skull (Table 1). For example, greatest skull length (20.08 v. 20.57); braincase width (9.05 v. 9.68); zygomatic breadth (11.57 v. 12.12); M^1 width (1.88 v. 2.06); I_1M_3 length (9.19 v. 9.40); M^3 width smaller relative to greatest skull length (Figure 13); and mastoid breadth narrower relative to mesopterygoid width (2.519 v. 2.704).

It differs from *H. s. rotiensis* in having a much smaller skull (Table 1). For example, greatest skull length (20.08 v. 20.76); braincase width (9.05 v. 9.59); dentary length (13.79 v. 14.10); greatest skull length smaller relative to M^3 width (Figure 13) and cranial height (3.142 v. 3.160); braincase width smaller relative to mastoid breadth (0.887 v. 0.923); cochlea width smaller relative to M^3M^3 breadth (Figure 14) and digit 4 metacarpal smaller (37.67 v. 39.44).

It differs from *H. s. sumbawae* in having cochlea width smaller relative to M^3M^3 breadth (Figure 14).

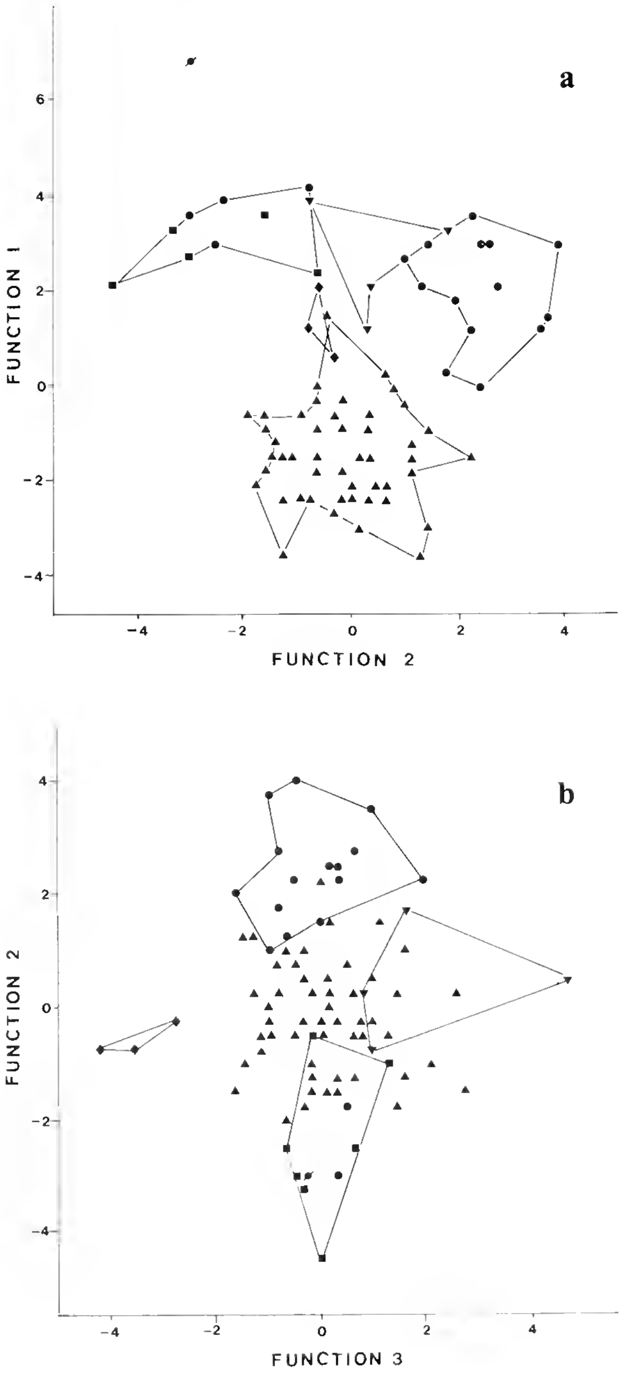

Figure 29 Canonical variate analysis of specimens from Nusa Tenggara **grouped by island**, based on skull characters (**a**, plot of functions 1 and 2; **b**, plot of functions 2 and 3) and (**c**) external characters, plot of functions 1 and 2 group. Island locality codes as for Figure 7.

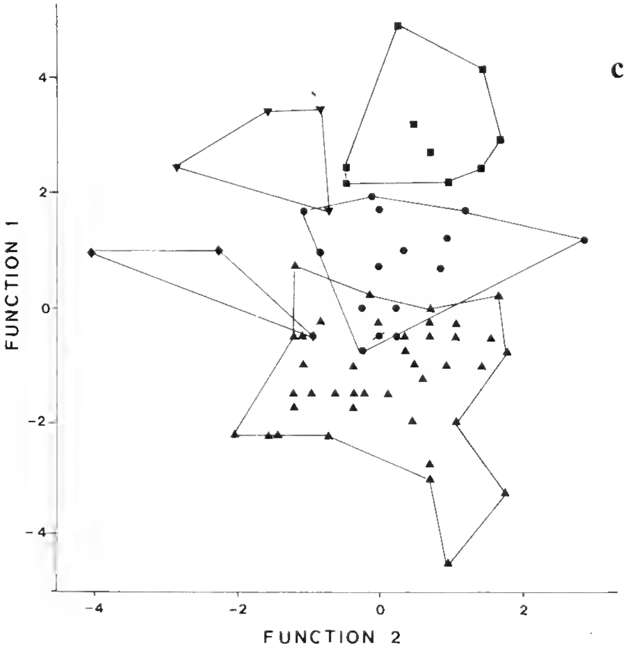

Figure 29 (cont).

It differs from *H. sumbae* subsp. indet. A in having skull generally smaller (Table 1). For example, greatest skull length (20.08 v. 20.78); braincase width (9.05 v. 9.72). Least interorbital width relative to greatest skull length greater (0.153 v. 0.142).

Externals

Glans penis and baculum

The glans penis and baculum (Figure 5i) very similar to other forms of *H. sumbae*. The baculum examined had dimensions: greatest length 0.80; greatest width 0.53; and height of cranial part of distal arm above base 0.43; anterior face of this cranial part almost vertical.

Hipposideros sp. indet.

WAM M30008-09, a male and female from Gua Cidolog, Cikopeah, near Sukabumi. On skull characters the female specimen was close to the *H. larvatus* group, whereas on external characters it was closest to *H. m. madurae* (Table 1, Figure28a,b). The male had missing values and was not included in the analysis. Glans penis similar to *H. madurae* and *H. sorenseni* but its baculum is a unique shape (see Figure 5j); while most similar to bacula from *H. l. larvatus* specimens from Krakatau Is, Ujong Kulon, Nias I. etc., its basal part differs considerably in shape. Rather than a squat short baculum base in dorsal profile, it is narrowed and rounded with greatest width at a point approximately one-third the greatest length rather at the most proximal part. Its dimensions are as follows: greatest length 1.15; greatest width 0.53; height of cranial part of distal bifurcating arm from its base 0.50.

Results and Discussion

(1) Univariate Statistics

Mean, standard deviation, maximum, minimum values and sample size of each taxon are presented in Table 1 for (a) skull and (b) external characters.

(2) Multiple Regression

A multiple regression of skull and external characters on sex, age (young adult, adult, mature adult) and locality groups reflecting species (*Hipposideros madurae, H. sorenseni, H. larvatus* and *H. sumbae*). The results of these analyses are presented in Table 2. The effects and interactions are discussed below.

Skull

Sex: Only nasal length (N1L) and M^3 width (M^3W) showed a significant relationship with sex alone ($P = 0.028$ and $P = 0.035$, respectively). However, there was a significant interaction between sex and age for cranial length (P1L) ($P = 0.003$) and between sex and species for rostrum height (RH) ($P = 0.035$), M^3M^3 breadth (M^3M^3B) ($P = 0.034$), C^1 width ($P = 0.036$) and M^2 length (M^2L) ($P = 0.048$). These characters are related to dentition, width of palate, robustness of rostrum and cranial length. These may relate to functional relationship concerned with masticating power but more likely these significant relationships are due to chance. This is because six of the seven significant relationships had a low significance ($P>0.01$) and given the large number interactions being tested (124) about 6 such interactions could be expected to be significant by chance alone. Only the interaction between age and sex for cranial length was highly significant ($P = 0.003$).

Age: Only M^1 length showed a simple and significant relationship with age ($P = 0.005$, respectively). However, there was a significant interactive relationship for cranial length between sex and age (discussed above) and for both rostrum length (RL) and cranial length between age and species ($P = 0.013$ and 0.012, respectively). These significant relationships again probably resulted from chance alone.

Species: All but one of 31 skull characters (cochlea width) differed significantly between the species — most of them were highly significant. These differences were generally similar between the sex and age grouping considered, although there were significant interactions between species and sex for: rostrum height (RH) ($P = 0.035$), M^3M^3 breadth (M^3M^3B) ($P = 0.034$), C^1 width (C^1W) ($P = 0.036$) and M^2 length (M^2L) ($P = 0.048$) and between species and age for rostrum length (RL) ($P = 0.013$) and cranial length (P1L) ($P = 0.012$).

Externals

Sex: Digit 3 and 5, phalanx 1 length (D3P1, D5P1) showed a simple and significant relationship with sex ($P = 0.004$ and $P = 0.006$, respectively); with Digit 3 phalanx 1 there was also a significant interaction between sex and or age and species ($0.05 < P<0.01$). These interactions resulted from the fact that females generally had a longer digit 3 phalanx 1 than males, but that in *H. larvatus* this was not the case, because for example, mature male had longer digit 3 phalanx 1 than mature females [19.08 (N=8) v. 18.84 (N=7);

Table 2 Multiple regressions on species of *Hipposideros (larvatus, sorenseni, madurae,* and *sumbae),* sex and age, based on skull and external characters. F values are presented for the basic effects and their interactions, significance levels are: *, 0.05> P> 0.01; **, 0.01> P> 0.001; and ***, P< 0.001.

	Main Effects			Interactions			
Character	Sex	Age	Species	Sex. Age. Species	Sex. Age	Sex. Species	Age. Species
GSL	0.050	0.031	77.327***	0.968	1.039	1.152	0.969
BW	0.263	0.918	54.140***	0.720	0.104	1.761	0.292
ZB	0.712	0.910	113.172***	1.615	0.648	1.954	0.578
MB	0.036	0.808	123.333***	0.612	0.402	1.979	0.965
CH	0.657	0.973	41.214***	0.512	1.189	0.454	1.136
RH	0.413	0.180	5.087**	1.260	1.725	2.956*	1.721
RL	3.624	1.604	3.496*	1.511	0.829	2.301	2.823*
LIOW	0.175	0.044	4.447**	0.536	1.571	0.310	0.579
PIL	2.101	3.931*	38.836***	2.223	5.927**	0.607	2.851*
NIL	4.938*	1.208	60.025***	0.762	0.113	2.528	0.704
PBL	2.113	1.141	37.758***	1.742	1.441	1.453	0.950
PML	1.093	2.987	9.501***	1.200	0.594	0.622	1.099
MF	0.111	0.054	6.681***	0.257	0.177	1.673	0.284
TBL	0.011	0.756	4.526**	1.882	1.323	0.540	1.246
TBB	0.100	0.049	84.956***	1.010	0.197	1.952	0.761
NIW	2.817	0.678	37.297***	0.801	0.575	2.017	0.768
CW	0.042	1.300	1.455	0.321	0.031	1.133	0.772
M^3M^3B	1.184	0.435	179.744***	0.403	1.601	2.979*	1.556
C^1C^1B	0.220	0.694	73.903***	0.606	1.785	1.788	0.827
C^1W	0.000	2.420	27.166***	0.962	1.436	2.917*	0.594
P^3L	0.148	0.170	17.428***	1.084	0.648	0.840	0.154
P^3W	0.013	0.581	38.027***	0.750	1.763	1.814	0.481
M^1L	0.014	5.604**	18.124***	1.852	0.967	0.076	0.855
M^1W	0.426	0.116	21.220***	1.128	0.534	0.521	0.599
M^2L	0.335	1.651	18.914***	0.322	0.219	2.702*	1.188
M^2W	0.178	0.108	19.295***	0.166	0.040	1.752	0.845
M^3L	3.052	2.610	21.653***	0.811	0.280	0.549	1.904
M^3W	4.510*	2.061	25.499***	0.335	0.404	1.622	0.848
I_1M_3L	0.107	0.231	106.295***	0.188	2.403	2.155	0.759
DL	0.182	0.204	141.044***	0.214	0.236	0.509	0.749
RAP	0.238	0.621	16.053***	1.804	0.114	0.103	0.519
SVL	0.566	1.273	21.841***	0.753	0.274	0.949	0.453
TVL	0.742	1.080	10.109***	1.804	3.160*	1.287	1.257
EL	0.067	1.755	1.499	0.710	0.263	0.628	0.785
TIL	0.096	0.251	58.231***	0.716	0.130	0.675	0.731
TOL	1.831	0.964	10.278***	0.397	1.079	2.455	2.082
FA	0.924	0.954	49.631***	1.901	1.645	0.999	1.316
D2MC	0.091	0.029	32.602***	0.364	1.938	1.184	1.346
D3MC	0.812	0.021	36.335***	0.713	2.050	0.700	1.124
D3P1	8.480**	2.904	29.678***	2.463*	3.797*	3.205*	1.144
D3P2	0.896	1.196	22.751***	0.290	0.273	0.923	0.688
D4MC	1.865	1.083	50.618***	0.209	1.139	1.138	0.844
D4P1	2.411	0.542	9.824***	0.289	0.527	2.774	1.757
D4P2	0.207	0.012	27.042***	0.619	0.067	0.267	0.954
D5MC	0.240	0.333	1.399***	0.817	1.452	1.029	1.249
D5P1	7.800**	2.332	9.823***	1.573	1.135	3.872	1.157
D5P2	0.498	0.015	34.280***	0.243	0.047	1.354	0.364

respectively]. Also adult females had longer digit 3 phalanx 1 than other age groups, but only in *H. madurae* and *H. larvatus*. There was also a weakly significant interaction between sex and age for the character tail to vent length (TVL) ($P = 0.046$).

Age: No characters were significantly influenced by age alone. However, tail to vent length showed a weak interaction between age and sex and as discussed above digit 3 phalanx 1 showed weakly significant interactions between age and/or sex and species.

Species: All external characters showed highly significant ($P<.001$) differences between the species, except for ear length (EL). Nearly all these differences were the same between sex and age grouping except for those discussed above (digit 3 phalanx 1 length and ear length).

(3) **Multivariate analysis**

Canonical variate (discriminant) analyses (DFA) was carried out on locality and taxonomic groupings using all 47 characters measured. Both sexes and age groups were combined in the following analysis. However, all these analyses were also carried out after deleting those characters shown in the multiple regression analyses to be significantly influenced by sex or age, despite the probability that these significant relationships may have resulted from chance alone. The deletion of these characters had little or no effect on the analyses or the conclusions. For this reason the results presented are from the analysis of the full character set.

All localities separate

The DFA of skull and external characters analysed separately produced two broad locality groups as shown by the plot of functions 1 and 2 (Figures 25a,b, respectively. These two groups, which are entirely separate on function 1, are (i) Nusa Tenggara and (ii) Madura, Java, Sumatra and associated islands (≡ Western group). Within these two broad groups are further distinct locality clusters.

Nusa Tenggara and Western groups

The DFA based on skull characters of specimens placed in the Nusa Tenggara or Western group extracted a single function with 99.5% of all cases allocated to their correct group (Figure 26a).

The characters that load heaviest on function 1 are (listed in decreasing order): M^3M^3 breadth (M^3M^3B), greatest skull length (GSL) and dentary length (DL) (see Table 3a). A stepwise discriminant analysis revealed that I_1M_3 length (I_1M_3L), nasal inflation length (NIL), palatal bridge length (PBL), rostrum length (RL) and nasal inflation width (NIW) were also important discriminants. These characters indicate that overall skull size, palatal width, shape of nasal inflation, length of rostrum and length of toothrows are important discriminants between the Nusa Tenggara and Western groups.

The DFA, based on external characters (this excludes *H. m. jenningsi*), for the Nusa Tenggara and Western groups extracted a single function (Figure 26b), with 100% of all cases correctly classified to the 'Nusa Tenggara' or 'Western' groups.

The characters loading heaviest on this function were digit 5 phalanx 1 length (D5P1), digit 3 phalanx 1 length (D3P1) and ear length (EL) (Table 3b).

Table 3 Canonical variate function coefficients for the Nusa Tenggara group and the Western group (Madura I., Java, Sumatra and associated islands) of *Hipposideros* specimens studied. Standardised values followed by (in brackets) unstandardised values (**a**) skull and (**b**) external characters.

(a)

Character	Function 1
GSL	−0.5994 (−1.1995)
BW	−0.3898 (−1.3072)
MB	0.3396 (1.4175)
RL	−0.1904 (−0.7726)
LIOW	−0.1186 (−0.6584)
PIL	0.3049 (0.7456)
NIL	0.3800 (1.2236)
PBL	0.3540 (1.7855)
NIW	−0.2777 (−1.6030)
M^3M^3B	0.7966 (4.4713)
C^1C^1B	−0.2379 (−1.0768)
P^3L	0.1213 (1.2764)
M^1W	0.1204 (0.9231)
M^2W	0.1384 (1.0702)
M^3L	0.1316 (2.6600)
M^3W	−0.1805 (−2.2049)
I_1M_3L	0.1924 (0.8058)
DL	0.5272 (1.3977)
Constant	−49.3789
Variance explained (%)	100

(b)

Character	Function 1
SVL	0.3832 (0.1597)
TVL	0.1429 (0.0604)
EL	−0.5383 (−0.5008)
TIL	0.2780 (0.2454)
FA	0.2337 (0.1386)
D3P1	0.5565 (0.6767)
D4MC	0.3326 (0.2397)
D4P1	−0.4993 (−0.8120)
D5MC	0.3125 (0.2533)
D5P1	−0.7281 (−1.1896)
D5P2	0.4754 (0.8730)
Constant	−24.7993
Variance explained (%)	100

Table 4 Canonical variate function coefficients for the first three functions for the Western group taxa (*H. l. larvatus; H. m. madurae; H. m. jenningsi; H. sorenseni*); standardised values followed by (in brackets) unstandardised values. **(a)** skull and **(b)** external characters.

(a)

Character	Function 1	Function 2	Function 3
GSL	0.8109 (1.6654)	0.5457 (1.1209)	—0.1452 (—0.2983)
BW	—0.1167 (—0.4114)	0.5014 (1.7677)	—0.2290 (—0.8072)
MB	—0.6901 (—3.4196)	0.4169 (2.0657)	0.3551 (1.7593)
CH	—0.6126 (—2.9179)	0.0115 (0.0546)	0.2570 (1.2242)
RH	0.2455 (1.0785)	—0.1109 (—0.4873)	0.0265 (4.5103)
LIOW	0.4032 (2.3477)	—0.6334 (—3.6880)	—0.0039 (—0.0230)
PIL	0.3517 (0.8099)	0.7697 (1.7727)	—0.0942 (—0.2170)
NIL	0.6827 (1.9649)	0.2663 (0.7665)	—0.7248 (—2.0862)
PBL	0.6197 (2.8994)	0.0835 (0.3906)	0.0357 (0.1672)
PML	0.5573 (2.9408)	0.1476 (0.7791)	—0.4238 (—2.2365)
TBB	—0.7980 (—3.3246)	—0.4145 (—1.7267)	0.2111 (0.8793)
NIW	—0.1326 (—0.9113)	0.2735 (1.8796)	—0.3201 (—2.2002)
CW	—0.2990 (—1.8797)	—0.5755 (—3.6181)	0.0386 (0.2426)
M^3M^3B	0.5046 (2.6945)	—0.8230 (—4.3943)	0.0786 (0.4195)
C^1C^1B	—0.8308 (—3.9437)	0.2609 (1.2386)	—0.1115 (—0.5293)
P^3L	—0.6359 (—8.1650)	—0.5378 (—6.9055)	—0.3778 (—4.8510)
P^3W	—0.1942 (—2.5283)	0.5608 (7.3000)	0.3343 (4.3513)
M^1W	0.3598 (2.9161)	0.3197 (2.5909)	—0.0829 (—0.6716)
M^3L	0.5792 (11.6451)	0.4151 (8.3463)	0.3407 (6.8502)
M^3W	0.4296 (5.4312)	0.2967 (3.7512)	0.0365 (0.4615)
I_1M_3	0.0671 (0.2776)	0.0518 (0.2143)	0.7001 (2.8949)
DL	—1.0822 (—3.4180)	—1.0652 (—3.3645)	—0.5902 (—1.8640)
Constant	42.2937	—14.8485	—17.1856
Variation explained (%)	72.1	17.4	10.6

(b)

Character	Function 1	Function 2	Function 3
TIL	0.8608 (0.6559)	0.3528 (0.2688)	—0.1414 (—0.1077)
TOL	0.3827 (1.0189)	—0.4860 (—1.2942)	0.4276 (1.1385)
FA	0.4753 (0.2519)	—0.1664 (—0.0882)	0.0245 (0.0130)
D3MC	—0.7691 (—0.5350)	0.5986 (—0.4164)	—0.5699 (—0.3965)
D4MC	0.3866 (0.2713)	0.3145 (0.2207)	1.4964 (1.0500)
D4P1	—0.5181 (—0.7573)	0.5622 (0.8217)	0.2315 (0.3384)
D4P2	—0.2898 (—0.4659)	0.3955 (0.6357)	0.5888 (0.9465)
D5MC	—0.1078 (—0.0810)	0.7453 (0.5601)	—1.3136 (—0.9873)
D5P2	0.3186 (0.5073)	—0.4868 (—0.7751)	—0.2507 (—0.3991)
Constant	—9.5566	—16.0724	—3.34420
Variation explained (%)	66.4	22.4	11.2

The Western Group (all localities separate)

DFA based on skull characters of specimens from within the Western group (Madura, Java, Sumatra and associated small islands) revealed at least four distinct clusters (Figure 27a). These were (1) *Hipposideros m. madurae*; (2) *H. m. jenningsi*; (3) *H. sorenseni* and (4) *H. l. larvatus*. The last group shows further separation, particularly Candi (W. Java), Aceh and Palembang (Sumatra) and Nias I.

The Western Group (grouped by species and subspecies)

The DFA based on all 31 skull characters of the taxa: *H. l. larvatus, H. m. madurae, H. m. jenningsi* and *H. sorenseni* with the Sukabumi specimen unallocated, extracted three significant functions which combined account for 100% of the variation (function 1, 72.0%; function 2, 17.4% and function 3, 10.6%). All cases were correctly allocated to their designated taxon. The single Sukabumi specimen grouped closely with *H. larvatus*. The four taxonomic groups cluster approximately equidistantly in discriminant function space (Figure 28). *Hipposideros m. madurae* and *H. larvatus* separate from each other and from *H. m. jenningsi* and *H. sorenseni* on function 1. Characters loading heaviest on this function relate to overall size of skull (Table 4a) [greatest skull length (GSL), mastoid breadth (MB), rostrum length (RL), distance outside upper canines (C^1C^1B) and dentary length (DL)]; they are a reflection of the larger overall size of *H. larvatus*. *H. m. jenningsi* and *H. sorenseni* separated from *H. m. madurae* and *H. larvatus* and from each other on function 2. Characters loading heaviest on function 2 are dentary length, width of posterior palate (M^3M^3B), and cranial length (PIL) (Table 4a).

The DFA, based on a subset of 13 *external characters* listed in Table 1 (excluded were SVL, TVL, and EL which were missing from a number of specimens) of the four taxa in the Western group, with the Sukabumi specimen unallocated, also extracted three significant functions which combined explained 100% the variation (function 1, 66.4%; function 2, 22.3%; and function 3, 11.3%), but with only 74.1% of cases correctly allocated to their given taxonomic group. Three taxa: *H. m. madurae, H. m. jenningsi* and *H. sorenseni* formed reasonably discrete clusters from each other in discriminant function space (Figure 28b). The separation between *H. m. madurae* and both *H. m. jenningsi* and *H. sorenseni* was principally on function 2. Characters loading most heavily on function 2 were digit 3 metacarpal length (D3MC), digit 4 phalanx 1 length (D4P1) and digit 5 metacarpal length (D5MC) (Table 4b). *H. m. jenningsi* was separated from the other three taxa principally on function 1. Characters loading most heavily on this function were: tibia length, (TIL) digit 3 metacarpal length (D3MC), and digit 4 phalanx 1 length (D4P1) (Table 4b). The *H. larvatus* cluster overlaps extensively with *H. sorenseni* and less so with *H. m. madurae*.

The Sukabumi specimen clusters closest to *H. m. madura*.

The separation of the Western Group taxa (*H. m. madurae; H. m. jenningsi; H. sorenseni;* and *H. larvatus*) using DFA on 31 skull and 13 external characters (Figure 28) was also achieved from a considerably reduced character set, because of the extent of correlation between many of these characters. For example, similar clusters were obtained using only 10 skull characters (ZB, RH, NIW, NIL, P^3W, TBB, RL, P^3L, M^3W and

C^1C^1B) and 6 external characters (TIB, TOL, D4P1, D5MC, D2MC, D3MC). These characters were selected using a stepwise discriminant analysis; characters are listed in decreasing order of importance.

The Nusa Tenggara Group

The DFA based on 31 skull characters of specimens from within Nusa Tenggara, grouped by island, extracted five significant functions which explained 100% of the variance (function 1 — 55.4%, function 2 — 23.6%, function 3 — 8.2%, function 4 — 6.6% and function 5 — 6.2%). A plot of functions 1 and 2 and functions 2 and 3 (Figures 29a, b) shows that all island populations were distinct with the possible exception of the Semau population. 97.7% of all specimens were classified correctly into their island of capture. The two misclassification involved the Semau population; in one case a specimen from Semau was classified to the Roti population; in another a Sumbawa specimens was classified to the Semau population. If the above DFA was run without the four Semau specimens, 100% of the remaining island specimens (Sumbawa, Timor, Roti, Savu and Sumba) were correctly classified. Placing the Semau specimens as ungrouped in the above DFA allocated these specimens accordingly: two to Sumba, one to Roti and one to Sumbawa.

From Figures 29a,b the population on Sumbawa (Inner Banda Arc) was separated from populations on islands in the Outer Banda Arc (Roti, Savu, Semau, Timor and Sumba) principally on the important function 1 which explained 55.4% of the variance and from Savu on the less important function 3 (8.2% of the variance). The canonical discriminant function coefficients that loaded heavily on function 1 (in descending order of importance) are: least interorbital width (LIOW); M^2 length (M^2L); rostrum length (RL); M^1 width (M^1W) and on function 3 are: braincase width (BW); cochlea width (CW); rostrum length (RL); M^1 width (M^1W), PM^3 width (P^3W), and zygomatic breadth (ZB) (Table 5a). These characters related to shape of skull and cochlea and particularly molar teeth. Islands in the outer Banda Arc were separated on functions 2 and 3 (Figures 29a, b). In addition to function 3, discussed above, characters that loaded heavily on function 2 were: cochlea width (CW); M^3M^3 breadth (M^3M^3B); M^3 width (M^3W); palatal bridge length (PBL); braincase width (BW) and premaxilla length (PML). These added shape of palate to the above important discriminating characters.

The DFA based on all 16 external characters (present in all Nusa Tenggara specimens) grouped by island, extracted two significant functions which combined explained 88.3% of the variance (function 1, 74.5% and function 2, 13.8%). 84.5% of all cases were correctly classified to their island group. The plot of functions 1 and 2 (Figure 29c) indicated that *H. s. rotiensis* clustered separately from *H. sumbae* subsp. indet. A (Semau) and *H. sumbae* subsp. indet. B (Savu) on function 2. Characters loading heavily on this function were: forearm length (FA); digit 3 phalanges 1 and 2 lengths (D3P1, D3P2), digit 4 metacarpal length (D4MC) and digit 4 phalanx 1 length (D4P1) (Table 5b). *H. s. rotiensis*/ *H. sumbae* subsp. indet. A separated from *H. s. sumbae*/ *H. sumbae* subsp. indet. B/ *H. s. sumbae* on function 1. Characters loading heavily on function 1 were: ear length (EL) and digits 3 and 4 phalanx 1 length (D3P1, D4P1) (Table 5b).

Table 5 Canonical variate function coefficients for the significant functions for the Nusa Tenggara island groups (Sumbawa, Sumba, Savu, Roti, Semau, Timor). Standardised values followed by (in brackets) unstandardised values. **(a)** skull and **(b)** external characters.

(a)

Character	Function 1	Function 2	Function 3
GSL	0.3478 (1.0891)	—0.0398 (—0.1245)	0.2469 (0.7731)
BW	0.0396 (0.1952)	0.4178 (2.0581)	0.6373 (3.1393)
ZB	—0.0268 (—0.0989)	—0.3634 (—1.3431)	—0.4465 (—1.6503)
CH	0.1273 (0.8477)	—0.2439 (—1.6238)	0.3206 (2.1346)
RL	0.5171 (2.8372)	0.0367 (0.2016)	—0.5156 (—2.8290)
LIOW	—0.7702 (—4.7293)	0.2908 (1.7857)	—0.1985 (—1.2187)
PBL	0.2953 (1.7465)	—0.4217 (—2.4946)	—0.3446 (—2.0384)
PML	0.1913 (1.1122)	—0.4047 (—2.3524)	0.0280 (0.1626)
MF	0.3069 (2.2622)	—0.0095 (—0.0699)	0.2015 (1.4856)
TBL	0.1825 (1.4729)	—0.1246 (—1.0051)	—0.3405 (—2.7475)
TBB	0.1315 (0.6375)	0.3325 (1.6124)	0.0167 (0.0808)
NIW	0.3724 (2.8261)	—0.3356 (—2.5462)	0.0395 (0.3000)
CW	—0.3585 (—2.5482)	—0.6693 (—4.7566)	0.5911 (4.2012)
M^3M^3B	0.1182 (0.8104)	0.6037 (4.1372)	—0.1933 (—1.3247)
C^1C^1B	—0.0973 (—0.5407)	0.3091 (1.7173)	0.3238 (1.7991)
P^3W	—0.1106 (—1.5210)	0.0474 (0.6511)	—0.4557 (—6.2660)
M^1W	—0.4869 (—3.9613)	0.0931 (0.7571)	0.4590 (3.7338)
M^2L	0.5520 (6.8713)	—0.0771 (—0.9597)	—0.1037 (—1.2903)
M^2W	0.1197 (1.1381)	0.2534 (2.4083)	0.1220 (1.1593)
M^3W	—0.2211 (—2.7501)	0.4649 (5.7829)	0.1539 (1.9148)
Constant	—69.0830	—21.9855	—23.0779
Variation explained (%)	55.4	23.6	8.2

(b)

Character	Function 1	Function 2
SVL	—0.2459 (—0.1185)	0.1767 (0.0851)
TVL	0.0851 (0.0448)	0.7291 (0.3836)
EL	0.8480 (1.1264)	—0.0330 (—0.0438)
TIL	0.3890 (0.6274)	—0.0582 (—0.0939)
FA	—0.2768 (—0.2014)	—0.8281 (—0.6024)
D2MC	—0.4262 (—0.3683)	0.2956 (0.2554)
D3P1	0.6980 (1.0567)	—0.6689 (—1.0127)
D3P2	—0.2062 (—0.2135)	0.6213 (0.6433)
D4MC	—0.1708 (—0.1869)	0.7281 (0.7966)
D4P1	0.5756 (1.2071)	0.0860 (0.1805)
D4P2	—0.4318 (—0.8417)	—0.3498 (—0.6819)
Constant	—20.0799	—12.0670
Variation explained (%)	74.5	13.8

The separation of the Nusa Tenggara group taxa (*H. s. sumbae, H. s. rotiensis, H. s. sumbawae*) using DFA on 31 skull and 16 external characters (Figure 29) was also achieved from a considerably reduced character set because of the extent of correlation between many of these characters. For example, very similar clusters were obtained using only 6 skull characters (GSL, CW, M^3M^3B, BW, PML, RL) and 6 external characters (EL, D3P1, D4MC, SVL, TVL, FA). These reduced character sets were selected using a stepwise discriminant analysis; characters are listed in decreasing order of importance.

General Discussion

This study clarifies considerably the taxonomic status of the *Hipposideros* previously attributed to *H. larvatus sumbae* from Sumba and other islands in Nusa Tenggara. This was its major focus. However, examination of an extensive series of related specimens, also previously attributed to *H. larvatus*, from Java, Sumatra and associated islands — and a few specimens from Peninsular Malaysia (2), Sarawak (1) and Thailand (1) has only partially resolved their taxonomic status.

Specimens from Nusa Tenggara are *Hipposideros sumbae*. Most islands in Nusa Tenggara with *H. sumbae* have a morphologically distinctive form of the species. Populations on Sumba I., Roti I. and Sumbawa I. are considered separate subspecies, as probably also are those from Savu I. and Semau I. Only single specimens were available from Timor I. and Flores I. (the latter with a dentary damaged during its development by a disease and/or accident).

Specimens from Java, Sumatra, Madura, Nias, Krakatau and Palau Laut Is are very distinctive morphologically from *H. sumbae*. Three species (*H. madurae, H. sorenseni, H. larvatus*) and a possible fourth species from Sukabumi, are described from Java.

The nomenclature of this group of species is very difficult to resolve. This is because Horsfield (1823) recognised four species from Java. These are: *H. insignis, H. deformis, H. vulgaris* and *H. larvatus*. Their collection locality is known only as 'Java'. Their holotype or "co-types" lodged in the British Museum of Natural History are unavailable to us to study directly and have never been even remotely adequately described. All authors since Horsfield (1823, 1824) have considered the first three forms synonymous with *H. larvatus*. Temminck (1835) considered *H. vulgaris* to be a female of *H. insignis*. The cotype of *H. insignis* (BMNH 60.5.4.16 and 79.11.21.94) according to Tate (1941) have 'skulls' that consist of fragments of toothrows only (BMNH 60.5.4.16) or have the basal part of the cranium destroyed (BMNH 79.11.21.94). The type of *H. vulgaris* (BMNH 79.11.21.575) has the back of its braincase broken. Tate (1941) was apparently confused about the specimen BMNH 79.11.21.94. He referred to it as both a cotype of *H. insignis* and as the holotype of *H. deformis* (which he could not photograph). Ms Paula Jenkins, British Museum (Natural History), confirms that BMNH 79.11.21.94 is in fact the holotype of *H. deformis* and that it has the base of the cranium broken. Ms Jenkins also adds that "the skull of the types of *H. larvatus* BMNH 79.11.21.93 is inside the dried skin and the specimen is in such poor condition that I am unwilling to attempt to remove the skull and provoke even more disintegration". A decision with which we concur.

Table 6 Forearm lengths for *Hipposideros* spp. measured in this study.

Species	Locality	Forearm length x, range, sample size
H. l. larvatus	W. Java Krakatau Pulau Laut Sumatra Nias	57.5 (53.2-62.1) 60
H. l. larvatus	Sarawak	56.9, N = 1
H. l. larvatus	Pen. Malaysia	58.5 (57.8-59.2) 2
H. madurae	Madura I. Semarang, C. Java	55.0 (53.0-57.9) 15
H. sorenseni	Pangandaran, C/W Java	57.5 (55.4-60.2) 7
H. sumbae	Nusa Tenggara	54.0 (49.9-57.1) 86
H. sp. indet.	Sukabumi	57.6 (56.5-58.7) 2
H. sp. cf. *H. grandis*	Chanthaburi, SE Thailand	54.0, N = 1

It is not possible to know for certain where in Java Horsfield's type of *H. larvatus, H. insignis, H. deformis* and *H. vulgaris* were collected, but it is likely that the bulk of his collections came from W. Java, although he travelled widely over Java (Horsfield 1822-1824). The forearm length for types of *H. larvatus, H. deformis* and *H. vulgaris* listed by Tate (1941) as 53, 53 and 56 mm, respectively, also do not help in allocating our Javanese taxa to one of these named Javanese forms, although 53 mm is the lowest value reported by us for 60 specimens from W. Java. Measurements of forearm lengths for our Javanese forms overlap and are not diagnostic (Table 6). Further we are unsure as to whether or not all of Horsfield's types were adult. On the basis of measurements of these Javanese types provided to us by Ms Paula Jenkins (see Appendix), we are able to confidently state that none of the types *H. insignis, H. deformis* or *H. vulgaris* represent the taxon *H. madurae*. Further, the measurements of these types are similar to our W. Javan specimens considered by us to represent *H. l. larvatus*, rather than those from Pangandaran (*H. sorenseni*). For this reason we concur with most recent workers in considering *H. insignis, H. deformis* and *H. vulgaris* consubspecific with *H. l. larvatus*. However, confirmation of this will depend on a more detailed comparison of the skull of the *H. l. larvatus* holotype with these other forms, perhaps using x-ray techniques. However, without baculum and glans penis of these types (which are unavailable — they are dry skins and the *vulgaris* holotype is a female) to compare with W. Javan and Pangandaran specimens, it will be difficult to distinguish if the types represent members of the W. Javan or the Pangandaran taxa from the skull measurements that can be taken from these damaged types.

This study has shown that specimens from populations in W. Java, Sumatra, Pulau Laut I., Krakatau Is and Nias I. are similar in skull, external morphology, glans penis and baculum (specimens from Carita, Krakatau Is, Ujong Kulon, Aceh and Nias I. had a glans penis and baculum available for examination). Hill (1963) placed the Sumatra and Nias I. specimens in the subspecies *H. larvatus neglectus*. This subspecies was described from Borneo by Sody (1936) on the basis of specimens from C. Borneo having a forearm of 62-63. These values overlap with the *H. l. larvatus* in this study and are larger than the single specimen from Sarawak examined by us (Table 7). This Sarawak specimen and two from Pahang, Peninsular Malaysia, examined by us (forearms 57.8-59.2) also had glans penis and baculum of the same form as our *H. l. larvatus* specimens as did a specimen of *H. larvatus* illustrated in Zubaid and Davison (1987). Further, when these three Malaysian specimens are included in the DFA they cluster closely with the *H. l. larvatus* specimens. For these reasons we suspect that *H. l. larvatus* and *H. l. neglectus* are synonymous.

The single specimen from Chanthaburi, S.E. Thailand, examined by us is, however, morphologically quite distinct from *H. larvatus*, for example, its overall skull morphology (it clusters closer to *H. madurae* than it does to *H. l. larvatus*) and its glans penis and baculum morphology is distinct from all other taxa dealt with in this study. The baculum (Figure 5k) is almost identical to those figured as *H. l. larvatus* in Topál (1975: Plate 6, 5-10) from Tuong Linh, N. Vietnam. Clearly the Vietnam and Thailand specimens are not representative of *H. l. larvatus* as defined by us. Our Thailand specimen would also appear to be much smaller than the measurements of *H. grandis* presented from Chiangmai, N. Thailand, by Shamel (1942). For example (our measurements, followed by Shamel's in brackets) are total body length 57.2 (69-71); tail length 31.8 (34-35); forearm length 54.0 (62.0-66.2); skull condylobasal length 18.2 (?) (20.5-20.5); maxillary tooth row length 8.2 (8.6-8.8). However, on geography our Thailand specimen would appear to be a small representative of the form *grandis*. If this is the case, then the distinctive appearance of the baculum and skull of our specimen would suggest that *H. grandis* is a species.

This study confirms a number of previous studies by us that Nusa Tenggara is a unique biogeographic region which has been the centre of considerable speciation of mammals (Kitchener *et al.* 1992a). As indicated in our study of *Taphozous* (Kitchener *et al.* 1992b), the islands in the Outer Banda Arc (Sumba, Savu, Roti, Semau, Timor) showed considerable morphological, if not genetic, variation from the islands of the inner Banda Arc (Sumbawa and Flores). This again suggests that there is either very restricted gene flow between populations of *Hipposideros sumbae* in the inner and outer Banda arcs, or that *Hipposideros sumbae* in these different island arcs experience considerably different selection pressures and environments that influence their morphology.

Specimens Examined (see Figure 1 for map of localities)

Hipposideros larvatus larvatus

Pulau Panjang, Krakatau Is. (loc 1); 6♂♂, 11♀♀; MZB (9433, 14515 A-F), WAM (M25925-35). *Pulau Rakata* (Krakatau Is) (loc. 2); 3♂♂, 3♀♀; WAM (23305-11). *Ujong Kulon*, W. Java (loc. 3); 2♂♂; MZB 10607A-B. *Carita*, W. Java (loc. 4); 8♂♂, 5♀♀; MZB 1458A-C, WAM (M26420-25, M26427, M26429-

30, M26433). *Candi*, W. Java (loc. 5); 2♀♀; MZB (14853, 14887). *Banten*, W. Java (loc. 6); 2♀♀; MZB (14850, 10598). *Cikajang*, W. Java (loc. 7); 2♂♂; MZB 14860-61. *Rawa Kalong*, *Pelabuan Ratu*, W. Java (loc. 8); 1♂; MZB 10604. *Ciampea* W. Java (loc. 9); 1♂, 3♀♀ MZB 172A-B,D, MZB 9425. *Pulau Laut*, nr W. Java (loc. 11); 3♂♂, 1♀; MZB (9442-43, 10616A-B). *Aceh*, N. Sumatra (loc. 12); 2♂♂, 1♀; MZB (11279-80, 11283). *Palembang*, S. Sumatra (loc. 13); 1♂, 1♀; MZB (14854, 14886). *Nias I.*, nr N. Sumatra (loc. 14); 3♂; WAM (M37184, M37226, M37314).

Hipposideros larvatus subsp. cf *larvatus*

Pahang, Pen. Malaya (loc. 15); 1♂, 1♀; WAM 21156-57. *Bako National Park*, Sarawak (loc. 16); 1♂; WAM 23752.

Hipposideros madurae madurae

Holotype: *Sampang*, Madura I. (loc. 17); 1♂; MZB 10613B. Paratypes: *Sampang*, Madura I. 1♂, 3♀♀; and *Sumenep*, Madura I. (loc. 18); 2♂♂, 1♀; MZB 10615A-C.

Hipposideros madurae jenningsi

Holotype: *Semarang*, C. Java (loc. 19); 1♀; MZB 14883. Paratypes: *Semarang*, C. Java; 3♂♂, 3♀♀; MZB (14851, 14855-56, 14862, 14880, 14884).

Hipposideros sorenseni

Holotype: *Gua Kramat*, Pangandaran, C. Java (loc. 20); 1♀; MZB 11333. Paratype: *Gua Kramat*, Pangandaran; 2♂♂, 3♀♀; MZB (10612A-F).

Hipposideros sp. cf. *H. grandis*

Chanthaburi, Thamai, Khao wong kot, Thailand (loc. 21); 1♂, WAM M26828.

Hipposideros sumbae sumbae

Waikabubak, Sumba I. (loc. 22); 1♂, 3♀♀; WAM (M30315-17, 30319). Waikelasawah, Sumba I. (loc. 23); 1♂, 1♀; WAM (M30338, M30348). Waeelonda, Sumba I. (loc. 24); 1♂, 3♀♀; WAM (M30448, M30452-53, M30455). *Bondokodi*, Sumba I. (loc. 25); 1♂, 3♀♀; WAM (M30490-91, M30493, M30495).

Hipposideros sumbae rotiensis

Holotype: *Sangoen*, Roti I., Nusa Tenggara (loc. 26); 1♂; WAM M35436. Paratypes: 7 km SW *Baa*, Roti I. (loc. 27); 2♂♂, 1♀; WAM (M35361, M35369, M35379). *Sangoen*, Roti I.; 3♂♂, 3♀♀; WAM (M35433, M35435-36, M35438, M35440, M35442). Camplong, W. Timor (loc. 28); 1♂; MZB 14852.

Hipposideros sumbae sumbawae

Holotype: *Gua Batu Tering*, 3 km S Desa Batu Tering, W. Sumbawa I. (loc. 29). Paratypes: *Gua Batu Tering*, 3 km S Desa Batu Tering; 14♂♂, 16♀♀; WAM (M31140, M31515-16, M31416-17, M31439-40, M31462-63, M31468, M31492, M31495-99, M31515-16, M31528), MZB (11392, 11394-405). *Desa sangeang*, E. Sumbawa (loc. 30); 22♂♂, 1♀; WAM (M31526, M31529, M31532-34, M31536-37, M31539-40, M31542-43, M31545, M31549-52, M31553, M31559, M31564, M31566, M31568-69, M31571). *Gua Cermin*, nr Labuan Bajo, W. Flores (loc. 31): 1♂; MZB 14243.

Hipposideros sumbae subsp. indet. A.

Desa Uiasa, Semau I. (loc. 32); 1♀; WAM M35563. *Desa Onansila*, Semau I. (loc. 33); 2♂♂, 1♀; WAM (M38007-08, M38016-17).

Hipposideros sumbae subsp. indet. B.

Desa Menia, E. Savu I. (loc. 34); 2♂♂, 1♀, WAM (M35116, M35213, M35259, M35263).

Hipposideros sp. indet.

Gua Cidalog, Cikopeah, nr Sukabumi, W. Java (loc. 10); 1♂, 1♀; WAM M30008-09.

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N. Cooper, Western Australian Museum, ran the computer analyses. J. Dell, Western Australian Museum, drew the graphs. A. Nevin, Western Australian Museum, typed the manuscript.

Appendix

Measurements (in mm) of the skull of the holotypes of the Javanese names *Hipposideros insignis* (mandible only), *H. deformis* and *H. vulgaris* (both with basal part of cranium damaged).

Character	*H. insignis* BM 60.5.4.16	*H. deformis* BM 79.11.21.94	*H. vulgaris* BM 79.11.21.575
Palatal bridge length		4.46	3.91
M^3 width		2.63	1.92
P^3 width		1.80	1.72
Least interorbital width		3.31	3.03
C^1C^1 outer breadth		5.81	5.40
Dentary length		15.41	15.09
I_1M_3 length	10.66	10.56	10.03
Ramus to angular tip length		5.80	5.43
Nasal inflation length		6.08	6.10
Cranial length		*c.* 17.0	

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Description of a new genus of goby from southern Australia, including osteological comparisons with related genera

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Abstract

The osteology of *Favonigobius suppositus* and *Favonigobius tamarensis* are described and compared with that of *Favonigobius lateralis*, the type species for the genus. Osteological comparisons are also made with members of *Papillogobius* and *Glossogobius*, genera that are closely related to *Favonigobius*. These comparisons, together with data on body proportions, the distribution of the papillae of the cephalic lateral-line system, meristic counts and larval development provide strong evidence that *Favonigobius suppositus* and *Favonigobius tamarensis* should not be placed in the genus *Favonigobius*. Therefore a new genus, *Afurcagobius* is proposed for these species and *A. suppositus* is designated as the type species. A key is provided for these two species and for other Australian genera and species with which, during recent years, they have been associated.

Introduction

The family Gobiidae, which comprises approximately 2000 species, is the second most diverse of all teleost families (Hoese 1984). The large size of the group and a tendency to evolve by reduction have led to difficulties in classifying many of the members of this family (Birdsong *et al.* 1988; Gill *et al.* 1992). These difficulties have often been compounded when genera have been erected with merely a reference to the type species, the descriptions of which themselves are often inadequate and without figures (Hoese and Lubbock 1982; Gill and Miller 1990; Gill *et al.* 1992).

The taxonomic status of *Favonigobius* was recently investigated by Gill and Miller (1990) and this resulted in the transfer of three species from this genus to a new genus, *Papillogobius*. A subsequent study of the morphology and osteology of *Favonigobius, Papillogobius* and *Glossogobius*, which incorporated a detailed analysis of morphometric and papillae pattern data, indicated that two of the four remaining species assigned to *Favonigobius* were more closely related to the last of these genera (Gill *et al.* 1992). Although Whitley (1934) and Koumans (1953) placed *Favonigobius suppositus* (Sauvage, 1880) in *Glossogobius*, there is now clear evidence that this species, and also *Favonigobius tamarensis* (Johnston, 1883), should be assigned to a new genus (Gill *et al.* 1992).

This paper describes a new genus of goby, which is endemic to southern Australia, and incorporates species previously referred to as *Favonigobius suppositus* and *Favonigobius tamarensis*.

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Materials and Methods

The methods for counting the meristic characters and for deriving pterygiophore formulae follow those described by Akihito *et al.* (1984). Vertebral counts and osteological examination were undertaken after clearing and double staining the specimens, using the method of Dingerkus and Uhler (1977). All bones of the skeleton were examined in detail after dissection and/or disarticulation in a heated solution of 5% KOH. Nomenclature of the bones follows Birdsong (1975) and Springer (1983).

Description of the cephalic lateral-line system and morphometric measurements follow those of Miller (1969, 1975, 1984) and Gill *et al.* (1992). Terminology of the cephalic lateral-line system follows that given by Miller (1986), which represents a modification of that provided by Sanzo (1911).

Measurements were made to the nearest 0.1 mm (interorbital nearest 0.01 mm) with dial calipers. Illustrations were prepared with the aid of a Wild M8 stereo-microscope and drawing tube attachment.

Details and drawings of the characters examined are given in Tables 1 & 2 and Figures 1-15.

Material from the following institutions was examined: the Australian Museum, Sydney (AMS); The Natural History Museum [formerly the British Museum (Natural History)], London (BMNH); Gulf Coast Research Laboratory, Ocean Springs, Mississippi (GCRL); Rijksmuseum van Natuurlijke Histoire, Leiden (RMNH); J. B. L. Smith Institute of Ichthyology, Grahamstown (RUSI) and the Western Australian Museum, Perth (WAM). Additional material from the collection of Peter Miller (PJM) and from the authors collection (HSG) was also examined.

Key to the Australian species of the genera *Afurcagobius, Favonigobius* and *Papillogobius* and the genus *Glossogobius*

1a Snout shallow (Fig. 1A & B); mouth horizontal/superior (Fig. 1A & B); head long (>27% SL); cephalic lateral-line with row a1 (Fig. 1A & B); 27 vertebrae 2

1b Snout steep (Fig. 1C & D); mouth oblique/terminal (Fig. 1C & D); head short (<25% SL); cephalic lateral-line without row a1 (Fig. 1C & D); 26 vertebrae 4

2a Tongue truncate; prepelvic area naked; nape scales small and indistinct; operculum naked; branchiostegal membrane attached to isthmus to well behind level of preopercular/opercular margin; row a1 of cephalic lateral-line short and connected to medial portion of row a (Fig. 1A) . . . . *Afurcagobius* 3

2b Tongue forked; prepelvic area scaled or naked; nape scales small and indistinct or large and well defined; operculum often lightly scaled; branchiostegal membrane usually only attached to isthmus to about level of preopercular/opercular margin; row a1 of cephalic lateral-line long and connected to anterior of row a (Fig. 1B) . . . . *Glossogobius*

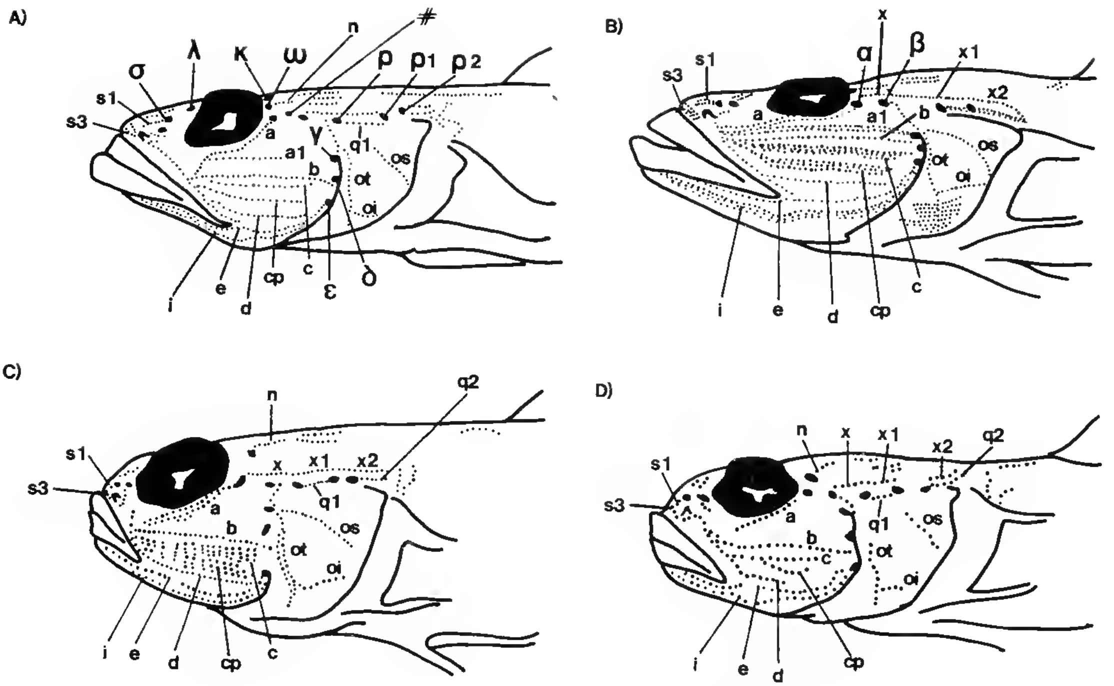

Figure 1 Cephalic lateral-line system in (A) *Afurcagobius*; (B) *Glossogobius*; (C) *Papillogobius*; (D) *Favonigobius*. Modified from Gill *et al.* (1992).

3a A I, 7; P 15-16 .... *A. suppositus*

3b A I, 8; P 16-18 .... *A. tamarensis*

4a D2 I, 9; A I, 9; D1 may bear large spot anteriorly and may have first ray extended; rows a, c and cp of cephalic lateral-line single (Fig. 1 D); row x short extending to pore β; rows x1 and x2 separate .... *Favonigobius lateralis*

4b D2 I, 8; A I, 8; D1 never bears large spot, first second and third rays maybe extended but second is always longest; rows a, c and cp of cephalic lateral-line transversely proliferated (Fig. 1C); row x usually long, extending to pore α; rows x1 and x2 contiguous or with small break .... *Papillogobius* 5

5a Branchiostegal membranes meeting isthmus below rear of preopercle and usually heavily pigmented; nape scales small and illdefined; cephalic lateral-line row e with distinct break (Fig. 1C); rows x1 and x2 contiguous .... *Papillogobius punctatus*

5b Branchiostegal membranes meeting isthmus below orbit and lightly pigmented; nape scales large and well defined; cephalic lateral-line row e continuous or with small break (Fig. 1); rows x1 and x2 usually with small break .... *Papillogobius exquisitus*

Systematics

Afurcagobius gen. nov.

Type species

Gobius suppositus Sauvage, 1880: 41 (type locality, Swan River, Western Australia).

Diagnosis

A genus of the subfamily Gobiinae, distinguishable from related genera possessing 26 or 27 vertebrae by, a pterygiophore formula of 3/II II I I 0/9, one epural and a longitudinal cephalic lateral-line system by the presence on the cephalic lateral-line system of an additional suborbital row of papillae, a1, which meets the medial section of row a anteriorly and is reduced posteriorly, and the absence of a large posteroventral process on the coracoid. The genus also differs from related genera by the following combination of characters: 27 vertebrae; operculum and preoperculum without scales or spines; snout shallow and long; basibranchial 4 absent or reduced; asteriscus greatly reduced or absent; prepelvic area without scales; rows a, c and cp of cephalic lateral-line system single and long; row c often joined anteriorly and/or posteriorly to row b; rows e and i single; row h long; row n single and longitudinal; row os short; rows x1 and x2 separate; row x short extending to pore β.

Description

Body moderately elongate. Eyes dorso-lateral. First ray of first dorsal never extended or free at tip. Second dorsal fin with eight soft branched rays. Anal fin with seven or eight soft branched rays. Caudal fin rounded, usually shorter than head. No deepening of caudal peduncle in adults. Pectoral fins without free rays. Pelvic disc complete, posterior edge rarely to anal fin; anterior membrane complete and well developed. Lateral series with 30-38 ctenoid scales. Transverse series with 9-13 ctenoid scales. Predorsal scales 0-4, embedded and very small. Prepelvic scales absent. Belly scales small and cycloid. Head, opercle and cheek naked. Anterior nostril tubular, without tentacles; posterior nostril pore-like, midway between anterior nostril and orbit. Mouth horizontal/superior; jaws subequal, posterior angle of lower jaw between pupil and posterior edge of orbit; chin without barbels or transverse fold. Teeth in jaws erect and caniniform, in several rows medially, outer row of teeth in both jaws enlarged; pharyngeal teeth caniniform. Tongue truncate to slightly notched. Branchiostegal membrane attached to lateral margin of isthmus to level of pectoral base. Gill rakers small and simple to serrate on first arch, spinulose on rest.

Cephalic lateral-line system with anterior and posterior oculoscapular canals carrying pores σ, λ, κ, ω, α, β, $\mathbf{p}$, $\mathbf{p}^1$, $\mathbf{p}^2$, and the preopercular canal carrying pores, γ, δ and ε posterior oculoscapular canal often carrying an additional pore (#) between pores α and β (Figure 1). Cheek sensory papillae in eight single rows; row a single and extending from pore α to row b; row a1 extending from row a to between verticals of pores α and β; row b extending from row c to pore δ or just below it; rows c and cp single and extending to vertical of pore β, row c often curving up to join row b both anteriorly and posteriorly;

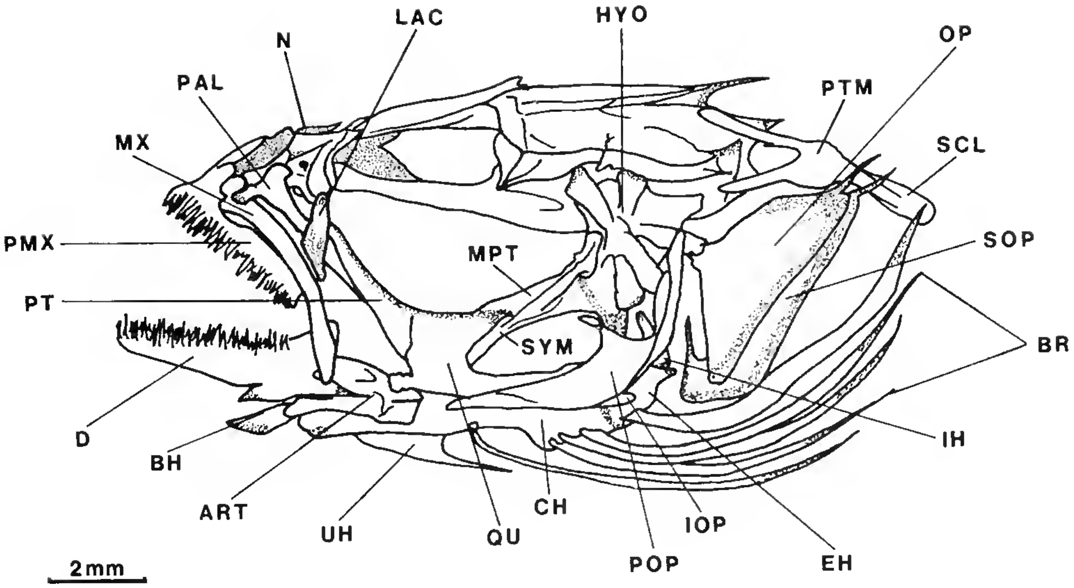

Figure 2 Articulated skull of *Afurcagobius suppositus*, female, 43.5 mm SL, lateral view.

row d extending from row c to vertical of pore β and bearing a short extension running parallel to jaw; rows e and i without break; row ot single and extending to pore γ; row oi extending from row ot to edge of opercle; row os extending from posterior edge of opercle to above level of pore γ but not joined to row ot; rows x and x1 contiguous and extending from pore β to pore $\mathbf{p}^1$; row x2 extending from pore $\mathbf{p}^2$ to above posterior opercular margin; rows q1 and q2 single; row n short and longitudinal; row s1 comprising 5-10 papillae; row s3 long and proliferated.

Skeleton possesses characters diagnostic of the subfamily Gobiinae as described by Miller (1973) (Figures 2-14). Ventromedial strut of exoccipital (V EO) with large expanded foot. Metapterygoid (MPT) and symplectic (SYM) fused; tip of metapterygoid overlapping quadrate (QU). Symplectic cartilage bound to hyomandibular (HYO) and preopercle (POP). Head of palatine bearing additional posteriorly projecting strut (PT2 PAL). Ectopterygoid (PT) long and thin, reaching and bound to PT2 PAL. Symplectic process of preopercle (SYM POP) large. Lateral process of cleithrum (LP CL) small or absent. Scapula (SCA) partially ossified. Posterior process of coracoid (COR) reduced. Asteriscus greatly reduced or absent.

Osteology of *Afurcagobius* and some related genera

In general, the overall shape and articulation of the skeletons of all the genera examined were consistent with Birdsong's (1975) description of *Microgobius signatus*. For this reason, the following description refers only to cases where there are differences from Birdsong's description and for ease of comparison follows his scheme.

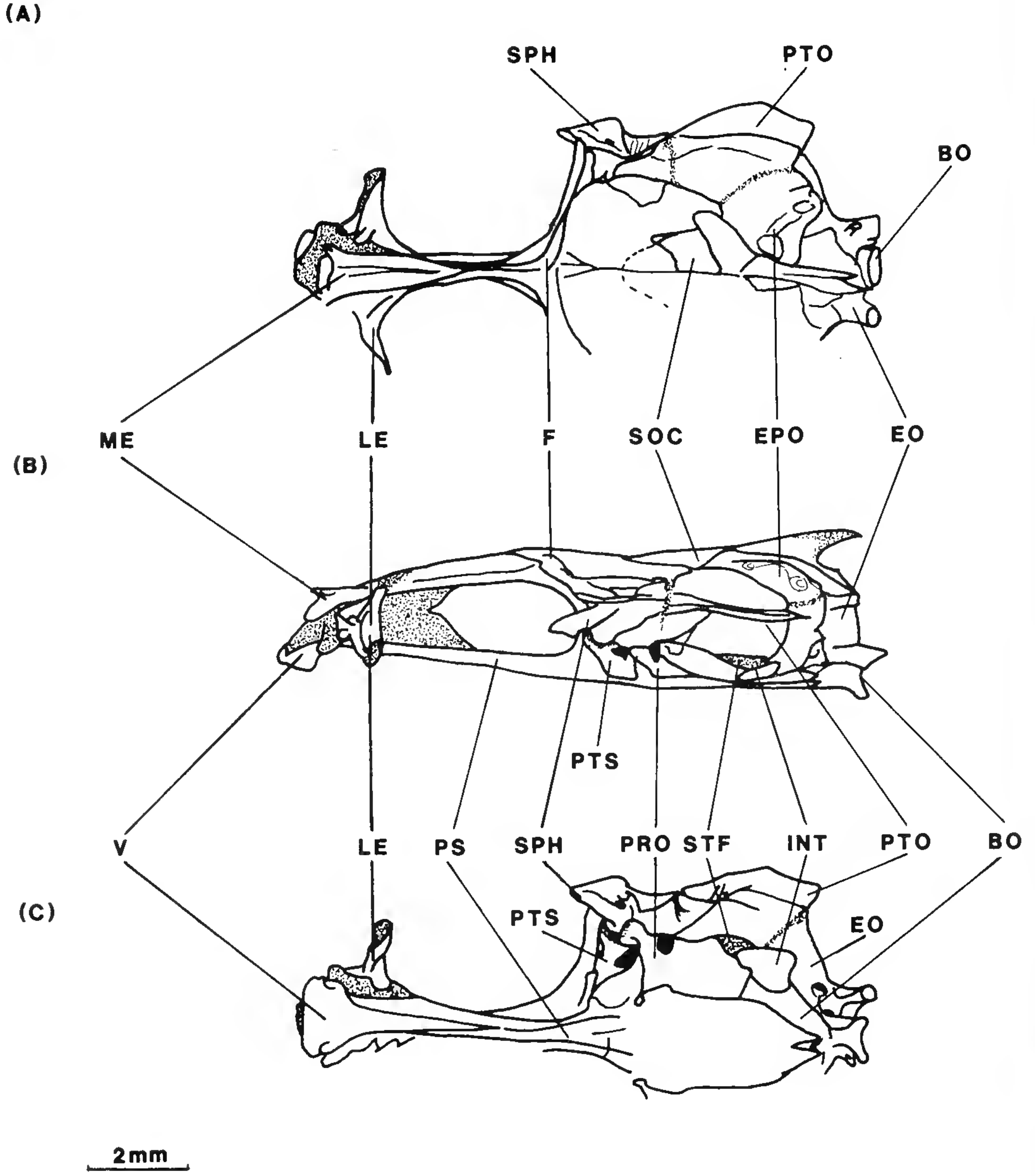

Figure 3 Cranium of *Afurcagobius suppositus*, female, 43.5 mm SL, (A) dorsal view; (B) lateral view; (C) ventral view.

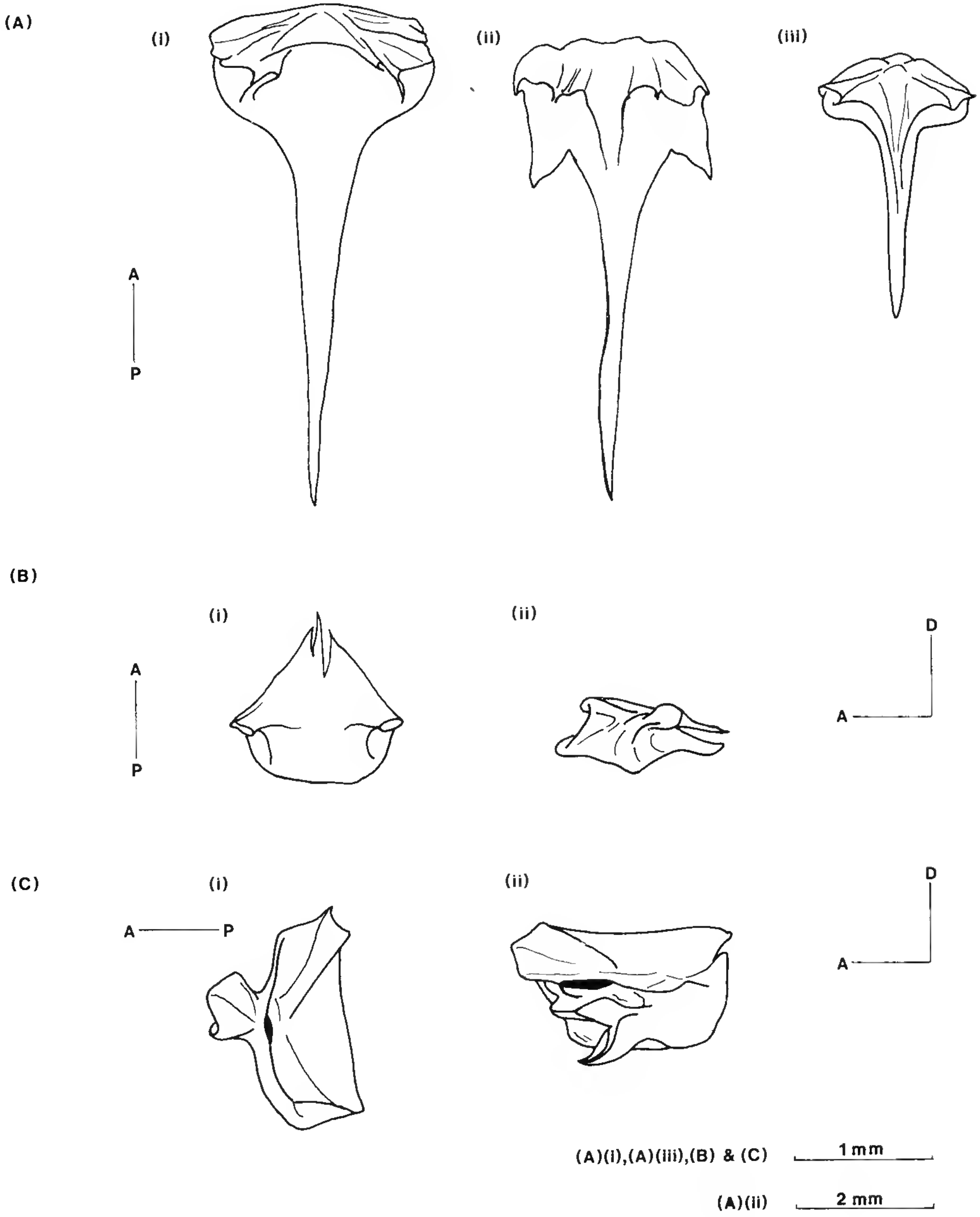

Figure 4 Disarticulated cranial bones of *Afurcagobius suppositus*, female, 43.5 mm SL, (A) vomer, ventral view, (i) *A. suppositus*, (ii) *G. giuris*, female, 71.0 mm SL, (iii) *P. punctatus*, female, 32.2 mm SL; (B) median ethmoid, (i) dorsal view, (ii) anterolateral view; (C) lateral ethmoid, (i) dorsal view, (ii) lateral view.

Head region (Figures 2-12)

Vomer (Figures 3,4).

In *Afurcagobius* the anteriorly broadened head of the vomer (V) bears a large ventral shelf. *Favonigobius* and *Papillogobius* bear no anterior ventral shelf, rather a median process extending onto the posterior process of the vomer. In *Glossogobius* a ventral shelf or a median process may be present, and in addition, the head of the vomer bears two posteriorly directed lateral processes

Median ethmoid (Figures 3,4).

In all genera the median septum of the median ethmoid (ME) extends and is firmly bound to the parasphenoid (PS). The median septum is unossified in *Afurcagobius* and *Glossogobius*, partially ossified in *Papillogobius* and maybe unossified or partially ossified in *Favonigobius*.

Lateral ethmoid (Figures 3,4).

As Birdsong 1975.

Frontal (Figures 3,5).

The frontals (F) are paired but not fused, the sagittal crest is absent or present only as a remnant in *Afurcagobius, Papillogobius* and *Favonigobius*, whereas in *Glossogobius* a small crest is present. A small foramen pierces the broadened posterior section of each frontal in *Favonigobius* and *Papillogobius* but is absent in *Afurcagobius* and *Glossogobius*. Posteriorly the medial edge of the frontal is most deeply cut away in *Afurcagobius* and *Glossogobius*, less so in *Favonigobius* and least of all in *Papillogobius*.

Sphenotic (Figures 3,5).

As Birdsong 1975.

Pterotic (Figures 3,5).

In the specimens of *Afurcagobius* and *Glossogobius* examined in this study the anterolateral surface of the pterotic bones (PTO) bear three to four finger-like processes which overlap the sphenotics (SPH). However, Hoese (pers. comm.) reports observing these processes only in larger specimens of *A. tamarensis* and in none of the specimens of *Glossogobius* (<65 mm) examined by him. These processes are absent in *Favonigobius* and *Papillogobius*.

Epiotic (Figures 3,5).

The posterolaterally directed process of each epiotic (EPO) is large and heavily sculptured in *Glossogobius*, slightly smaller in *Afurcagobius* and present as little more than slight sculpturing in both *Papillogobius* and *Favonigobius*.

Supraoccipital (Figures 3,6).

The anterior lateral margins of the supraoccipital (SOC) are most deeply cut away in *Papillogobius*, less so in *Favonigobius* and *Afurcagobius tamarensis* and least of all in *A. suppositus* and *Glossogobius*. This reduction is inversely proportional to the reduction in the overlapping frontals (F). The anterior and posterior edges of the sagittal crest meet at an acute angle forming a posteriorly directed spur in all genera.

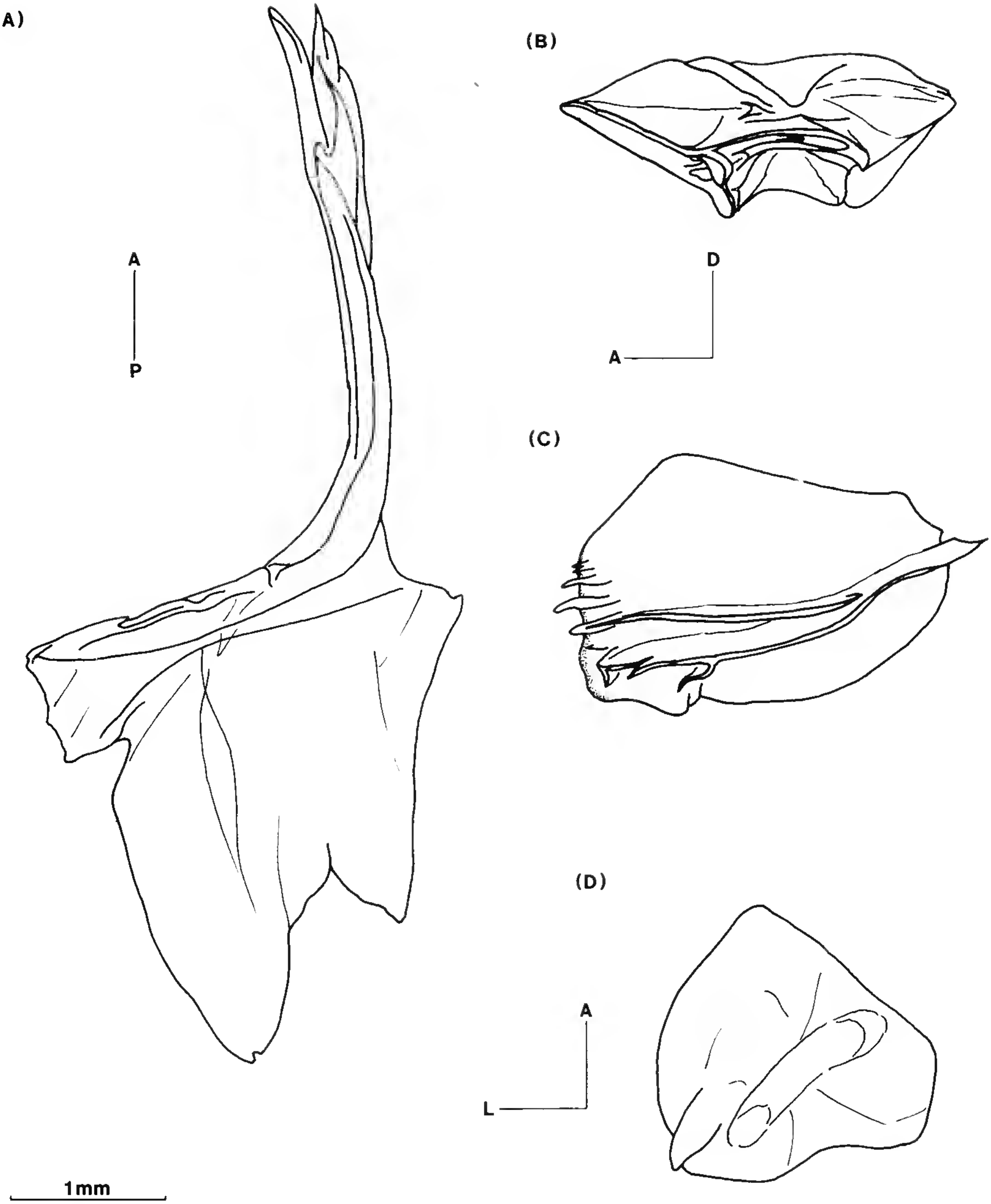

Figure 5 Disarticulated cranial bones of *Afurcagobius suppositus*, female, 43.5 mm SL, (A) frontal, dorsal view; (B) sphenotic, lateral view; (C) pterotic, lateral view; (D) epiotic, dorsal view.

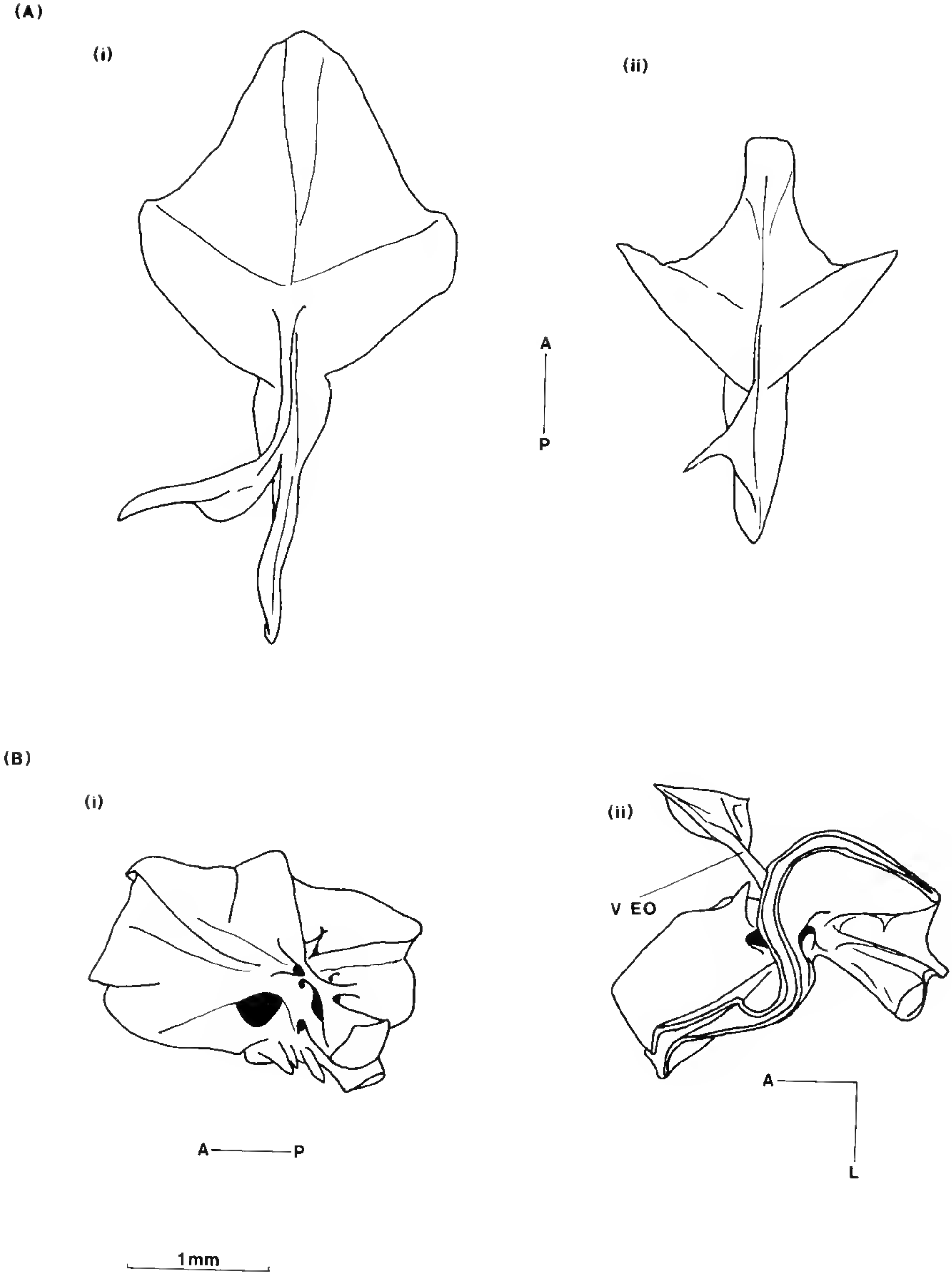

Figure 6 Disarticulated cranial bones of *Afurcagobius suppositus*, female, 43.5 mm SL, (A) supraoccipital, dorsal view, (i) *A. suppositus*, (ii) *P. punctatus*, female, 32.2 mm SL; (B) exoccipital, (i) lateral view, (ii) dorsal view.

Exoccipital (Figures 3,6).

The internal ventromedial strut (V EO) of each exoccipital (EO) bears a large foot in both *Afurcagobius* and *Glossogobius.* In *Favonigobius* the foot is small, whereas in *Papillogobius* the foot is greatly reduced or absent.

Basioccipital (Figures 2,3 and 7).

As Birdsong 1975.

Intercalar (Figures 3,7).

In contrast to the condition described by Birdsong 1975 for *Microgobius signatus*, the paired intercalars (INT) are well separated from the parasphenoid (PS) in the four genera examined. The posterolaterally directed process is always present although highly variable in size and form in *Afurcagobius, Glossogobius* and *Papillogobius.* In *Favonigobius*, however, the process is either absent or greatly reduced. Both *Papillogobius* and *Favonigobius* often bear an indent on the anterior edge of the intercalar. This indent maybe present as either a simple indent, or as a break in the bone leading to a foramen.

Subtemporal fossa (Figure 3).

In all four genera the subtemporal fossae (STF) are relatively small cartilaginous areas, each is bound by the prootic (PRO) anteriorly and medially, the pterotic (PTO) anteriorly and laterally and the intercalar (INT) posteriorly.

Prootic (Figures 3,7).

In *Afurcagobius* and *Glossogobius* the internal lamina of each prootic (PRO) forms a large anterior process which is synchondrally joined to the internal surface of the pterosphenoid (PTS). Neither *Favonigobius* or *Papillogobius* bear such a process. The anterior notch forming the ventral and lateral walls of the trigemino-facial foramen is deeper in *Afurcagobius* and *Glossogobius* than in either *Papillogobius* or *Favonigobius.*

Pterosphenoid (Figures 3,7).

The pterosphenoid bones (PTS) are similar in shape and attachment points to those in *Microgobius signatus.* However, in *Afurcagobius* and *Glossogobius* the ventromedial process is bifid, the lateral and medial extensions of which are synchondrally bound to the prootic (PRO) and parasphenoid (PS) respectively. In *Papillogobius* and *Favonigobius* the ventromedial process is pierced by a foramen and is splayed at its tip to form a highly sculptured spear shaped attachment point. This sculptured surface is very firmly bound to the overlying parasphenoid from which it could only occasionally be separated. Even after heating in 5% KOH the bone normally broke at the foramen.

Parasphenoid (Figures 3,8).

As Birdsong 1975.

Lacrymal (Figures 2,8).

The lacrymal bones (LAC) are poorly ossified fan shaped bones in all four genera.

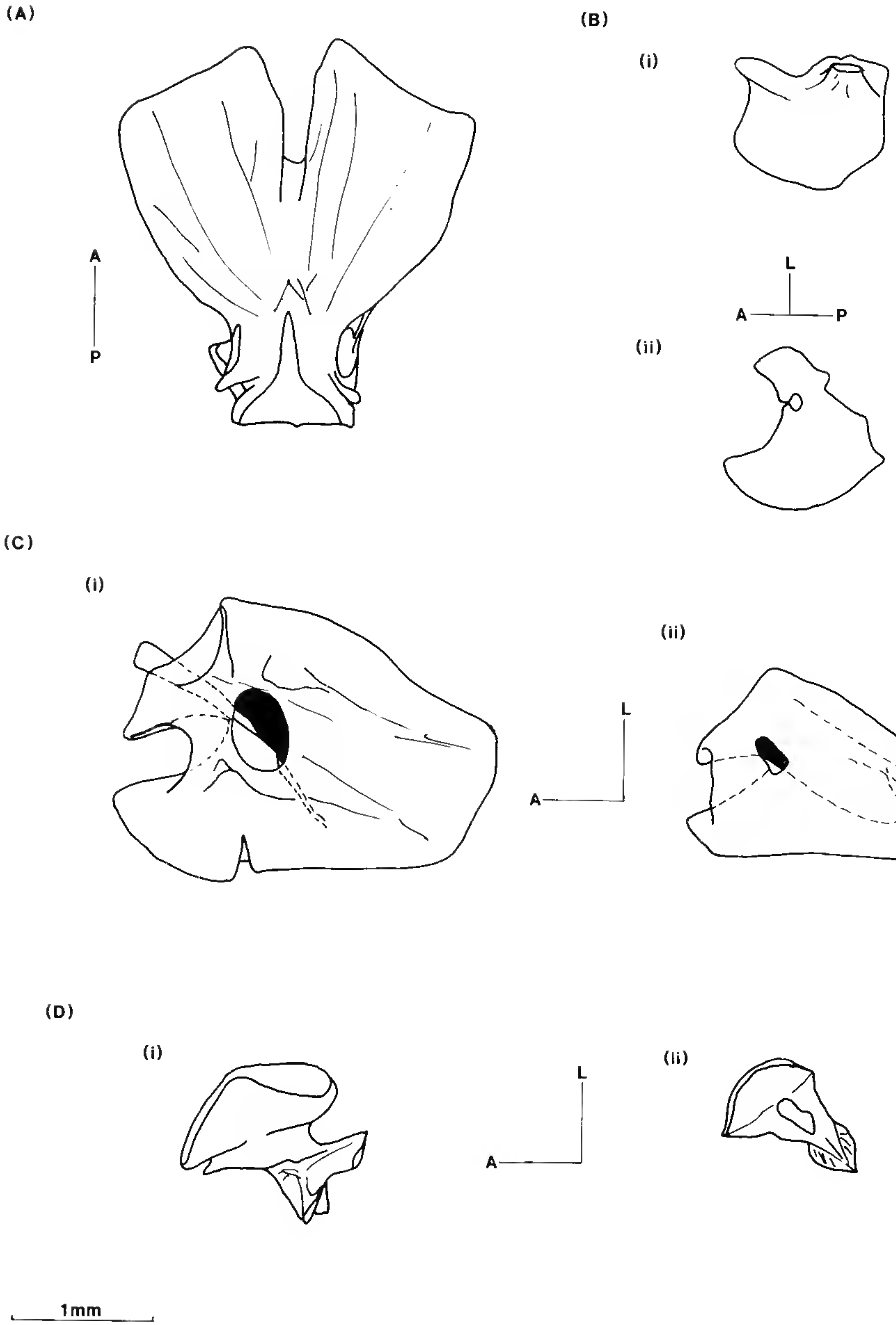

Figure 7 Disarticulated cranial bones of *Afurcagobius suppositus*, female, 43.5 mm SL, (A) basioccipital; (B) intercalar, ventral view, (i) *A. suppositus*, (ii) *P. punctatus*, female, 32.2 mm SL; (C) prootic, ventral view, (i) *A. suppositus*, (ii) *P. punctatus*, female, 32.2 mm SL; (D) pterosphenoid, ventral view (i) *A. suppositus*, (ii) *P. punctatus*, female, 32.2 mm SL.

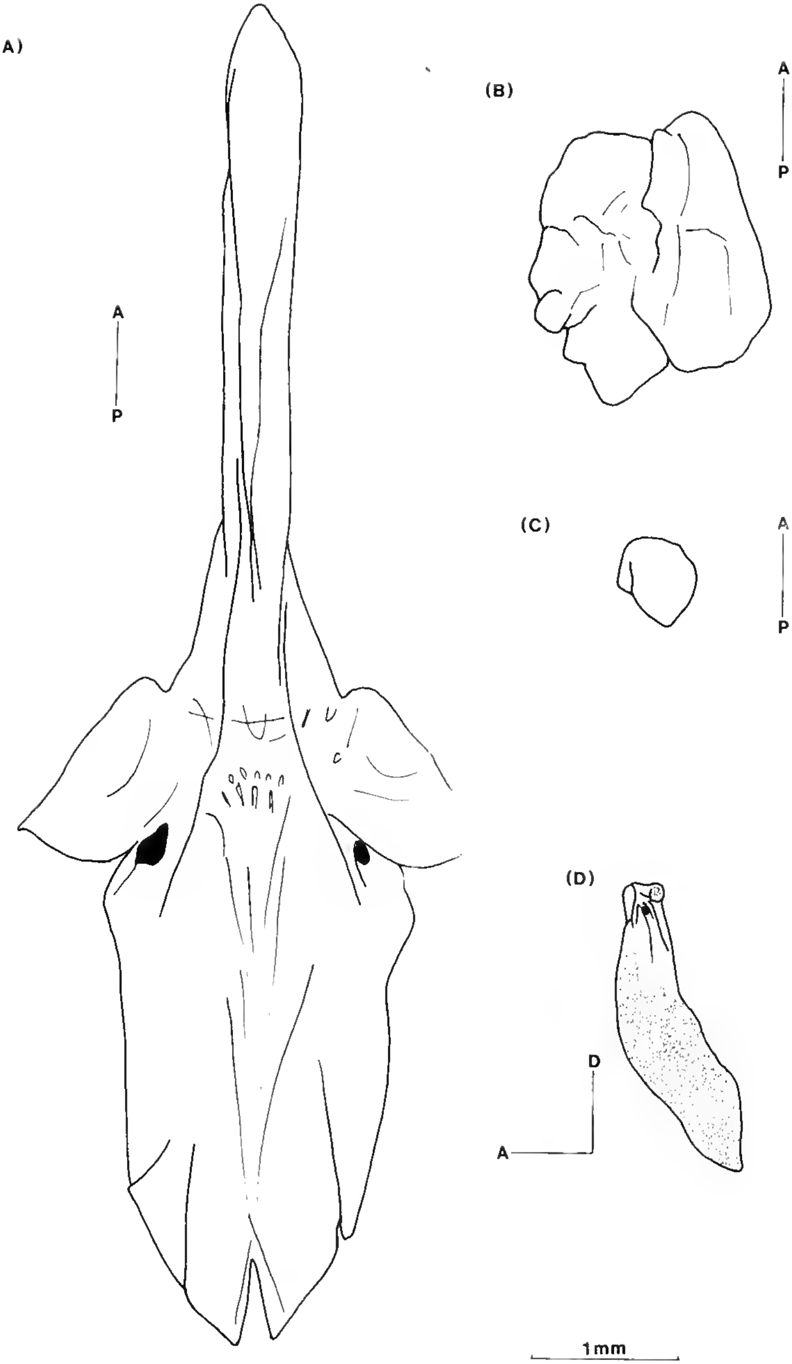

Figure 8 Disarticulated cranial bones of *Afurcagobius suppositus*, female, 43.5 mm SL, (A) parasphenoid, ventral view; (B) sagitta, dorsal view; (C) lapillus, dorsal view; (D) lacrymal.

Nasal (Figure 2).

In *Afurcagobius, Glossogobius* and *Papillogobius* the nasal (N) bones are greatly reduced and usually only ossified in the larger specimens. These bones are relatively large and well ossified in *Favonigobius.*

Otoliths (Figure 8).

The sagittal otoliths in *Afurcagobius* and *Glossogobius* are characterised by the presence of both anterior and posterior processes. In *Favonigobius* the sagittae bear only posterior processes while in *Papillogobius* these otoliths are highly sculptured anteriorly but bear no processes. In all four genera the lapillus and asteriscus are small and lightly sculptured. The asteriscus is particularly small and is often absent in *Afurcagobius* and *Glossogobius.*

Upper jaw (Figures 2,9).

Birdsong (1975) shows the premaxilla (PMX) extending posteriorly well beyond the postmaxillary process (PM PMX) and the teeth in his figures of *Microgobius signatus* (Figures 1,7). In the four genera examined their is no such extension, the postmaxillary process marking the posterior extent of this bone. The postmaxillary process is lower and longer in *Afurcagobius* and *Glossogobius* than in *Favonigobius, Papillogobius* or *Microgobius signatus.* However, Hoese (pers. comm.) reports that this is only the case in larger specimens of *A. tamarensis* and *Glossogobius* and that in smaller specimens the process is a similar shape and size to that found in the other genera. In all four genera the premaxillary teeth are in four rows anteriorly and two rows posteriorly, the outer row bearing 12-20 large recurved caninoid teeth and the inner rows bearing 30-40 smaller caninoid teeth.

The lateral head of the maxilla (L MX) is pierced by a large foramen in both *Afurcagobius* and *Glossogobius.* A small foramen is often present in *Papillogobius.* In *Favonigobius* the lateral head is deeply recessed but only rarely bears a foramen. In *Afurcagobius* and *Glossogobius* the posterior extent of the maxilla is rarely ossified and bears a thin cartilaginous tip. In all but the smallest specimens of *Favonigobius* and *Papillogobius* examined the maxilla was fully ossified.

Lower jaw (Figures 2,9).

In all four genera examined the coronoid process (COR D) of the dentary (D) is relatively short. The posterior margin of the dentary is usually unossified in *Afurcagobius* and *Glossogobius.* As with the maxilla in all but the smallest specimens of *Favonigobius* and *Papillogobius* the dentary is fully ossified.The ventromedial shelf although narrower is longer than that described by Birdsong and as such appears as a process rather than a shelf. In *Afurcagobius, Glossogobius* and *Papillogobius* the tip of this process is rarely ossified. The tip is ossified in *Favonigobius.* In all the genera examined the teeth are in three rows; the outer row comprising 6-10 large caninoid teeth and the inner rows 35-50 smaller caninoid teeth.

Posterodorsally the articular bone (ART) bears a complex articulation point that accepts the articular process of the quadrate (QU) as follows; anterolaterally there is a simple socket upon which the tip of the articular process articulates; just posterior to this

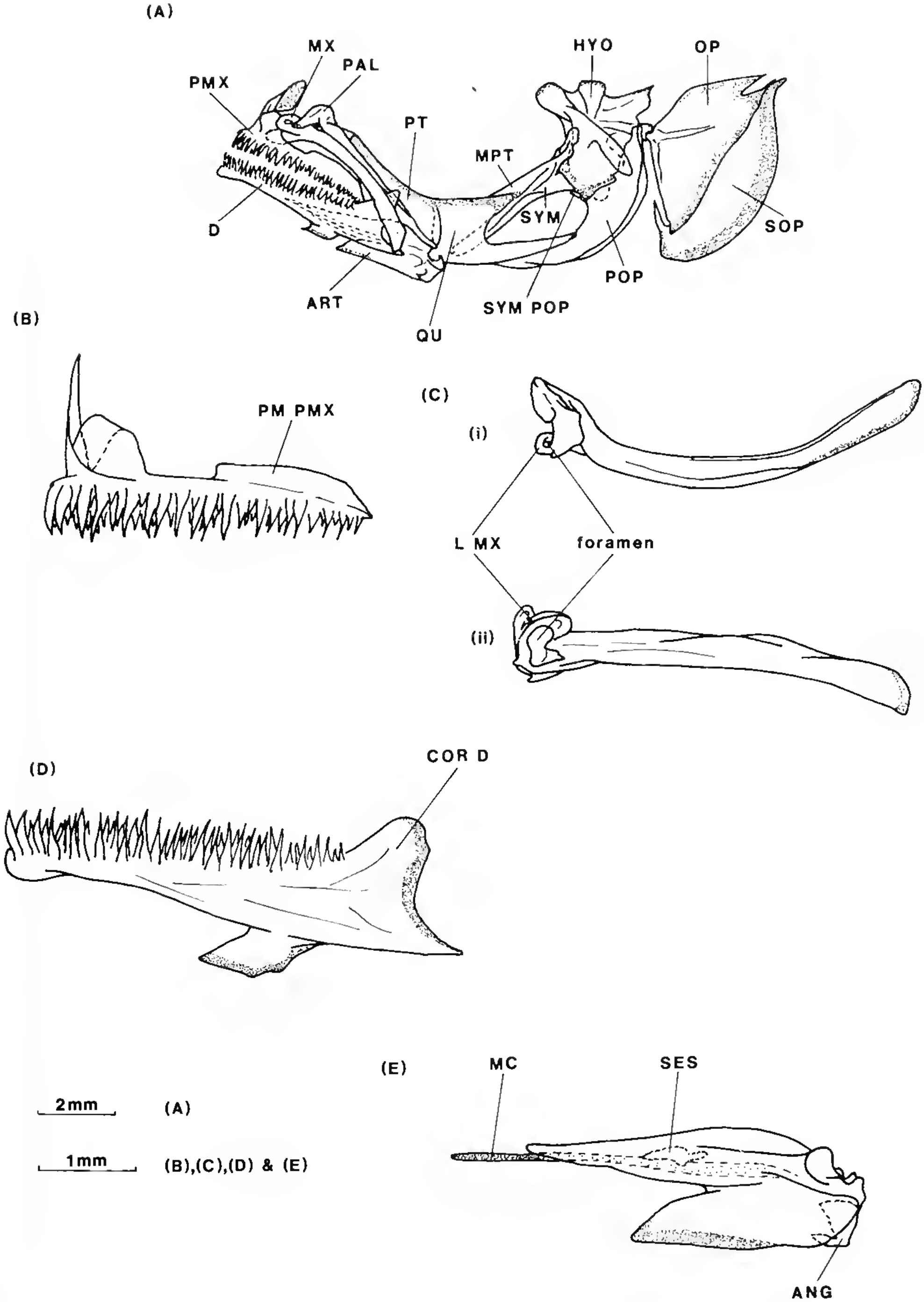

Figure 9 Suspensorium, opercular bones and jaws of *Afurcagobius suppositus*, female, 43.5 mm SL, (A) articulated suspensorium, lateral view; (B) premaxilla, lateral view; (C) maxilla, (i) dorsal view, (ii) lateral view; (D) dentary, lateral view; (E) articular, lateral view.

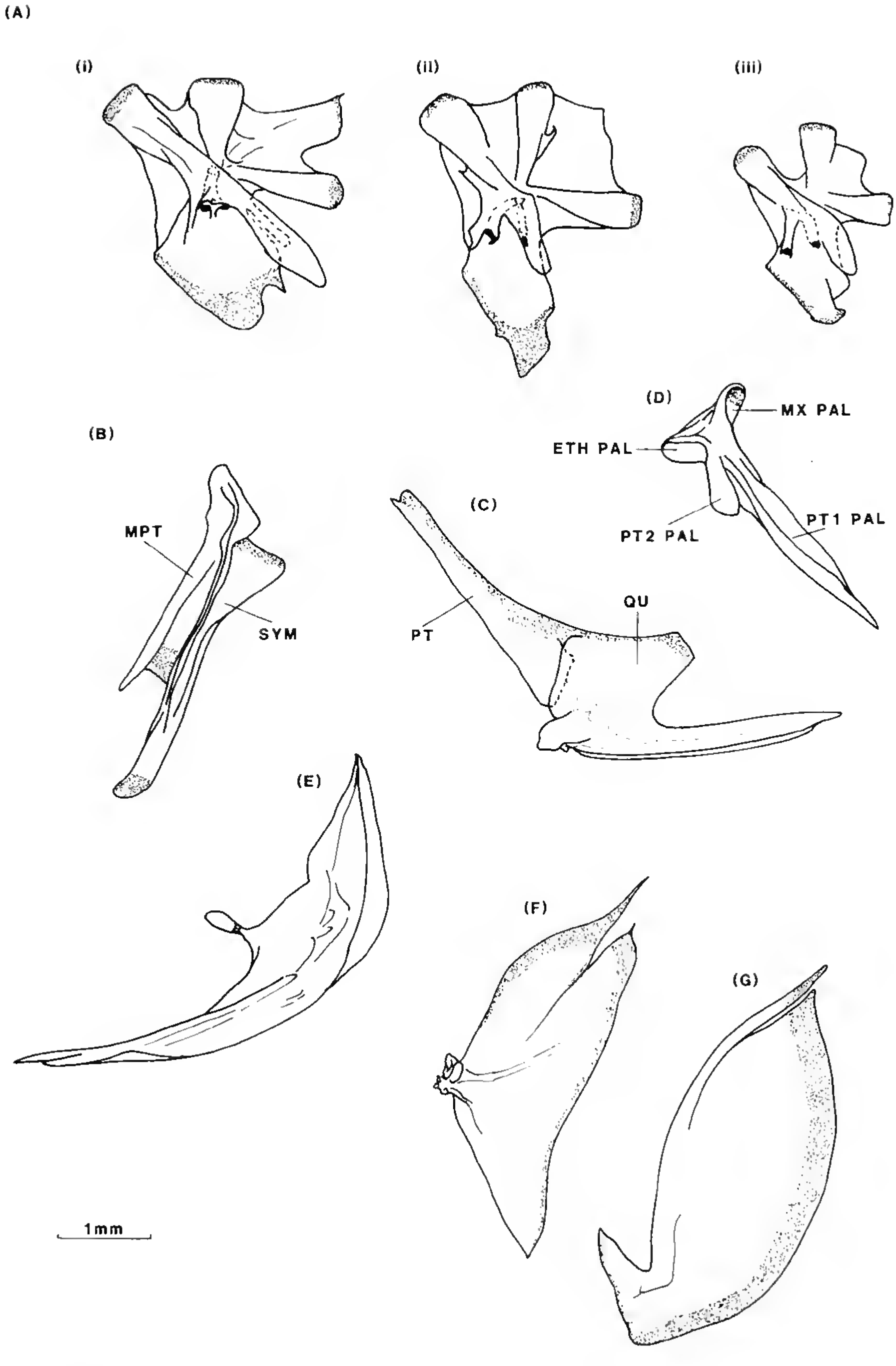

Figure 10 Suspensorium, opercular bones and jaws of *Afurcagobius suppositus*, female, 43.5 mm SL, (A) hyomandibular, lateral view, (i) *A. suppositus*, (ii) *F. lateralis*, female, 41.3 mm SL, (iii) *P. punctatus*, female, 32.2 mm SL; (B) metapterygoid and symplectic, lateral view; (C) ectopterygoid and quadrate, lateral view; (D) palatine, ventral view; (E) preopercle, lateral view; (F) opercle, lateral view; (G) subopercle, lateral view.

socket, but on the medial surface, is a smaller socket on which the medial articulation point of the quadrate bears and running posteriorly a channel surrounds the articular process posteroventrally. Posteriorly, the lateral wall of the channel bears a small hook which firmly clasps the articular process of the quadrate (the medial wall occasionally bears a smaller hook). The tip of the ventral ramus of the articular remains unossified in *Afurcagobius* and *Papillogobius.*

Meckel's cartilage (MC), sesamoid articular (SES) and angular bones (ANG) are as described by Birdsong 1975.

Hyomandibular and Palatine arch (Figures 2,9 and 10).

Both the posterolaterally directed flange and the posterodorsal sheet of the hyomandibular (HYO) tend to be larger in *Afurcagobius* and *Glossogobius* than in *Favonigobius* and *Papillogobius.* In *Papillogobius* the dorsal sheet of the hyomandibular is usually greatly reduced or missing.

In all the genera examined the metapterygoid (MPT) and symplectic (SYM) are fused to form a single complex bone which could not be separated even after heating in KOH. In all four genera the anterior strut of the metapterygoid overlaps the quadrate (QU). No differences in the form of this complex bone were observed between the sexes.

The dorsal arm of the quadrate (QU) is unossified dorsally and is heavily sculptured posterolaterally and posteromedially. The posteromedial sculpturing receiving the cartilaginous extension of the symplectic (SYM). The articular process of the quadrate is developed to produce two ball joints which articulate with the articular bone (ART) as described above.

The ectopterygoid (PT) is a simple triangular shaped bone in all genera and extends toward the head of the palatine (PAL) in *Afurcagobius, Glossogobius* and *Favonigobius.* In *Papillogobius* the ectopterygoid is often short, extending only half way up the palatine. When short, a thin sliver of bone, the medial process of the ectopterygoid, arising on the ventromedial surface of the ectopterygoid is firmly bound to the second ectopterygoid process of the palatine (PT2 PAL). In *Afurcagobius* and *Glossogobius* the dorsal surface of the ectopterygoid is unossified, whereas in *Papillogobius* and *Favonigobius* the bone is fully ossified.

Opercular series (Figures 2,9 and 10).

Both the dorsal and posterior margins of the opercle (OP) and the posterior and anteroventral margins of the subopercle (SOP) are unossified in *Afurcagobius* and *Glossogobius.* In *Papillogobius* the dorsal and dorsoposterior margins of the opercle are unossified, whereas in *Favonigobius* only the dorsoposterior margin is unossified. In both *Papillogobius* and *Favonigobius* the anteroventral margin of the subopercle is fully ossified.

The preopercle (POP) in *Afurcagobius* and *Glossogobius* bears a large symplectic process extending and synchondrally bound to the symplectic (SYM), in *Papillogobius* the symplectic process is large but only occasionally reaches the symplectic and in *Favonigobius* the process is present as a remnant only.

The remaining bones of the series are as described by Birdsong 1975.

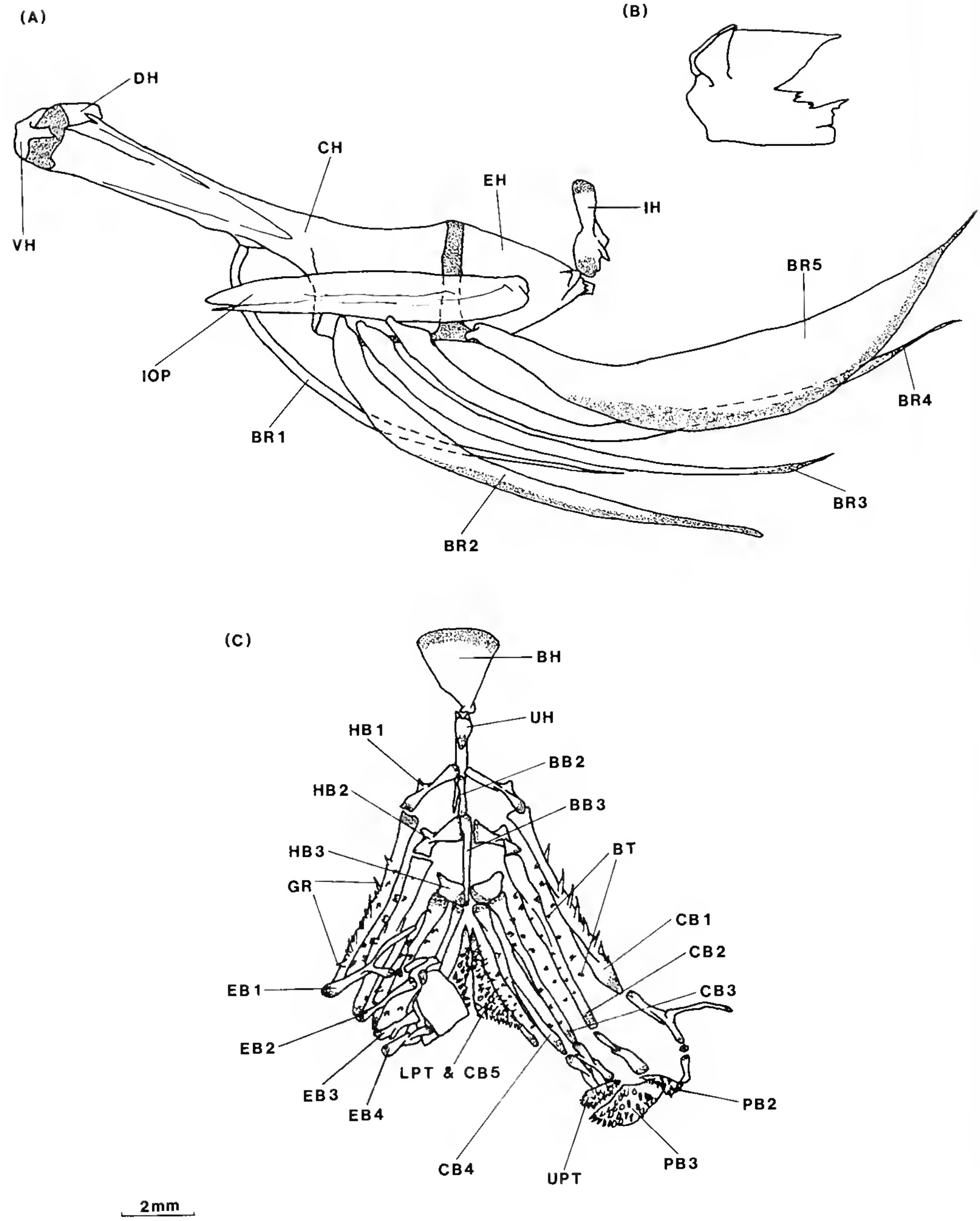

Figure 11 Hyal and branchial bones of *Afurcagobius suppositus*, female, 43.5 mm SL, (A) hyal bones, lateral view; (B) urohyal, lateral view; (C) branchial bones, dorsal view.

Hyoid arch (Figures 2,11).

In *Papillogobius* the second branchiostegal ray (BR 2) is broad and blade-like and broader than rays three and four. In the other genera branchiostegal ray two is broadest at its base and approximately the same size as rays three and four.

In all four genera the ventral and dorsal hypohyals (VH and DH) are synchondrally joined. These bones sit in a groove located on the anterodorsal surface of the ceratohyal (CH), to which they are firmly bound by cartilage.

In *Glossogobius* the basihyal (BH) is preceded by two plates of cartilage which give support to the bilobed tongue. These plates are not present in the other three genera. The basihyal is rounded to truncate and the urohyal (UH) is notched or V-shaped in all the genera examined.

Branchial arches (Figs 2,11).

In *Glossogobius* the junctions of pharyngobranchials two and three (PB 2 and 3) and pharyngobranchial three and the pharyngeal tooth plate (UPT) are each overlain by a cartilaginous plate. This plate is absent in the other genera.

Basibranchial 4 (BB 4) is greatly reduced or absent in *Afurcagobius*. When present, and in all the other genera, it is unossified.

The gill rakers (GR) of the first branchial arch comprise a large central blade and one or two small lateral blades. The lateral blades are most highly developed in *Papillogobius*, less so in *Favonigobius* and least of all in *Afurcagobius* and *Glossogobius*. There are 6-9 rakers on the ceratobranchial (CB) in all genera; 0-2, 1-2 and 1-3 rakers on the epibranchial (EB) in *Afurcagobius* and *Glossogobius*, *Papillogobius* and *Favonigobius* respectively and no rakers are present on the hypobranchial (HB) of any of the genera. The medial face of ceratobranchial one and the medial and lateral faces of ceratobranchials two to four all bear a row of five to eight patches of branchial teeth (BT). Each patch bears from one to twelve teeth which are very small in *Afurcagobius* but relatively large in *Glossogobius*, *Papillogobius* and *Favonigobius*.

Pectoral girdle and paired fins (Figure 12).

The cleithrum (CL) bears a large lateroventral process which is T-shaped in cross-section in *Papillogobius*. This process is large but simple in *Favonigobius* and small or absent in both *Afurcagobius* and *Glossogobius*.

The scapula (SCA) is partially ossified in *Afurcagobius* and *Glossogobius*, but is completely unossified in both *Papillogobius* and *Favonigobius*.

In *Afurcagobius* the coracoid (COR) always bears a large anteroventral process and a small posteroventral process. Both processes are large in *Glossogobius*, *Papillogobius* and *Favonigobius*.

In all the genera examined the medial portions of radials two, three and four (RAD 2, 3 and 4) maybe fused in larger specimens, radial four is a roughly rectangular shaped bone. There are usually 15-16 pectoral rays in *A. suppositus*, *Favonigobius* and *Papillogobius*; 16-18 in *A. tamarensis* and 14-22 in *Glossogobius* (Akihito and Meguro 1975; Allen and Coates 1990; Hoese and Allen 1990).

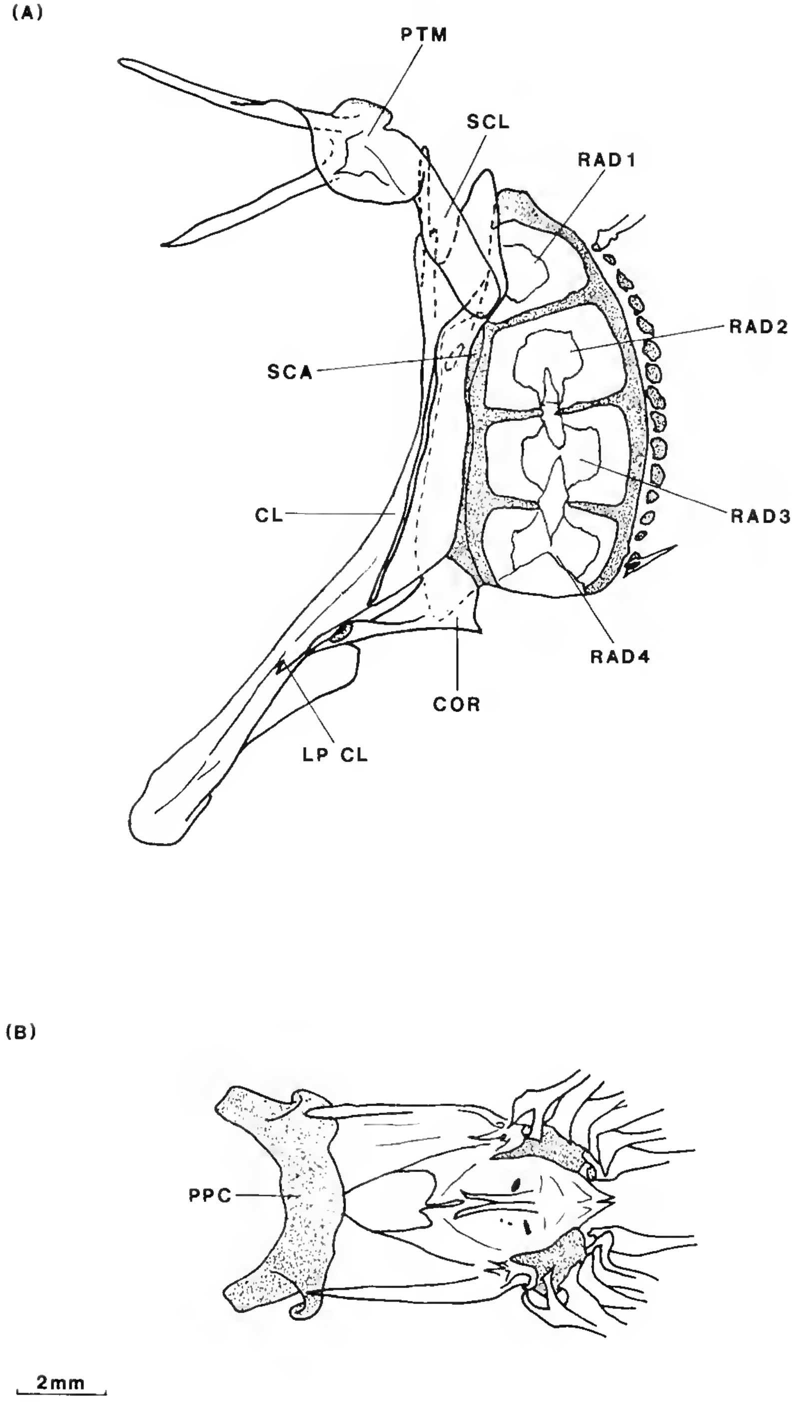

Figure 12 Pectoral and pelvic girdles of *Afurcagobius suppositus*, female, 43.5 mm SL, (A) pectoral girdle, lateral view; (B) pelvic girdle, ventral view.

Pelvic girdle and fins (Figure 12).

The medial shelf of each pelvic bone bears an anteriorly directed process at the symphysis with its partner. The processes are the largest in *Favonigobius* and reach to the pectoral/pelvic cartilage (PPC). In *Papillogobius* the processes reach about three quarters way to the cartilage, whilst in *Afurcagobius* and *Glossogobius* they only reach about half way to the cartilage. The medial shelf bears from one or two (*Afurcagobius* and *Glossogobius*) to up to approximately 12 (*Papillogobius* and *Favonigobius*) small fenestrations at the base of each ventral process. The ventral processes are divergent for at least half of their length.

Vertebral column and median fins

Vertebral column (Figures 13,14).

Afurcagobius suppositus and *Glossogobius* have 11 precaudal (PCV) and 16 caudal vertebrae (CV). *Afurcagobius tamarensis* has 10 precaudal and 17 caudal vertebrae. *Papillogobius* and *Favonigobius* both have 10 precaudal and 16 caudal vertebrae. However, the vertebral count for the species of *Glossogobius* which are endemic to Papua New Guinea is highly variable (precaudal, 10-15; caudal, 15-18)(Hoese and Allen, 1990; Hoese, pers. comm.). The precaudal and caudal vertebrae in *Papillogobius* and *Favonigobius* are difficult to distinguish since the parapophyses (PAP) of the final two precaudal vertebrae each bear a posteromedial process which is fused with its partner, thereby forming a haemal arch (HA) without an associated haemal spine. In contrast the haemal arches of the caudal vertebrae are formed by the fusion of the distal portions of the ventrally curved parapophyses. In this case a haemal spine is formed. Since radiographs were used to obtain many of the vertebral counts available for the gobies (see in particular Akihito *et al.*, 1984; Birdsong *et al.*, 1988) it would not have been possible to distinguish vertebrae with this type of haemal arch from those without an arch i.e. precaudal vertebrae. Thus both of the above studies give counts of 10 precaudal and 16 caudal vertebrae for members of *Papillogobius* and *Favonigobius*. Therefore, since the two types of haemal arch are not homologous and to concur with these published counts the presence of a haemal spine (HS) in the caudal vertebrae has been used to differentiate the vertebral types (Akihito *et al.*, 1984). As the vertebral formula appears to be one of the better characters available for helping to characterize major groupings in the gobies (Birdsong *et al.*, 1988), it would be prudent to distinguish between "true" precaudal vertebra (without a haemal arch or spine), "pseudocaudal" vertebrae (with an arch but no spine) and "true" caudal vertebrae (with an arch and a spine). I therefore propose that, when cleared and stained material is available the vertebral formulae is given in two parts; the first giving precaudal and caudal counts based on the presence or absence of a haemal spine and the second giving the "true" precaudal and pseudocaudal count of the precaudal vertebrae. Although this approach may appear unwieldy it allows direct comparison with published counts and with any future counts taken from radiographs alone and, more importantly, does not lose information. Although posteromedial processes are often present on the last precaudal vertebra of *Afurcagobius* and *Glossogobius* they are small and never met in the

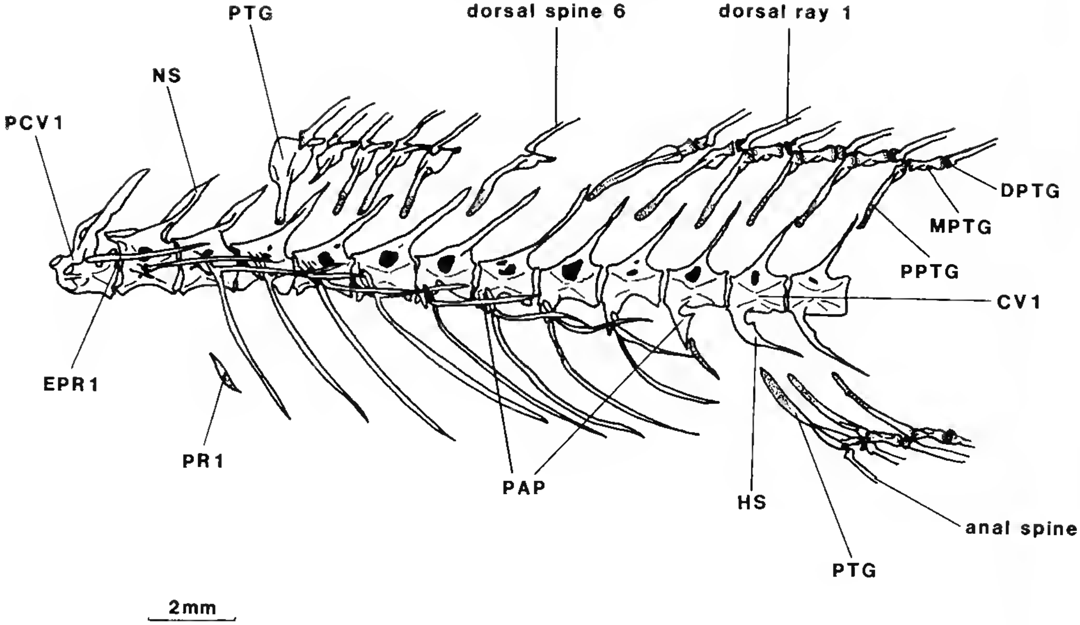

Figure 13 Vertebral column of *Afurcagobius suppositus*, female, 43.5 mm SL, lateral view.

specimens I examined. Hoese (pers. comm.) reports, however, that they did meet in some of the species of *Glossogobius* that he examined.

A reduced pleural rib (PR) is often present in connective tissue lateral to the second precaudal vertebrae of *Afurcagobius, Glossogobius* and *Favonigobius.* In *Papillogobius* this second pleural rib articulates with the epipleural rib (EPR), but it is significantly smaller than the third pleural rib. The epipleural and pleural ribs of the more anterior vertebrae may be fused. This condition is most prevalent in *Afurcagobius.* In *Afurcagobius tamarensis*, and in species of *Glossogobius* with 10 precaudal vertebrae the final precaudal vertebra bears both a pleural and an epipleural rib (Hoese, pers. comm.). There is a pleural but no epipleural rib in *A. suppositus* and species of *Glossogobius* with more than 10 precaudal vertebrae, whereas in both *Papillogobius* and *Favonigobius* the final precaudal vertebrae bears an epipleural rib but no pleural rib.

Although the vertebral zygopophyses are generally larger in *Papillogobius* and *Favonigobius* than in *Afurcagobius* and *Glossogobius*, they are similar in position and shape and are as follows. The first vertebrae bears small dorsal postzygapophyses; the second to fourth or fifth vertebrae bear well developed dorsal pre- but poorly developed postzygapophyses; from vertebrae 5-6 up to vertebrae 16-17 the dorsal prezygapophyses are poorly developed or absent; the dorsal prezygapophyses on vertebrae 16-17 to 23 or 24 get progressively larger, while the the final three bear no dorsal prezygapophyses; vertebrae 6 to 24 bear dorsal postzygapophyses which are relatively well developed in *Papillogobius* and *Favonigobius*; vertebrae 10 to 13 bear large ventral

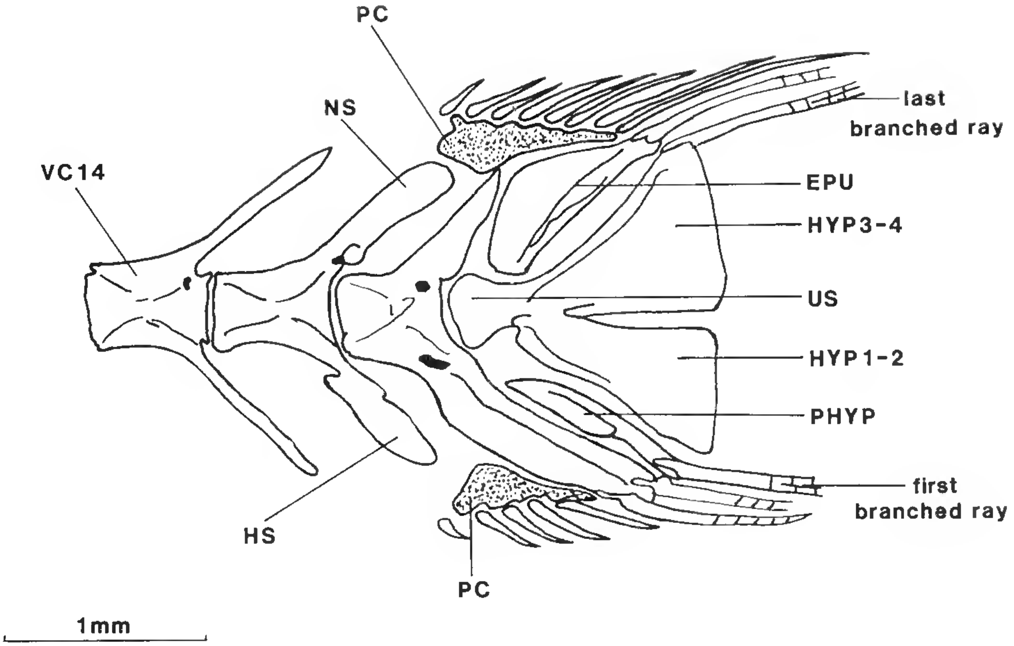

Figure 14 Caudal skeleton of *Afurcagobius suppositus*, female, 43.5 mm SL, lateral view.

postzygapophyses; vertebrae 14 to 22 bear poorly developed postzygapophyses, and finally vertebrae 20 to 26 bear increasingly well developed ventral prezygapophyses.

The penultimate vertebra (vertebra 26 in *Afurcagobius* and *Glossogobius*, and vertebra 25 in *Papillogobius* and *Favonigobius*) is modified in the manner described by Birdsong 1975. The haemal spine usually receives one or two, but may receive upto three, segmented and unbranched rays.

Caudal fin (Figure 14).

These genera have a total of 17 segmented caudal rays, 14 of these rays are branched and three are unbranched. The 14 branched and segmented caudal rays are generally arranged as follows. The first ray inserts on the parahypural (PHYP), the next five insert on hypurals one and two, the next seven on hypurals three and four and the final branched ray on hypural five (HYP 1-5). Above and below the branched rays are one and one to three unbranched rays inserting on the epural (EPU) and last haemal spine (HS), respectively. There are six to eight unsegmented procurrent rays preceding the segmented rays. This arrangement may vary by the addition, deletion or substitution of a ray or rays on any particular caudal element.

Hypural five is often absent in *Afurcagobius suppositus*.

Spinous dorsal fin (Figure 13).

The overall morphology and arrangement of the elements of the dorsal fin are as described by Birdsong, excepting that the seventh dorsal spine and associated pterygiophore (PTG) are lacking.

Second dorsal fin (Figure 13).

The second dorsal fin is composed of one spine and eight soft rays in *Afurcagobius* and *Papillogobius*, one spine and nine soft rays in *Favonigobius* and one spine and 7-12 soft rays in *Glossogobius* (Akihito and Meguro 1975; Allen and Coates 1990; Hoese and Allen 1990). The two anterior pterygiophores (PTG) insert into interneural spaces eight and nine respectively. The arrangement of the pterygiophore elements is as described by Birdsong 1975. The final ray appears as two distinct elements arising from the final pterygiophore, but, as in most recent works, it is counted as one ray (Akihito *et al.* 1984; Birdsong *et al.* 1988; Murdy 1989; Gill and Miller 1990).

Anal fin (Figure 13).

The anal fin is composed of one spine and seven soft rays in *Afurcagobius suppositus*, one spine and eight soft rays in *Afurcagobius tamarensis* and *Papillogobius*, one spine and seven to nine soft rays in *Glossogobius* (Akihito and Meguro 1975; Allen and Coates 1990; Hoese and Allen 1990) and one spine and nine soft rays in *Favonigobius*. The two anterior pterygiophores (PTG) insert anterior to the first haemal spine. However Hoese (pers. comm.) reports that there is variability in the *Glossogobius* species from Papua New Guinea, with between one and five pterygiophores inserting anteriorly to the first haemal spine. The arrangement of the pterygiophore elements is as described by Birdsong. As for the dorsal fin, the final ray appears as two distinct elements which are counted as one ray.

Etymology

The name *Afurcagobius* is derived from *furca*, fork, and refers to the lack of a forked tongue. This is the most obvious distinguishing character between this genus and the morphologically similar genus *Glossogobius*.

Afurcagobius suppositus (Sauvage, 1880)

Figures 1, 15 and 16; Tables 1-2

Eleotris obscurus Castelnau, 1873: 134 (type locality, Fremantle, Western Australia) (in Sauvage, 1880: 41; non *Gobius obscurus* Peters, 1855).

Gobius suppositus Sauvage, 1880: 41 (type locality, Swan River, Western Australia).

Glossogobius vomer Whitley, 1929: 135, pl. 32, fig. 1 (type locality, Swan River, Western Australia) (in Whitley, 1934).

Material examined

WAM P. 1815-7, 2 specimens, 43-45 mm SL, Harvey River, WA; WAM P. 3054, 1 specimen, 71 mm SL, Gin Gin Brook, WA; WAM P. 14187, 1 specimen, 66 mm SL, Moore River, WA; WAM P. 21755, 1 specimen, 59 mm SL, Gin Gin Brook, WA; WAM P. 24820, 1 specimen, 72 mm SL, Hardy Inlet, WA; WAM P. 25069-001, 1 specimen, 83 mm SL, Yunderup, WA; WAM P. 26019-001, 2 specimens, 72-75 mm SL, Denmark River, WA; WAM P. 27026-001, 1 specimen, 74 mm SL, Moore River, WA; WAM P. 29738-001, 7 cleared and stained specimens, Swan River, WA; HSG, 73 specimens, 34-83 mm SL, Swan River, WA, osteological data were taken from 46 of these specimens; HSG, 1 specimen, 53 mm SL, Peel-Harvey Estuary, WA; HSG, 1 specimen, 59 mm SL, Princess Royal Harbour, Albany, WA; HSG, 3 specimens, 67-80 mm SL, Swan River, WA; HSG, 1 specimen, 51 mm SL, Warren River, WA.

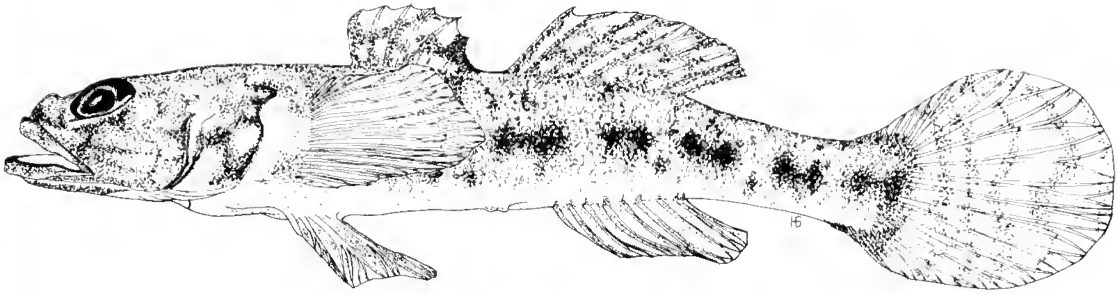

Figure 15 *Afurcagobius suppositus*, female, 48.0 mm SL, Swan River, W.A.

Diagnosis

A species most similar to *Afurcagobius tamarensis* but distinguished from it by the anal count I, 7 (cf. I, 8), the pectoral count 15-16 (cf. 16-18), the transverse scale count 10-13+1 (cf. 9-10) and the vertebral count 11 + 16 (cf. 10 + 17). This species differs from the superficially similar species from the genera *Favonigobius, Papillogobius* and *Glossogobius* by a combination of the following characters (mode in parentheses): predorsal scales 0-4 (0-2); scales in lateral row 30-38 (34-36); prepelvic area naked; cheek and operculum naked; tongue truncate; cephalic lateral-line row a1 short.

Description

Body proportions are given in Table 1; other features as for genus. Body moderately elongate, laterally compressed towards tail and highest just anterior to first dorsal fin (juveniles) to middle of first dorsal fin (adults). Postorbital profile shallow. Snout shallow, longer than eye diameter in larger adults (>45 mm) but shorter in juveniles and smaller adults (<45 mm), juveniles and small adults bearing a small bump on the end of the snout. Head proportions vary greatly with size, sex and breeding condition.

Fin ray and scale counts are given in Table 2. First dorsal fin (D1) arising above proximal third of pectoral fin; last ray arising above distal third of pectoral fin; no rays free at tip; usually only three quarters height of second dorsal (D2), never taller. D2 commencing above or just posterior to anus; last ray above or just posterior to vertical of penultimate anal ray and tip only extending to proximal third of caudal peduncle. Anal fin commencing below D2 2/3; tip of last ray behind posterior tip of D2. Pectoral fin extending back to origin of D2 and occasionally to D2 1. Pelvic disc relatively short, only occasionally extending to anus in males. Caudal fin rounded and usually slightly shorter than head.

Coloration

Fresh specimens light brown to black dorsally and pale ventrally, preserved specimens usually much paler. Lateral series bearing seven or occasionally six dark blotches which are often very pale or indistinct in preserved specimens; anteriormost a large blotch below D1 I-III; second below D1 V-VI and is often pale or missing; third and fourth below D2 1-3 and D2 4-7 respectively; fifth just posterior to D2; sixth at centre of caudal peduncle and seventh on caudal peduncle at base of caudal fin. In dorsal view; three to

Table 1 Body proportions of *Afurcagobius suppositus* from the Swan River, W.A. and *A. tamarensis* from Margate, Tasmania. Range and, in parentheses, mean ± standard deviation.

Species	*A. suppositus*		*A. suppositus*		*A. tamarensis*	
Sex	Males		Females		Females	
SL(mm)	43.0-83.4		49.7-79.9		24.5-41.7	
n	10		10		5	
%SL,						
H	27.1-31.9	(30.0±1.97)	28.0-31.7	(29.4±1.04)	27.3-27.7	(27.6±0.47)
HW	12.2-15.6	(13.7±1.07)	12.4-14.7	(13.4±0.62)	12.1-13.0	(12.5±0.36)
Mw	10.0-17.0	(13.1±2.23)	10.9-13.4	(12.1±0.84)	7.5-9.6	(8.3±0.82)
SN/D1	36.4-39.3	(37.9±0.96)	36.1-40.1	(37.7±1.10)	35.0-37.3	(35.7±0.90)
SN/D2	54.4-58.1	(56.2±1.19)	55.3-58.3	(56.5±1.05)	53.2-54.4	(53.8±0.47)
SN/AN	52.6-57.2	(55.4±1.48)	53.6-58.9	(56.2±1.48)	49.5-53.5	(51.7±1.52)
SN/A	57.2-61.5	(59.2±1.41)	59.2-63.3	(61.2±1.32)	55.6-58.4	(57.1±1.01)
SN/V	28.2-33.7	(31.4±1.40)	29.6-32.5	(31.0±0.91)	25.4-28.4	(27.1±1.10)
CP	23.0-27.0	(24.6±1.21)	20.5-25.2	(23.5±1.38)	26.0-28.4	(27.2±1.00)
D1b	10.7-12.0	(11.5±0.44)	10.2-12.0	(11.2±0.61)	10.4-12.1	(11.4±0.63)
D2b	19.2-22.5	(20.7±1.16)	18.4-21.9	(19.9±1.10)	17.1-20.6	(19.3±1.38)
D1/2	5.6-8.0	(6.8±0.87)	6.2-8.6	(7.6±0.78)	5.6-8.0	(6.8±0.89)
Ab	15.1-17.6	(16.1±0.84)	13.7-17.0	(15.4±1.18)	13.8-16.8	(15.7±1.18)
Cl	24.3-30.7	(28.0±1.97)	23.0-27.7	(25.7±1.22)	24.4	
Pl	21.4-25.7	(23.7±1.54)	20.7-24.2	(22.8±1.22)	17.3-21.5	(19.8±1.78)
Vl	19.6-24.4	(22.5±1.61)	19.4-22.1	(21.2±0.80)	24.5-27.5	(25.8±1.31)
Vd	15.3-20.1	(17.2±1.58)	15.9-19.0	(17.6±0.99)	13.3-15.1	(13.9±0.76)
Ad	13.3-17.4	(15.0±1.36)	13.9-17.3	(15.6±1.00)	11.6-14.2	(12.9±1.07)
Aw	7.7-10.7	(9.5±0.74)	8.1-12.1	(10.0±1.24)	7.8-8.9	(8.6±0.48)
CPd	7.9-9.5	(8.8±0.50)	7.9-9.6	(8.6±0.53)	7.4-8.8	(8.2±0.51)
V/AN	22.2-25.7	(24.1±1.18)	21.4-28.0	(25.2±1.88)	23.9-26.2	(24.8±1.05)
%CP,						
CPd	29.5-40.6	(36.0±3.40)	33.0-43.2	(36.8±2.83)	28.1-31.6	(30.1±1.57)
%H,						
SN	25.0-31.9	(27.6±2.07)	23.9-29.4	(27.4±1.73)	18.7-26.4	(21.9±2.85)
E	20.7-29.0	(23.7±2.89)	18.9-25.5	(22.0±2.33)	27.3-34.8	(31.4±2.94)
PO	46.5-54.8	(51.9±2.39)	50.4-57.2	(53.6±2.04)	45.3-50.6	(48.0±2.01)
CHd	20.4-36.9	(28.4±5.64)	23.5-34.1	(26.9±3.31)	13.3-20.4	(16.9±2.60)
Hw	42.5-48.9	(45.7±1.89)	42.4-49.3	(45.6±1.88)	43.9-47.5	(45.4±1.52)
Mw	35.1-54.1	(43.7±6.27)	34.3-45.0	(41.1±3.06)	27.1-35.2	(30.1±3.20)
%E,						
I	21.4-45.1	(35.1±8.37)	28.7-51.7	(40.2±7.24)	12.8-17.7	(14.0±2.10)
%V/AN,						
V	77.4-110.1	(93.5±9.01)	63.9-89.1	(80.2±6.61)	95.6-111.6	(104.3±6.11)

Abbreviations used. Ab: anal fin base; Ad and Aw: body depth and width at origin of anal fin; Cl: caudal fin length; CHd: cheek depth; CP and CPd: caudal peduncle length and depth; D1b and D2b: first and second dorsal fin bases: D1/2: distance between last ray of first dorsal fin and first ray of second dorsal fin; E: eye diameter; H and Hw: head length and width; I: interorbital width; Mw: maxillary width; Pl: pectoral fin length; PO: postorbital distance; SL: standard length; SN: snout length; SN/A and SN/V: distance from the snout to the verticals passing through the origin of the anal fin and the origin of the pelvic disc; SN/D1 and SN/D2: distance from the snout to the verticals passing through origins of the first and second dorsal fins; V/AN: distance from the origin of the pelvic disc to the anus; Vd: body depth at the origin of the pelvic disc; Vl: pelvic disc length.

Table 2 Meristics of *Afurcagobius suppositus* from the Swan River, W.A. and *A. tamarensis* from Margate, Tasmania and Botany Bay, N.S.W. Range and, in parentheses, mode are given.

Counts SL(mm) n	*A. suppositus* 34.4-83.4 73	*A. tamarensis* 24.5-45.8 7
D1	VI	VI
D2	I,8	I,8
A	I,7	I,8
P	15-16	16-18
V	I,5	I,5
C	9/8	9/8
LL	30-38 (34-36)	30-34 (33)
TR	10-13+1 (12-13)	9-10
PD	0-4 (0-2)	0-1
P-VC	3/II II I I 0/9	3/II II I I 0/9
VC	11 + 16	10 + 17

four diffuse bars across nape; a heavily pigmented spot in mid-line of nape anterior to D1; large saddle across D1 and smaller saddles across anterior, medial section and posterior of D2 and caudal peduncle. Head usually heavily pigmented epidermally and dermally; epidermal pigmentation present as mottling over whole head; dermal pigmentation extending from corner of jaw to below orbit and over snout anteriorly, to just behind interorbital posteriorly and extending as a thin line over cheek and preoperculum laterally, often most obvious in preserved or pale specimens. Preoperculum and operculum bearing dark mottling epidermally and dorsally bearing dermal pigmentation. Dorsal and caudal fins with series of brown or black reticulating lines; D1 bearing prominent dark spot between D5 and distal margin. Pectoral fin transparent. Pelvic and anal fins pale, darker during breeding season.

Pigmentation varies with site of capture, sex, breeding condition and preservation, and is usually strongest in breeding males. Although some specimens show virtually no pigmentation, the dermal pigmentation of the head, preoperculum, operculum, and mid-line nape spot and the epidermal pigmentation of the first dorsal spot are usually obvious (Figures 15 and 16).

Distribution

This species is found in estuaries, coastal lakes and rivers of south-western Australia, extending from the Moore River (30° 59′S 115° 42′E) in the north to Esperance (33° 52′S 121° 54′E) in the south-east. The species is common in the freshwater streams of the south-west (Gill unpubl. data) and shows a strong preference for heavy cover (Humphries 1991; Humphries and Gill in prep.).

Size

Reaches about 110 mm.

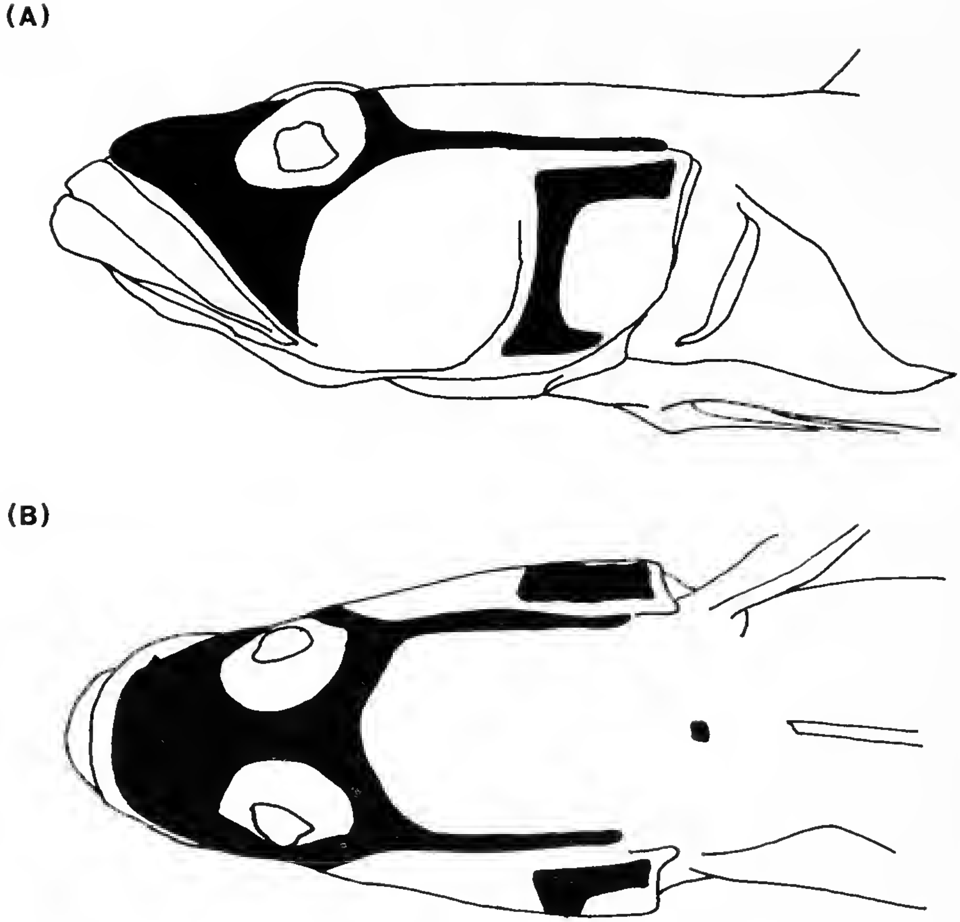

Figure 16 Dermal pigmentation of *Afurcagobius suppositus*, (A) lateral view; (B) dorsal view.

Etymology

The name *suppositus* is derived from the latin, *suppono*, to substitute or falsify, presumably referring to the substitution of this name, by Sauvage (1880), for that of *obscurus* (Castelnau 1873) which was preoccupied by *Gobius obscurus* Peters 1855.

Afurcagobius tamarensis (Johnston, 1883)

Tables 1-2

Gobius tamarensis Johnston, 1883: 120 (type locality, Tamar River, Tasmania, Australia).

Gobius tasmanicus Whitley, 1929: 62 (type locality, Tamar River, Launceston, Tasmania)(Hoese, pers. comm.).

Material examined

HSG, 2 specimens, 40-46 mm SL, Botany Bay, NSW; HSG, 5 specimens, 25-42 mm SL, Margate, Tasmania. Osteological data were taken from all specimens.

Diagnosis

Anal elements I, 8; pectoral elements 16-18; vertebral count 10 + 17. A species most similar to *Afurcagobius suppositus* but distinguished from it by the anal count I, 8 (cf. I, 7), the pectoral count 16-18 (cf. 15-16), the transverse scale count 9-10 (cf. 10-13+1) and the vertebral count 10 + 17 (cf. 11 + 16). This species differs from the superficially similar species from the genera *Favonigobius, Papillogobius* and *Glossogobius* by a combination of the following characters: predorsal scales 0-1; scales in lateral row 30-34 (33); prepelvic area naked; cheek and operculum naked; tongue truncate; cephalic lateral-line row a1 short.

Description

Body proportions are given in Table 1; other features as for genus. Body moderately elongate, laterally compressed towards tail and highest at middle of first dorsal fin. Postorbital profile shallow. Snout shallow, shorter than eye diameter in juveniles and small adults (<45 mm), the figure by Scott (1935) (67.5 mm, TL) indicates snout longer than eye diameter in larger adults.

Fin ray and scale counts are given in Table 2. First dorsal fin (D1) arising above proximal third of pectoral fin; last ray arising above distal third of pectoral fin; no rays free at tip; usually full height of second dorsal (D2). D2 commencing above or just posterior to anus; last ray above or just posterior to vertical of penultimate anal ray and tip only extending to proximal third of caudal peduncle. Anal fin commencing below D2 1/2; tip of last ray behind posterior tip of D2. Pectoral fin extending back to origin of D2 and occasionally to D2 1. Pelvic disc usually extending to anus and often well onto genital papilla. Caudal fin rounded and usually slightly shorter than head.

Coloration

Specimens examined were in ethanol and had no discernible markings; except in the lack of dermal head pigmentation, the description by Hoese and Larson (1980) and Plate 49 in Allen (1989) indicate that the coloration is similar to that of *A. suppositus.*

Distribution

This species lives on silt or mud bottoms in the estuaries and coastal lakes of New South Wales, Victoria, Tasmania and South Australia and often penetrates into fresh water (Hoese and Larson 1980).

Size

Reaches about 110 mm (Hoese and Larson 1980).

Etymology

The trivial name, *tamarensis*, refers to the type locality (Tamar River).

Discussion

Afurcagobius, Glossogobius, Favonigobius and *Papillogobius* each possess the osteological and canal pore characters described by Miller (1973) as diagnostic of the subfamily Gobiinae, namely: one epural bone; fan-hypurals usually not fused; five branchiostegal rays; four pectoral radials; metapterygoid bridge between hyomandibular and quadrate; scapula reduced (foramen open) or absent and preopercular canal with no more than three primary pores. In addition, all possess a pterygiophore formula of 3/II II I I 0/9, a full longitudinal papillae pattern and are superficially similar. This marked similarity, combined with the erection of many gobiid genera without formal descriptions, has led to much confusion over the status of what I now term *Afurcagobius suppositus* and *A. tamarensis* and accounts for the placing of these species in several different genera by different workers (Castelnau 1855; Sauvage 1880; Johnston 1883; Whitley 1934; Scott 1935; Koumans 1953; Hoese and Larson 1980).

Detailed osteological and morphological examination confirm the close relationship of these genera and suggests that *Afurcagobius* is more closely related to *Glossogobius* than to either of the other two genera. A current study by Hoese and Allen (pers. comm.) suggests that *Glossogobius* has undergone an extensive radiation within Papua New Guinea and to a lesser extent within northern Australia. Associated with this radiation is a plasticity of many characters that may usually be considered conservative within a genus. Notwithstanding this plasticity of characters *Afurcagobius* shares the following characters with the majority of *Glossogobius* species (variations for *Glossogobius*, as kindly supplied by D. F. Hoese, are given in parentheses): 27 vertebrae (26 in dwarf species and up to 31); pterotic bearing finger-like projections (maybe absent in small specimens); prootic bearing large anterior process; ventromedial process of pterosphenoid bifid; sagittal otoliths bearing anterior and posterior processes; asteriscus greatly reduced or absent; dorsal surface of ectopterygoid unossified; postmaxillary process of premaxilla low (in larger specimens); presence of row a1 of cephalic lateral-line system; scales in transverse series >9 (7-12); snout long and shallow (occasionally short, but usually longer than in *Favonigobius* or *Papillogobius*); mouth horizontal (up to 45° in some species) and superior and a maximum SL greater than 100 mm (25 mm in dwarf species). In addition to these similarities, the larvae of *Afurcagobius suppositus* and *Glossogobius olivaceus* hatch possessing a large yolk sac, a condition which is not found in either *Favonigobius lateralis* or *Papillogobius punctatus* (Dotsu *et al.* 1988; Neira unpubl. data).

The similarities exhibited by *Afurcagobius* and *Glossogobius* are not solely morphological. The majority of the species found in Papua New Guinea and all of the seven species of *Glossogobius* found in northern Australia penetrate well into fresh water (Allen 1989; Hoese and Allen 1990), a situation also found with *Afurcagobius* in southern Australia. In contrast members of *Favonigobius* and *Papillogobius* are strictly marine/estuarine (Hoese and Larson 1980; Allen 1989; Gill and Miller 1990).

Although *Afurcagobius* and *Glossogobius* are very similar, they are nevertheless distinguishable, each bearing two unique characters. Thus, in *Afurcagobius* the coracoid bears a reduced posteroventral process and the cephalic lateral-line system bears a posteriorly shortened row a1 which meets the medial section of row a anteriorly. In *Glossogobius* the basihyal is preceded by two cartilage plates which give support to the forked tongue and row a1 is long and meets the most anterior section of row a.

Comparative material

Acentrogobius gracilis (Jenyns, 1835): WAM P. 25118-004, 21 specimens, 27-55 mm SL, Dampier Archipelago, West Lewis Island, WA, 17 November 1974.

Acentrogobius griseus (Day, 1878): BMNH (uncatalogued), 2 specimens, 34-75 mm SL, Sawak Lake, about 30 km NW Samawak Town, 19 July 1973.

Acentrogobius janthinopterus (Bleeker, 1852): PJM, 1 specimen, Lizard Island, Queensland, 15 September 1981.

Acentrogobius viridipunctatus (Cuvier and Valenciennes, 1837): PJM coll. No. 0, 4 specimens, 38-66 mm SL; PJM coll. No. 4, 2 specimens 50-58 mm SL.

Arenigobius bifrenatus (Kner, 1865): WAM P. 11959-62, 4 specimens, 58-74 mm SL, Preston Point, Swan River, WA, 18 January 1965; WAM P. 16758, 1 specimen, 89 mm SL, Moore River, WA, 7 June 1969; WAM P. 24388-92, 5 specimens, 39-82 mm SL, Hardy Inlet, WA, 26 March 1974; WAM P. 25064-005, 1 specimen, 91 mm SL, Hardy Inlet, WA, 20 March 1974; PJM, 6 specimens, 70-81 mm SL, Swan River, WA.

Arenigobius frenatus (Gunther, 1861): AMS I. 19896-002, 4 specimens, 36-57 mm SL.

Barbuligobius boehlkei Lachner and McKinney, 1974: WAM P. 28284-027, 10 specimens, 21-24 mm SL, N.W. side of Six Mile Island, Israelite Bay, WA, 4 April 1984; WAM P. 29933-018, 1 specimen, 24 mm SL, Rottnest Island, WA, December 1986.

Bathygobius andrei (Sauvage, 1880): PJM 1461, 2 specimens, 65-107 mm SL, 1984; PJM 1469, 3 specimens, 67-89 mm SL, May 1984.

Bathygobius burtoni (O'Shaughnessy, 1875): PJM, 8 specimens, 16-50 mm SL, Mile 6, kei Victoria, Kamerun, 4 December 1976.

Bathygobius casamancus (Rochebrune, 1880): PJM, 6 specimens, 29-57 mm SL, Baia des Gatas, 10 km E Mindelo Island, San Vincente.

Bathygobius curacao (Metzelaar, 1919): GCRL V73:10318, 1 specimen, 34 mm SL, Limon Bay, Colon, Panama, 13 November 1972; GCRL V75:14019, 3 specimens, 26-36 mm SL, Limon Bay, Colon, Panama, 20 April 1971; GCRL V76:14598, 3 specimens, 33-36 mm SL, Limon Bay, Colon, Panama, 16 January 1976.

Bathygobius cyclopterus (Cuvier and Valenciennes, 1837): PJM, 6 specimens, 44-61 mm SL, Port Shelta, Hong Kong, 28 July 1983.

Bathygobius fuscus (Ruppell, 1830): PJM, 6 specimens, 38-53 mm SL, Kat-O shore, Hong Kong, 2 June 1966.

Bathygobius krefftii (Steindachner, 1866): WAM P. 27078-005, 7 specimens, 27-56 mm SL, Arrawarra Headland, NSW, 25 December 1980.

Bathygobius laddi: WAM P. 27967-034, 54 specimens, 12-33 mm SL, Fitzroy Reefs, Point Quobba, WA.

Bathygobius mystacium Ginsburg, 1947: GCRL V:11141, 11 specimens, 26-61 mm SL, San Blas, Isla Miru, Panama.

Bathygobius soporator (Cuvier and Valenciennes, 1837): GCRL V72:9987, 6 specimens, 36-74 mm SL, Boca del Rio Cienquita, Golfo de Honduras, Cortes, Honduras, 19 June 1971.

Bryaninops amplus Larson, 1985: HSG 75-321, 2 specimens, 10-15 mm SL, near Palfrey Island, Lizard Island area, Queensland, 13 November 1975, det. D. F. Hoese; HSG 75-442, 4 specimens, 7-14 mm SL, North Point, Lizard Island, Queensland, 28 November 1975, det. D. F. Hoese; HSG 80-18, 4 specimens, 8-23 mm SL, Rib Reef, Great Barrier Reef, Queensland, 4 December 1980, det. H. Larson.

Bryaninops ridens Smith, 1959: HSG 75-14, 1 specimen, 16 mm SL, Eagle Island, Lizard Island area, Queensland, 7 November 1975, det. H. Larson; HSG 75-96, 1 specimen, 13 mm SL, lagoon, Lizard Island, Queensland, 7 February 1975, det. D. F. Hoese.

Cabillus lacertops Smith, 1959: WAM P. 24481-001, 1 specimen, Clerke Reef Lagoon, Rowley Shoals, WA, 3 October 1973.

Cabillus tongarevae (Fowler): WAM P. 29041-023, 1 specimen, 29 mm SL, Ashmore Reef, Timor Sea, 12 September 1986.

Cristatogobius sp.: WAM P. 29595-018, 1 specimen, 25 mm SL, Madang, PNG, 29 September 1987; WAM P. 29595-031, 3 specimens, 25-28 mm SL, Madang, PNG, 29 September 1987.

Cryptocentroides cristatus (Macleay, 1881): WAM P. 28812-001, 1 specimen, 64 mm SL, Moreton Bay, Queensland, 28 September 1974; WAM P. 28837-005, 1 specimen, 32 mm SL, Port Hacking, NSW.

Drombus sp.: PJM, 1 specimen, 43 mm SL, Lizard Island, Queensland, 15 September 1981.

Exyrias belissimus (Smith, 1959): WAM P. 27662-030, 1 specimen, 74 mm SL, Clerke Reef, Rowley Shoals, WA, 23 July 1982; WAM P. 29054-003, 1 specimen, 77 mm SL, West Island, Ashmore Reef, Timor Sea, 17 September 1986; WAM P. 29928-019, 7 specimens, 37-77 mm SL, Pulo Blau, Cocos-Keeling Island, Indian Ocean, 26 February 1989.

Exyrias puntang (Bleeker, 1851): WAM P. 25231-004, 5 specimens, 30-77 mm SL, Ambon, Molucca Island, Batu Kuning Stream, Kutekote, 19 January 1975; WAM P. 26955-001, 2 specimens, 55-60 mm SL, Mowbray River, Mossman, Queensland, 13 September 1980; WAM P. 29595-025, 4 specimens, 37-93 mm SL, Madang, PNG, 29 September 1987; PJM, 6 specimens, 41-85 mm SL, Lizard Island, Queensland, 15 September 1981.

Favonigobius lateralis (Macleay, 1881): AMS I. 16386-001, syntypes, 3 specimens, 46-49 mm SL, King George's Sound, WA; AMS I. 9733-9735, paratypes (var. *obliquus*), 5 specimens, 33-44 mm SL, Rose Bay, Port Jackson, NSW; WAM P. 24393-6, 4 specimens, 46-50 mm SL, Hardy Inlet, WA; WAM P. 24413-7, 2 specimens, 45-46 mm SL, Hardy Inlet, WA; WAM P. 24900, 2 specimens, 40-50 mm SL, Hardy Inlet, WA; WAM P. 28806-001, 6 specimens, 25-32 mm SL, Moreton Bay, Queensland; HSG, 40 specimens, 33-55 mm SL, Port Hacking, NSW; HSG, 12 specimens, 30-43 mm SL, Rockingham Bay, WA; HSG, 103 specimens, 29-55 mm SL, Swan-Avon Estuary, WA, osteological data were taken from 63 specimens and 9 were lodged at the Western Australian Museum, WAM P. 29736-001.

Glossogobius aureus Akihito and Meguro, 1975: PJM H. B., 2 specimens, 132-133 mm SL.

Glossogobius biocellatus (Cuvier and Valenciennes, 1837): PJM, 1 specimen, 53 mm SL, Gazi, Kwale District, Kenya, 20 August 1982.

Glossogobius brunnoides (Nichols, 1951): WAM P. 28202-001, 6 specimens, 60-79 mm SL, Teti River, PNG, 12 October 1983; WAM P. 28204-002, 1 specimen, 71 mm SL, Rau Creek, Mt. Hagen, PNG, 5 October 1983.

Glossogobius celebius (Cuvier and Valenciennes, 1837): WAM P. 29613-008, 6 specimens, 45-104 mm SL, Bogia, PNG, 19 October 1987.

Glossogobius concavifrons (Ramsay and Ogilby, 1887): WAM P. 27803-007, 1 specimen, 65 mm SL, tributary of Tedi, Tabubil airstrip, PNG, 17 September 1982.

Glossogobius giuris (Hamilton, 1822): WAM P. 25414-005, 2 specimens, 71-78 mm SL, Stn. B1-3, Carson River, Western Australia, 12 December, osteological data were taken from these specimens; WAM P. 25424-010, 5 specimens, 35-112 mm SL, Stn. C5-1, Drysdale River, WA, 19 August 1975; WAM P. 25867-003, 20 specimens, 49-81 mm SL, Maitland River, WA; PJM H. B., 4 specimens, 65-133 mm SL.

Glossogobius koragensis Herre, 1935: WAM P. 27838-001, 20 specimens, 23-65 mm SL, Chambri Lake, Sepik River, PNG, 22 October 1982.

Glossogobius olivaceus (Temminck and Schlegel, 1845): PJM, 6 specimens, 99-133 mm SL, Hamana Lake, Japan, 1983.

Glossogobius sparsipapillus Akihito and Meguro, 1976: PJM coll. No. 6, 3 specimens, 88-97 mm SL, Thailand.

Glossogobius tenuiformis Fowler, 1934: RUSI 24741, 5 specimens, 31-39 mm SL, Pongolo Floodplain.

Glossogobius sp.: PJM coll. No. 6, 1 specimen, 88 mm SL.

Hazeus baliuris (Cuvier and Valenciennes, 1837): PJM, 1 specimen, 49 mm SL, Gulf of Thailand 1964; PJM, 7 specimens, 65-81 mm SL.

Istigobius cambelli (Jordan and Snyder, 1901)(labelled *"hongkongensis"*): PJM, 6 specimens, 53-74 mm SL, Sharp Island, Hong Kong, 27 April 1965.

Istigobius ornatus (Ruppell, 1830): WAM P. 27274-025, 17 specimens, 39-67 mm SL, Gantheume Point, Broome, WA, 18 January 1981; WAM P. 28155-011, 61 specimens, 19-48 mm SL, Daru, PNG, September 1983; PJM, 8 specimens, 34-54 mm SL, Kuste vorden Leuchtturm der Altstadt, Galle, 6 February 1981; PJM, 2 specimens, 72-84 mm SL.

Lesueurigobius freisii (Malm, 1874): PJM, 2 specimens, 63-67 mm SL, Irish Sea, west of Isle of Man, 27 May 1952; PJM, 5 specimens, 58-69 mm SL, NW Brada, 20 May 1960.

Oplopomops diacanthus (Schultz, 1943): PJM, 1 specimen, 34 mm SL, Malne, 30 September 1954.

Oplopomus caninoides (Bleeker, 1852): PJM, 2 specimens, 43-47 mm SL, Momboza, June 1985.

Oplopomus oplopomus (Cuvier and Valenciennes, 1837): WAM P. 25168-014, 1 specimen, 65 mm SL, Shark Bay, WA.

Oplopomus sp.: WAM P. 23350-001, 1 specimen, 56 mm SL, Exmouth Gulf, WA.

Papillogobius exquisitus (Whitley, 1950): AMS IB. 1413, holotype, 46 mm SL, Toukley, NSW, 20 March 1945; AMS I. 17355-004, 30 specimens, 28-47 mm SL, Sugar-Loaf Bay, NSW; AMS I. 25396-002, 2 specimens, Cowan Creek, NSW, 4 December 1984; HSG, 18 specimens, 26-39 mm SL, Rozzell Bay, NSW, osteological data were taken from five specimens.

Papillogobius melanobranchus (Fowler, 1934): RUSI 10149, I specimen, 22 mm SL, Kosi Bay, Zululand, osteological data were taken; WAM P. 25667-005, 11 specimens, 22-26 mm SL, Pt. Warrender, WA.

Papillogobius punctatus Gill and Miller, 1990: WAM P. 29724-001, holotype, 51 mm SL, Joel Terrace, Swan-Avon Estuary, WA; WAM P. 29723-001, paratypes, 5 specimens, 39-43 mm SL, Sandy Beach, Swan-Avon Estuary, WA; WAM P. 29725-001, paratype, 39 mm SL, Joel Terrace, Swan-Avon Estuary, WA; WAM P. 29726-001, paratypes, 5 specimens, 41-53 mm SL, Joel Terrace, Swan-Avon Estuary, WA; WAM P. 29727-001, paratype, 43 mm SL, Joel Terrace, Swan-Avon Estuary, WA; WAM P. 29728-001, paratypes, 2 specimens, 44-45 mm SL, Point Belcher, Swan-Avon Estuary, WA; WAM P. 29737-001, paratypes, 6 cleared and stained specimens, Joel Terrace, Swan-Avon Estuary, WA; AMS I. 29327-001, paratypes, 5 specimens, 36-45 mm SL, Joel Terrace, Swan-Avon Estuary, WA; HSG, 72 specimens, 27-47 mm SL, osteological data were taken from 52 specimens.

Papillogobius reichei (Bleeker, 1853): RMNH 4672, 1 specimen, 44 mm SL, Padang, Sumatra, 1853; RUSI 74-80, 4 specimens, 34-44 mm SL, Inhaca Islands; RUSI 10149, 24 specimens, 16-37 mm SL, Kosi Bay, Zululand, osteological data were taken from 4 specimens; RUSI 16790, 4 specimens, 23-35 mm SL, Mahe, Seychelles.

Parachaeturichthys polynema (Bleeker, 1853): PJM, 6 specimens, 64-84 mm SL, Plover Cove, Hong Kong, May 1967.

Parkraemeria ornata Whitley, 1951: AMS I. 26707-001, 1 specimen, south bank, Lake Merimbula, NSW, 17 March 1976; AMS I. 27222-001, 3 specimens, Shelley Beach, north of Townsville, Queensland, 1978.

Pleurosicya mossambica Smith, 1959: HSG 75-28, 2 specimens, 8-15 mm SL, lagoon, Lizard Island, Queensland, 29 January 1975, det. D. F. Hoese; HSG 77-65, 3 specimens, 14-16 mm SL, Bird Island, Lizard Island area, Queensland, 14 February 1977, det. H. Larson; HSG 78-151, 1 specimen, 23 mm SL, Decapolis Reef, Great Barrier Reef, Queensland, 2 December 1978, det. D. F. Hoese; HSG 81-3, 1 specimen, 16 mm SL, Mrs Watsons Bay, Lizard Island, Queensland, 18 September 1981, det. H. Larson.

Pleurosicya muscarum (Jordan and Seale, 1906): HSG 75-95, 1 specimen, 15 mm SL, lagoon, Lizard Island, Queensland, 7 February 1975, det. D. F. Hoese.

Porogobius sp.: PJM, 1 specimen, Port Hearcourt, Nigeria.

Silhouettea aegyptia (Chabanaud, 1933): PJM, 5 specimens, 26-29 mm SL.

Silhouettea dotui (Takagi, 1957): PJM, 1 specimen, 41 mm SL, Teradomari, Santo-gun, Niigata Prefecture, Japan, 17 August 1980; PJM, 1 specimen, 35 mm SL, Hichirinagahama, Aomoki Prefecture, Japan, 1 September 1980.

Yongeichthys caninus (Cuvier and Valenciennes, 1837): PJM coll. No. 5, 5 specimens, 84-92 mm SL, Thailand.

Yongeichthys criniger (Cuvier and Valenciennes, 1837): WAM P. 27779-001, 28 specimens, 29-59 mm SL, mouth of Daintree River, Queensland, 2 September 1982; PJM coll. No. 0, 3 specimens, 61-93 mm SL; PJM, 5 specimens, 82-97 mm SL, Thailand.

Yongeichthys thomasi (Boulenger, 1916): PJM, 4 specimens, 19-40 mm SL, Port Hearcourt, Nigeria; PJM, 10 specimens, 25-40 mm SL.

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Abbreviations used in text and figures

ANG	angular
AR PMX	articular process of premaxilla
ART	articular
ASC PMX	ascending process of premaxilla
BB	basibranchial
BH	basihyal
BO	basioccipital
BR	branchiostegal ray
BT	branchial tooth patch
C	centrum
CB	ceratobranchial
CH	ceratohyal
CL	cleithrum
COR	coracoid
COR D	coronoid process of dentary
CV	caudal vertebra
D	dentary
DH	dorsal hypohyal
DPTG	distal radial
EB	epibranchial
EH	epihyal
EO	exoccipital
EPO	epiotic
EPR	epipleural rib
EPU	epural
ETH PAL	ethmoid process of palatine
F	frontal
GR	gill raker
HB	hypobranchial
HS	haemal spine
HYO	hyomandibular
HYP	hypural
IH	interhyal
INT	intercalar
IOP	interopercle
L MX	lateral head of maxilla
LAC	lacrymal
LE	lateral ethmoid
LP CL	lateral process of cleithrum
LPT	lower pharyngeal tooth plate
MC	Meckel's cartilage
ME	medial ethmoid
MPT	metapterygoid
MPTG	medial radial
MX	maxilla
MX PAL	maxillary process of palatine
N	nasal
NA	neural arch
NC	neural canal
NS	neural spine
OP	opercle
PAL	palatine
PB	pharyngobranchial
PC	procurrent cartilage

PCV	precaudal vertebra
PHYP	parhypural
PM PMX	postmaxillary process of premaxilla
PMX	premaxilla
POP	preopercle
PPC	pectoral pelvic cartilage
PPTG	proximal radial
PR	pleural rib
PRO	prootic
PS	parasphenoid
PT PAL	ectopterygoid process of palatine
PT	ectopterygoid
PTG	pterygiophore
PTM	posttemporal
PTO	pterotic
PTS	pterosphenoid
QU	quadrate
RAD	pectoral radials
RC	rostral cartilage
SCA	scapula
SCL	supracleithrum
SES	sesamoid articular
SOC	supraoccipital
SOP	subopercle
SPH	sphenotic
STF	subtemporal fossa
SYM	symplectic
UH	urohyal
UPT	upper pharyngeal tooth plate
US	urostyle
V	vomer
V EO	ventromedial strut of exoccipital
VH	ventral hypohyal

Abbreviations used as orientation guide

A, anterior; D, dorsal; L, lateral; M, medial;
P, posterior; V, ventral; EX, external; IN, internal.

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Three new species of the spider family Linyphiidae from Australia (Araneae)

A.F. Millidge*

Abstract

Two new species of the genus *Dunedinia* Millidge are described: *D. occidentalis* sp.nov. from caves in Cape Range, Western Australia, and *D. opaca* sp.nov. from South Australia. *Chthiononetes* gen.nov. is erected for *C. tenuis* sp.nov., another linyphiid species from a cave in Cape Range.

Introduction

Among the spiders collected from caves in Cape Range, Western Australia, by Dr. W.F. Humphreys and associates, were two members of the Linyphiidae, a spider family which is poorly represented in Australia, but much more numerous in New Zealand. One of the species requires erection of a new genus, while the other is a member of the New Zealand genus *Dunedinia* Millidge. A further *Dunedinia* species, from South Australia, is also described in this paper.

Materials and Methods

All material is lodged in the Western Australian Museum, Perth and the South Australian Museum, Adelaide. The figures are drawn from alcohol-preserved specimens, and the palps figured are the right hand palps. All measurements are in mm.; scale lines on the figures are 0.1 mm.

Systematics

Family Linyphiidae Blackwall

Genus *Dunedinia* Millidge

Remarks

This genus was erected for three species from New Zealand (Millidge 1988:42) but one member was also known from South Australia, and this is described for the first time in the present paper. It also appears probable that *Laetesia forsteri* Wunderlich (1976) from Sydney, New South Wales, should be transferred to *Dunedinia*.

Dunedinia is close to *Laetesia* Simon (Millidge 1988:35) but the chaetotaxy is different and there are differences in the genitalia. The palpal organs of *Dunedinia* are basically similar to those of *Laetesia*, but the suprategular apophyses are somewhat differently shaped and the embolic divisions are somewhat simpler; in addition, the membraneous

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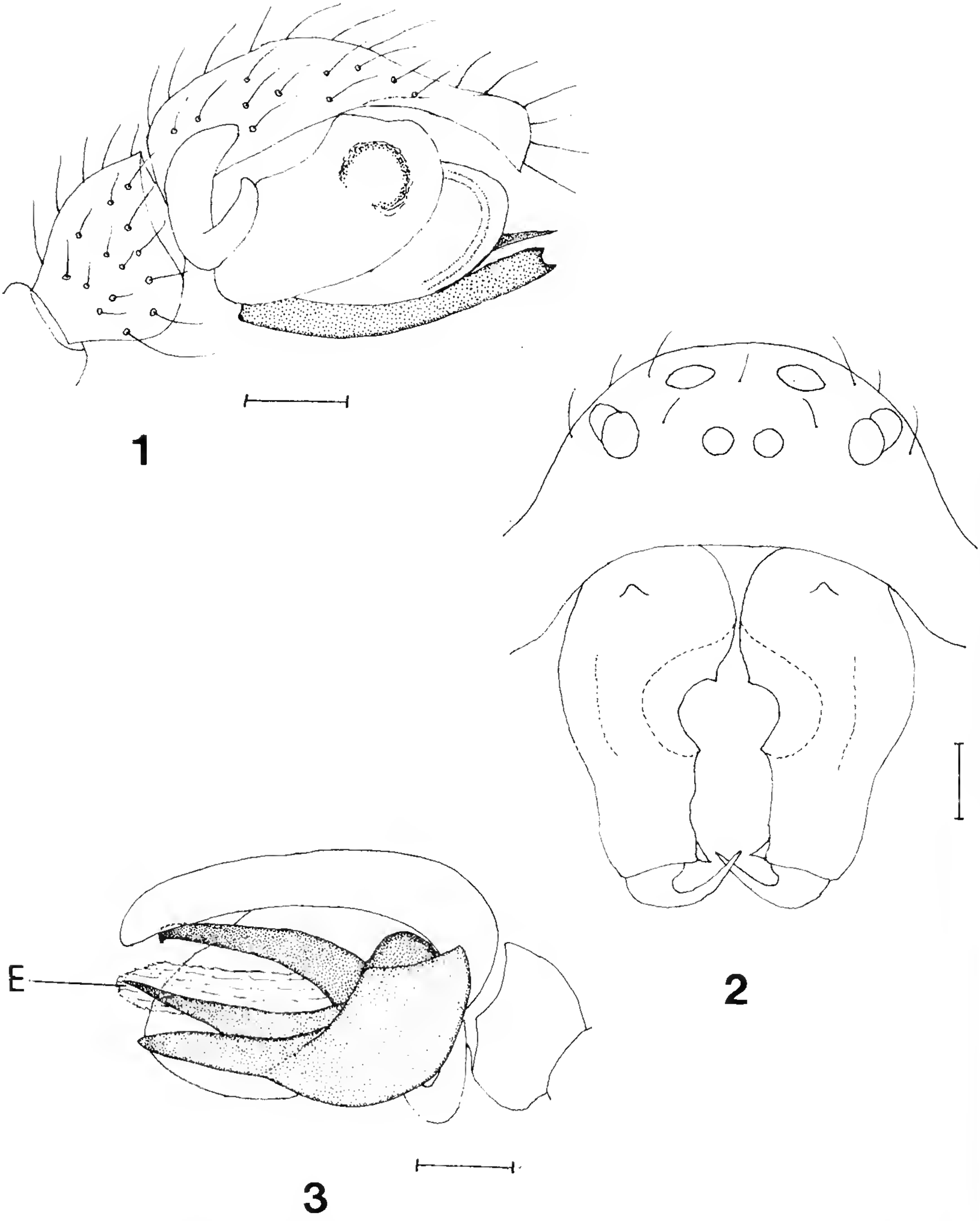


Figures 1-3 *Dunedinia occidentalis*, sp. nov., ♂. 1, palp, ectal. 2, chelicerae, anterior. 3, palp, mesal. E: embolus.

tegular apophysis present in *Laetesia* is absent in *Dunedinia*. The male chelicerae in *Dunedinia* are bowed as in *Dictyna*, whereas in *Laetesia* they are usually not (exception: *Laetesia minor* Millidge). Females of *Dunedinia* have the external genitalia very close to those of *Laetesia* in some species, but there are differences internally in the form of the spermathecae; in *Laetesia* the spermatheca has a tubular subsidiary chamber of the type common in members of the Linyphiinae (s. str.), while in *Dunedinia* this side chamber is absent. There was an error in the original generic description (Millidge 1988) where it was stated that *Dunedinia* resembled *Laetesia* in the presence of the side chamber; that this was not so was clearly shown by the figures given (Millidge 1988: figures 206, 207 cf. figures 187-189).

Of the two species dealt with in this paper, *D. opaca* is entirely typical of the genus, while *D. occidentalis* is somewhat abnormal in the detail of the embolic division of the palp.

Dunedinia occidentalis sp. nov.

Figures 1-3

Holotype

Male from cave C.106, Cape Range, Western Australia (22°04'S, 114°01'E), 21 June 1989 (M.S. Harvey); deposited in Western Australian Museum, Perth (92/184).

Paratypes

None.

Etymology

Species name is Latin adjective meaning "western".

Diagnosis

The male is diagnosed by the bowed chelicerae (Figure 2) and by the palp (Figures 1,3); the suprategular apophysis is longer and less hooked than in other *Dunedinia* species, and the embolic division lacks the median apophysis normally present in members of the genus. The female is not known.

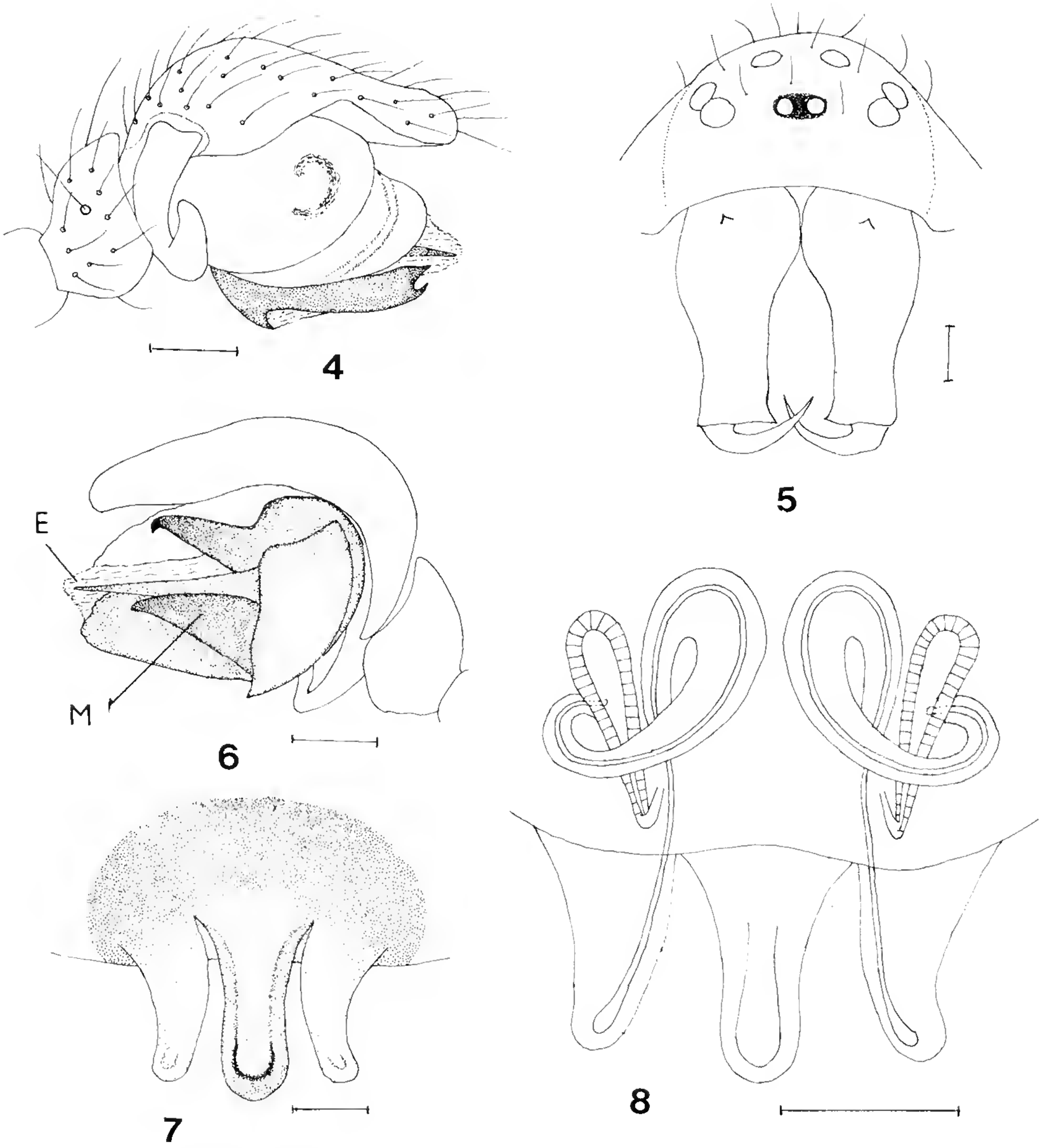
Description

Male

Total length 2.5. Carapace, length 1.35, orange-brown, margins suffused with grey; a few short bristles in ocular area. Eyes rather small, with posteriors ca. 2d. apart. Chelicerae bowed (Figure 2). Abdomen black, with two elongated white spots on each side. Sternum orange, suffused with grey. Legs orange, moderately stout with tibia I l/d ca. 8. Lengths: leg I: fem. 1.0, pat. 0.27, tib. 0.93, metat. 0.90, tars. 0.55; leg IV: most segments missing. Tibial spines short and weak, 2211 (but tibiae IV missing); TmI ca. 0.4. Leg lengths, spines and trichobothria normal for genus. Palp (Figures 1,3).

Distribution

Known only from one cave in Cape Range, Western Australia. It is perhaps not a true cave species, and possibly it will be found in the open in suitable (probably moist) situations.



Figures 4-8 *Dunedinia opaca*, sp. nov. 4, male palp, ectal. 5, male chelicerae, anterior. 6, male palp, mesal. 7, female epigynum, ventral. 8, female epigynum, internal, dorsal. E: embolus. M: median apophysis of embolic division.

Dunedinia opaca sp. nov.

Figures 4-8

Holotype

Male from low vegetation at edge of pond, Inman Valley, near Victor Harbor, South Australia, October 1981 (A.F. Millidge); deposited in South Australian Museum, Adelaide (SAM N1992676)

Paratypes

5 females, 2 subadult males, taken with the holotype; deposited in South Australian Museum (SAM N1992677-682) and Western Australian Museum (WAM 92/2126).

Etymology

Species name is Latin adjective meaning "dark, gloomy".

Diagnosis

This species is closely related to the New Zealand species *D. denticulata* Millidge. The female is diagnosed by the epigynum, which is very similar to that of *D. denticulata*, but has the lateral scapes more curved than in that species (Figure 7 cf. Millidge 1988, figure 203). The male is diagnosed by the palp, which differs from that of *D. denticulata* by the somewhat different shapes of the anterior ventral projection of the embolic plate and of the median apophysis (M, Figure 6, cf. Millidge 1988, figure 191). The male chelicerae are bowed.

Description

Female

Total length 2.2-2.3. Carapace, length 0.95-1.05, brown to dark brown, suffused anteriorly with black. Eyes of moderate size, with posteriors ca. 1 d. apart. Abdomen black, with dorsally four white spots (variable in size) anteriorly, and several white spots or a white stripe on sides. Sternum slightly rugose, orange suffused to variable degree with black. Legs orange-brown, with femora sometimes suffused basally with dark brown or black; fairly short and stout, with tibia I l/d ca. 5.5. Lengths: leg I: fem. 0.73, pat. 0.28, tib. 0.69, metat. 0.57, tars. 0.50; leg IV: fem. 0.89, pat. 0.33, tib. 0.82, metat. 0.67, tars. 0.44. Tibial spines 2211; TmI 0.35-0.40, trichobothrium absent on metatarsus IV. Epigynum (Figures 7,8).

Male

Total length 2.3. Carapace length 1.25. Colour as female, except: white abdominal markings weaker, legs heavily suffused with dark brown on femora and tibiae. Eyes as female. Chelicerae bowed (Figure 5). Leg lengths: leg I: fem. 0.89, pat. 0.30, tib. 0.84, metat. 0.78, tars. 0.55; leg IV: fem. 1.0, pat. 0.30, tib. 0.93, matat. 0.82, tars. 0.50. Tibial spines (2211) short and weak; tibia I l/d ca. 8. TmI ca. 0.35; trichobothrium absent on metatarsus IV. Palp (Figures 4,6).

Distribution

Known only from damp situation at type locality, South Australia.

Genus *Chthiononetes* gen. nov.

Type species

Chthiononetes tenuis sp. nov.

Etymology

From the Greek "chthionos", meaning "from the underworld", and "netes", a spinner; gender masculine.

Diagnosis

Females are diagnosed by the epigynal form (Figure 15), but particularly by the internal form (Figure 16) which distinguishes this genus from *Laetesia* and *Dunedinia*. Males are diagnosed by the bowed chelicerae (Figure 14), and particularly by the form of the palpal organ (Figures 9-12), which distinguishes this genus from *Laetesia* and *Dunedinia*. The cave habitat is also a diagnostic character.

Description

Specimens of the single species have a total length of 2.4-2.8. Carapace unmodified in both sexes, apart from some bristles in and around the ocular area (Figure 13); these bristles less developed in the female. Eyes rather small, with posteriors 1.5-2 d. apart. Male chelicerae bowed and with small basal pointed boss anteriorly (Figure 14); weak lateral files present in both sexes. Abdomen more or less unicolorous. Legs relatively long, with tibia I l/d 13-14 in both sexes. Dorsal tibial spines are 2211, short and slender in female, very weak in male; femora and metatarsi spineless. Metatarsal trichobothria appear to be absent. Female palp clawless. Tracheal form simple, with 4 slender tubes confined to the abdomen. Epigynum with 3 short, very lightly sclerotized scapes posteriorly; the outlines of the internal structures visibly to a varying degree through the lightly sclerotized integument (Figure 15). Median scape with socket; lateral scapes so short as to be scarcely visible, hold the genital openings. Internally, spermathecae elongated, bent over at the anterior end, with tubular subsidiary chamber; seminal duct makes one turn around base of spermatheca and then takes looped course to genital opening (Figure 16). Male palpal tibia without apophyses; large paracymbium present (Figure 9). Suprategular apophysis large, hooked anteriorly (Figure 10), more or less identical with those of *Dunedinia*. The embolic division of the palpal organ is a broad plate (Figure 11), from the inner (lateral) side of which (Figure 12) arises the long, curved embolus (E) and a prominent sclerotized median apophysis (M).

Included species

Only the type species.

Distribution

Known only from caves in Cape Range, Western Australia.

Taxonomic position

Laetesia, *Dunedinia*, *Laperousea* Dalmas and *Chthiononetes* form a group of closely related genera which lies in the subfamily Linyphiinae s.str. (Millidge, 1984). *Chthiononetes* differs from the other 3 genera mainly in the characters of the male and female genitalia.

Chthiononetes tenuis sp. nov.

Figures 9-16

Holotype

Male from Cave C.106, Cape Range, Western Australia, 19 July 1987 (W.F. Humphreys); deposited in Western Australian Museum, Perth (WAM 92/179).

Paratypes

Cape Range. 1 ♀, Cave C.106, 24 September 1988 (W.F. Humphreys *et al.*) (WAM 92/180); 4 ♀, 1 ♂, 2 immature, Cave C.106, 21 June, 1989 (M. Harvey) (WAM 92/185-189); 1 ♀, 1 ♂, Cave C.324, 27 August, 1989 (M. East) (WAM 92/193-194); 1 ♀, 1 immature, Cave C.106, 24 September 1988 (J.M. Waldock) (WAM 92/185/83); 4 ♀, 2 ♂, Cave C.18, 26 June 1989 (B. Vine, M. Harvey, D. Brooks) (WAM 92/157-163); 1 ♂, Cave C.162, 21 June 1989 (W.F. Humphreys) (WAM 92/192); 6 ♀, 2 ♂, 3 immature, Cave C.106, 21 September 1983 (J.C. Lowry), "abundant, especially with flood debris" (WAM 92/164-178); 1 ♂, Cave C.106, 11 August 1988 (B. Vine, D. Brooks) (WAM 92/181); 2 ♀, Cave C.18, 13 August 1988 (W.F. Humphreys *et al.*) (WAM 92/155-156).

Etymology

A Latin adjective meaning "slender".

Diagnosis

The female is diagnosed by the epigynum (Figure 15), and particularly by the internal structure (Figure 16). The male is diagnosed by the bowed chelicerae (Figure 14) and by the palp (Figures 9-12), and particularly by the shape of the median apophysis of the embolic division. The cave habitat is also a diagnostic character.

Description

Female

Total length 2.45-2.8. Carapace, length 1.0-1.1, orange-brown to pale yellow, faintly suffused with grey on margins; a few short bristles in ocular area. Abdomen grey to grey-yellow or grey-brown. Sternum pale orange, suffused with grey on margins. Legs pale yellow to orange-brown, femora slightly darker. Leg lengths: leg I: fem. 1.29, pat. 0.29, tib. 1.27, metat. 1.22, tars. 0.67; leg IV: fem. 1.44, pat. 0.33, tib. 1.33, metat. 1.33, tars. 0.67. Metatarsi without trichobothria. Epigynum (Figures 15,16).

Male

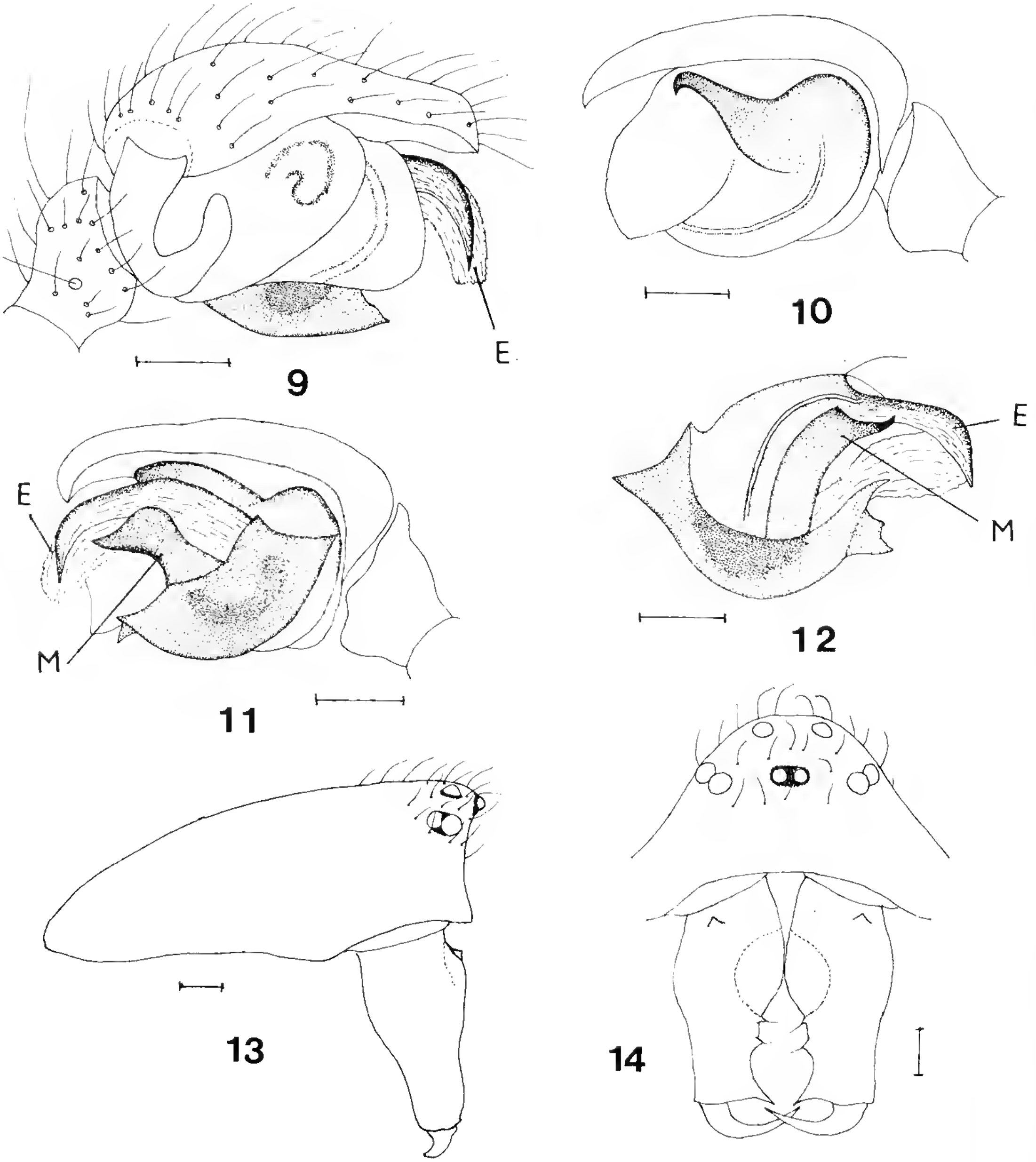
Total length 2.4-2.8. Carapace length 1.05-1.35. Colour as female. Carapace with numerous strong bristles in and around ocular area (Figure 13). Chelicerae bowed (Figure 14). Leg lengths: leg I: fem. 1.11, pat. 0.27, tib. 1.11, metat. 0.98, tars. 0.67; leg IV: fem. 1.18, pat. 0.29, tib. 1.11, metat. 1.11, tars. 0.67. Metatarsi without trichobothria. Palp (Figures 9-12).

Distribution

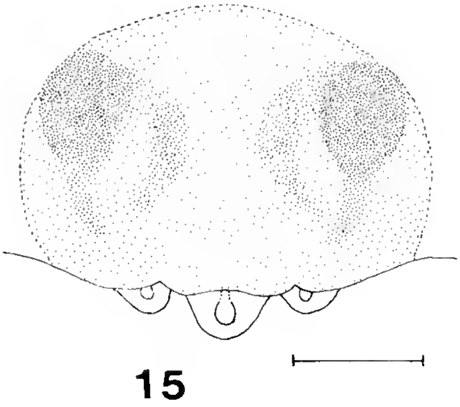
Known only from caves in Cape Range, Western Australia.

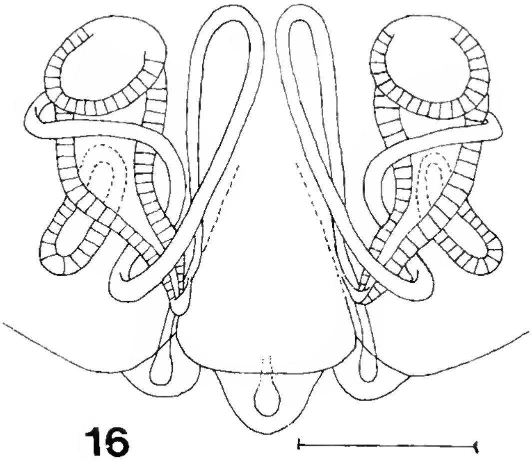
Acknowledgement

I am indebted to Mark Harvey for giving me the opportunity to study the Cape Range linyphiids.



Figures 9-14 *Chthiononetes tenuis*, sp. nov., ♂. 9, palp, ectal. 10, palp, mesal, embolic division removed. 11, palp, mesal. 12. embolic division, inner (lateral) side. 13. carapace, lateral. 14. chelicerae, anterior. E: embolus. M: median apophysis of embolic division.





Figures 15-16 *Chthiononetes tenuis*, sp. nov., ♀. 15, epigynum, ventral. 16, epigynum, internal, dorsal.

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A re-evaluation of the Gondwanan invertebrate *Waiparaconus* as a coelenterate

John S Buckeridge*

Abstract

The remains of *Waiparaconus*, an enigmatic calcareous invertebrate, have been known from Palaeocene deposits in the Middle Waipara Gorge of Canterbury, New Zealand, since the early 1870s. More recently, similar material has been collected from the late Cretaceous of Antarctica and Western Australia, and the Eocene of South America, demonstrating a Gondwanan distribution. These marine fossils have previously been interpreted as either rudistid molluscs or lepadomorph cirripedes, and even though it is clear that the remains are neither of these, many writers continue to include them within the Cirripedia. This paper re-examines the disposition of *Waiparaconus* from the Waipara Greensands, analyses gross morphology, and concludes these remains are most reasonably interpreted as an internal skeleton. It is proposed that *Waiparaconus* lies within the Waiparaconidae, a new family of the Anthozoa. At ordinal level, *Waiparaconus* shows similarity to the pennatulacean octocorals, but inclusion within this order is not warranted, both because of the uniquely waiparaconid imbrications (which are interpreted as attachment sites for rachides or polyps), and an unclear understanding of its mode of life. The austral endemism, and age of *Waiparaconus* suggest a Gondwanan origin for the family.

Introduction

In 1871 Julius von Haast described some "fossil shells" he had collected from the "....thick greensand strata overlying the Septarian clays..." of the middle Waipara Gorge, Canterbury, New Zealand, as "....allied to *Radiolites*", a rudistid bivalve. The same horizons were later collected by Thomson (1920) who, after rejection of any affinities with the Plantae, classified them as inorganic. Their similarity to the heavily calcified lepadomorph peduncles such as *Euscalpellum eocenense* (Meyer) from the southern United States prompted Withers (1951) to ally them with other "monstrously developed peduncles" within the cirripede genus *Euscalpellum*. Withers acknowledged that although none of the "peduncles" were associated with capitular valves, they were sufficiently like *Euscalpellum eocenense* to be included within the same genus. The position in the Lepadomorpha was maintained by Newman, Zullo and Withers (1969), although they gave only very brief reference to the solid peduncles. Buckeridge (1983) re-examined the material and concluded that it was not cirripede. In doing so, he proposed the replacement name *Waiparaconus*, but did not pursue formal systematic location. This paper specifically addresses the issue of systematic placement.

Buckeridge (1983) noted that the reconstruction proposed by Withers (1951) identified the broader end as the upper (= younger) part of the structure. This gave rise to

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confusion with respect to the direction of "plate" (= imbrication) growth, for if Withers' plan were adopted, it would follow that these imbrications must all have been pendant, a condition unknown amongst cirripedes. Further, no known *confirmed* cirripede, either fossil or extant, possesses a solid calcareous peduncle.

Subsequently, Seilacher (1984), and Seilacher and Seilacher-Drexler (1986) have again placed *Waiparaconus* within the Cirripedia, this interpretation being based primarily upon what they considered to be isolated capitular valves found with the New Zealand material.

Since Haast's original report, similar material has been described from a number of regions: Antarctica, New Zealand and South America (Withers 1951); Antarctica (Newman and Ross 1971); New Zealand and Australia (Buckeridge 1983). All of this material has been recovered from late Cretaceous-Eocene strata, and has a distinct "southern oceans" distribution. This paper has arisen following extensive fieldwork at New Zealand locations (during 1985-1992), study of the Western Australian specimens, the material described by Withers (1951), and that collected by W.J. Zinsmeister from Seymour Island, Antarctica (Zullo, Feldmann and Wiedman 1988).

Waiparaconus has been recovered from strata with complex faunal assemblages at Seymour Island, Antarctica, and at Kaynaba, near Dandaragan, Western Australia. In New Zealand it occurs very abundantly in restricted horizons in the Waipara Greensands of Canterbury, thousands being preserved in thanatocoenoses as the sole macrofossil (Figure 1). An examination of the inferred "capitular valves" of Seilacher and Seilacher-Drexler (1986) and of similar material, including that held at the Canterbury Museum, Christchurch, N.Z., suggests that they may better be interpreted as broken fragments of the broader ends of the stalks. Although most stalks appear to be remarkably well preserved, some, especially from the Waipara type location, are fractured around the broader end. The resultant fragments are arcuate, and in thin section could appear similar to cross-sections through cirripede capitular valves, especially when fragments of smaller individuals have been entrapped within the internal cavity of larger stalks. Excavation of specimens held both by Canterbury Museum and the New Zealand Institute of Geological and Nuclear Sciences, Lower Hutt, plus further field collecting, has failed to reveal any material that possesses the shape or growth patterns characteristic of lepadomorph capitular valves.

Systematics

Phylum Cnidaria Hatschek, 1888

Class Anthozoa Ehrenberg, 1834

Subclass Octocorallia? Haeckel, 1866

Order Incertae sedis

Discussion

Waiparaconus Buckeridge, 1983, is represented in the fossil record as arcuate, calcareous, non septate, conical tubes. In section, the tubes are comprised of concentric

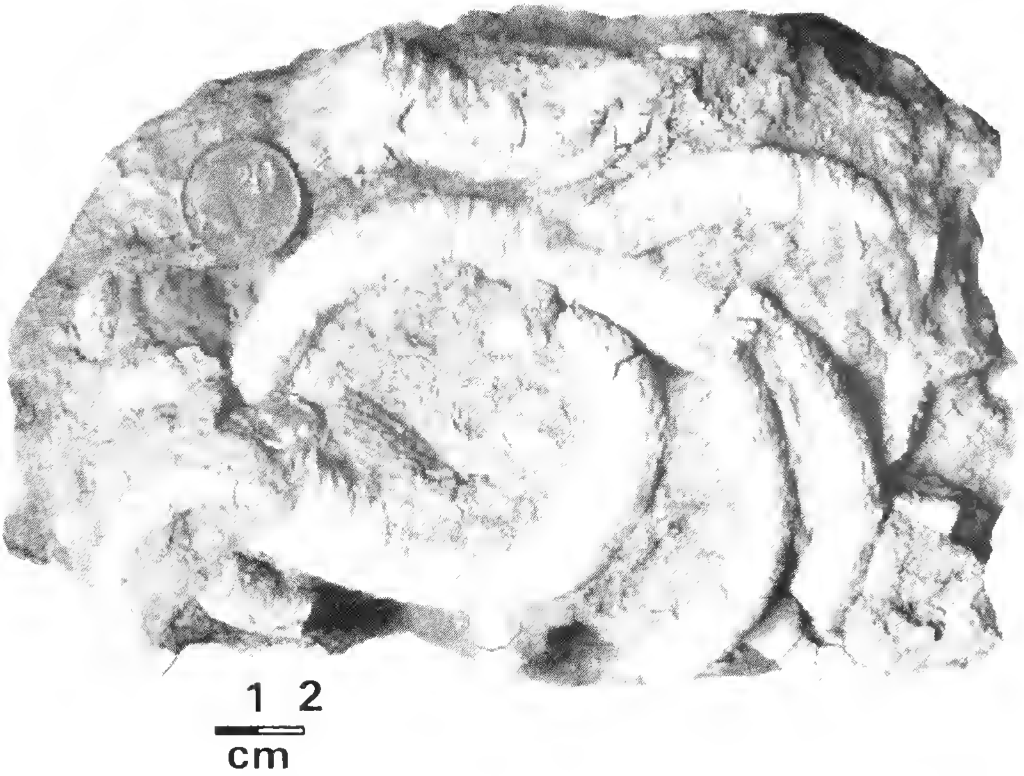

Figure 1 *Waiparaconus zelandicus* (Withers). **G050d**: Numerous stalks from the Waipara Greensands (Landenian), Middle Waipara Gorge, New Zealand, showing preservational disposition. The rigid calcareous stalks are relatively brittle, and are likely to have either been protected by soft tissue during transportation, or to have only been transported a short distance.

laminae of fine radiating calcite crystals, features which can be interpreted as anthozoan. *Waiparaconus* is unlike any known octocoral, particularly in its gross morphology and symmetry; it seems however, to represent an octocoral-like internal skeleton. It was developed as a series of concentric calcareous cones, and retains structures that can be interpreted as attachment sites for polyps, or polypiferous rachides. The informal ordinal location, and the tentative inclusion within Subclass Octocorallia reflect the uncertainty that still surrounds not only the total morphology of the organism but detail of its mode of life.

Family Waiparaconidae fam. nov.

Diagnosis

Massive, calcareous, internal skeleton comprising an elongate, semicircular, arcuate cone, with a central cavity, opening from a fine tube at the narrower, (proximal) end to occupy the entire diameter at the broader (distal) end; length characterised by medium to small imbrications, (possibly attachment sites for polypiferous rachi), each of which may

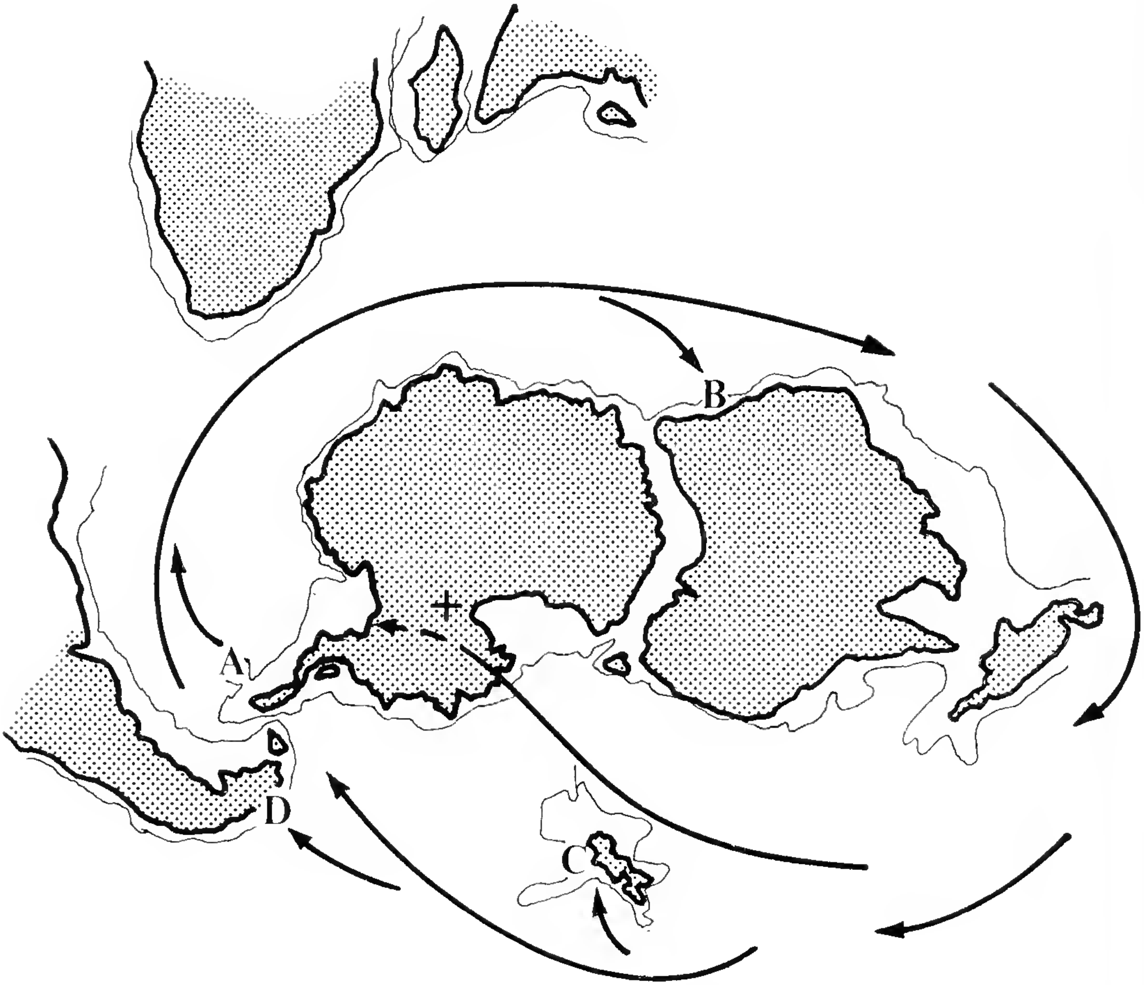

Figure 2 Known distribution the Waiparaconidae. Palaeogeographic reconstruction of the southern hemisphere at the close of the Cretaceous. The fine line surrounding the stippled areas represents the continental shelf at that time, with the "+" marking the south pole location. Arrows show oceanic circulation routes for the period Campanian-Maastrichtian, as inferred from foraminiferal biogeography (adapted from Huber, B T, 1988; BMR Palaeogeographic Group, 1990). An origin for *Waiparaconus* near Antarctica (site "A"), or Australia (site "B"), is likely, with subsequent colonization of New Zealand (site "C") at the close of the Cretaceous, and southern South America (site "D") in the early Cainozoic.

be totally or partially fused to adjacent imbrications; in fully fused varieties, imbrications become less abundant toward the distal end, where they are also increasingly submerged beneath more recently deposited calcareous lamellae.

Discussion

Amongst living octocorals, *Waiparaconus* shows greatest similarity to the Pennatulacea (sea pens), an order characterised by a calcareous or horny shaft, surrounded by coenenchyme which may contain calcareous spicules. Polypiferous rachi arise from the upper (proximal) part of the shaft, with the lower portion anchoring the colony in the bottom sediment. In the pennatulaceans, the rachi are generally arranged bilaterally, whereas in *Waiparaconus* rachi would have emerged from all sides of the shaft, each attached directly to an "imbrication". Like the pennatulaceans, the lower (distal) part of the shaft was probably buried in sediment, acting to anchor the colony. Most specimens show greater wear (corrosion?) at the distal end, suggesting that the protective soft tissue may have been restricted to the middle and upper portions of the stalk. A cross-section through the stalk of *Waiparaconus zelandicus* with its fine radiating calcite crystals superimposed on concentric growth rings (Figure 3) is very like the structure observed the New Zealand Oligocene pennatulacean "*Graphularia*" *longissima* Squires. The lack of imbrications on any pennatulacean shaft is the prime reason for excluding *Waiparaconus* from that order.

Distribution

Late Cretaceous (Santonian) to Palaeocene (Landenian), ?Upper Eocene (Bartonian); austral. Associated with glauconitic or glauconitic chalk horizons.

New Zealand, Teurian (= Landenian). Australia, Santonian. Antarctica, Middle Campanian. South America, ?Bartonian.

Palaeogeographic reconstructions of the late Cretaceous to early Palaeocene show only a partial break-up of the Gondwana supercontinent (Figure 2) at this time. The dispositions of the continents provide a continuity for *Waiparaconus* to range from Western Australia to the southern, circum-Pacific Weddellian Province of Zinsmeister, (1976). Circum-polar currents are inferred from foraminiferal studies (Huber, 1988), and may have provided a opportunity for *Waiparaconus* to disperse.

Palaeoecology

All material recovered to date is associated with glauconitic and glauconitic chalk sediments. Glauconite typically forms near the edge of the continental shelf, in warm waters (15-20° C), with low sedimentation rates. Similar conditions, resulting in glauconite formation, occur today off the west coast of Australia. The Western Australian *Waiparaconus* is preserved in the slightly glauconitic Gingin Chalk (Carter and Lipple, 1982), and water depths in that region during the late Cretaceous are interpreted as having been mid shelf or shallower, with widespread carbonate shoals (BMR Palaeogeographic Group, 1990). The New Zealand *Waiparaconus* shows strong evidence of having been transported, and is restricted to thin horizons adjacent to scour-and-fill and cross bedding. Most of the specimens lie sub-parallel to bedding planes, and are randomly oriented in this plane (Figure 1).

Waiparaconus from Waipara is less well preserved than specimens from other localities, and show characteristics that have been interpreted by Withers (1951) as weathering. This surface damage is however better described as solution pitting, a diagenetic feature, as pits tend to form where quartz grains, (which are common in the Waipara Greensand at this locality), come in contact with the calcareous stalks (Figure 4).

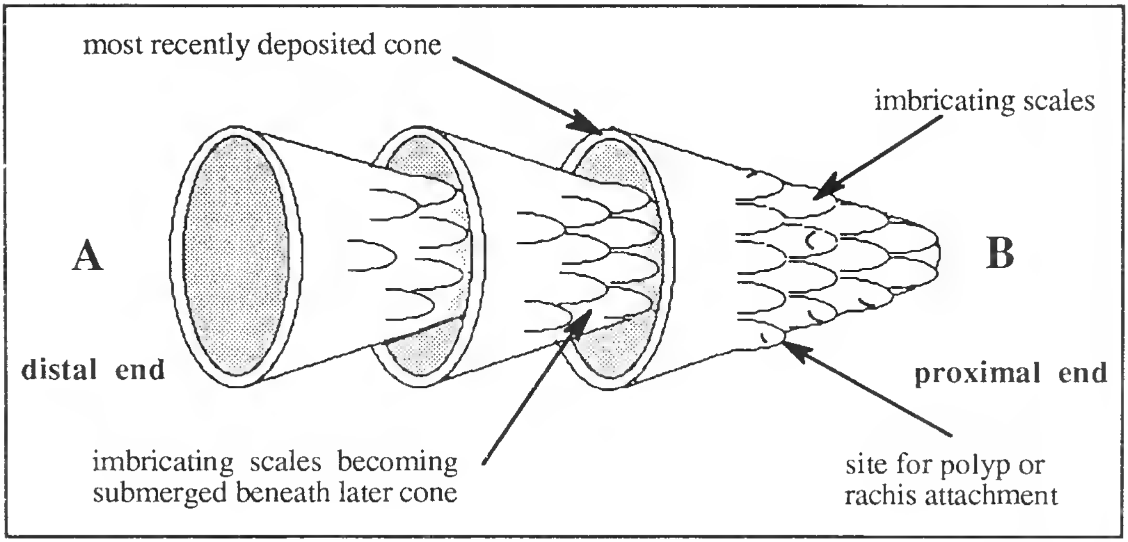

Figure 3 *Waiparaconus* structure. Exploded diagram of "Model 1", illustrating sequential growth in *Waiparaconus zelandicus*. Growth was accompanied by the deposition of successive cones of calcite with associated imbrications. In this process, older cones and imbrications (at end A) become submerged beneath younger (at B). Calcite deposition occurred over most of the shaft length, and although new layers thinned out toward the distal end, this part became broader as the structure lengthened.

Morphology

Buckeridge (1983) dealt specifically with the New Zealand and Australian material, all of which possess fully fused stalks. Further consideration of the specimens described in Withers (1951) shows that stalks in material from outside Australasia were less completely fused. In light of this, and to more fully appreciate the systematic location of *Waiparaconus*, specimens from the Lopez de Bertodano Formation, Seymour Island, Antarctica were examined. Unfortunately the South American (Tierra del Fuego) specimen could not be located.

In all specimens, the stalks are composed of calcite. The manner in which this was laid down may be interpreted in two different ways: In "Model 1", deposition occurred as a series of concentric cones, each cone being made up of fine calcite needles radiating out from about the geometric centre of the structure (Figure 3). These cones developed a series of imbrications on the outer surface, and these are particularly well preserved at the proximal end of all stalks. In specimens from New Zealand and Australia, the imbrications become progressively isolated towards the distal end. This is interpreted as being due to burial beneath successive, newer layers of calcite as the structure increased in size.

In "Model 2", growth would have occurred in precisely the opposite direction. This plan is favoured by Seilacher (1984), and Seilacher and Seilacher-Drexler (1986) who interpreted the "imbricated end" as the portion buried in the sediment, with filamentous anchors extending out from the imbrications. Seilacher proposed that the open end (here termed distal) housed diminutive capitular valves and associated soft parts.

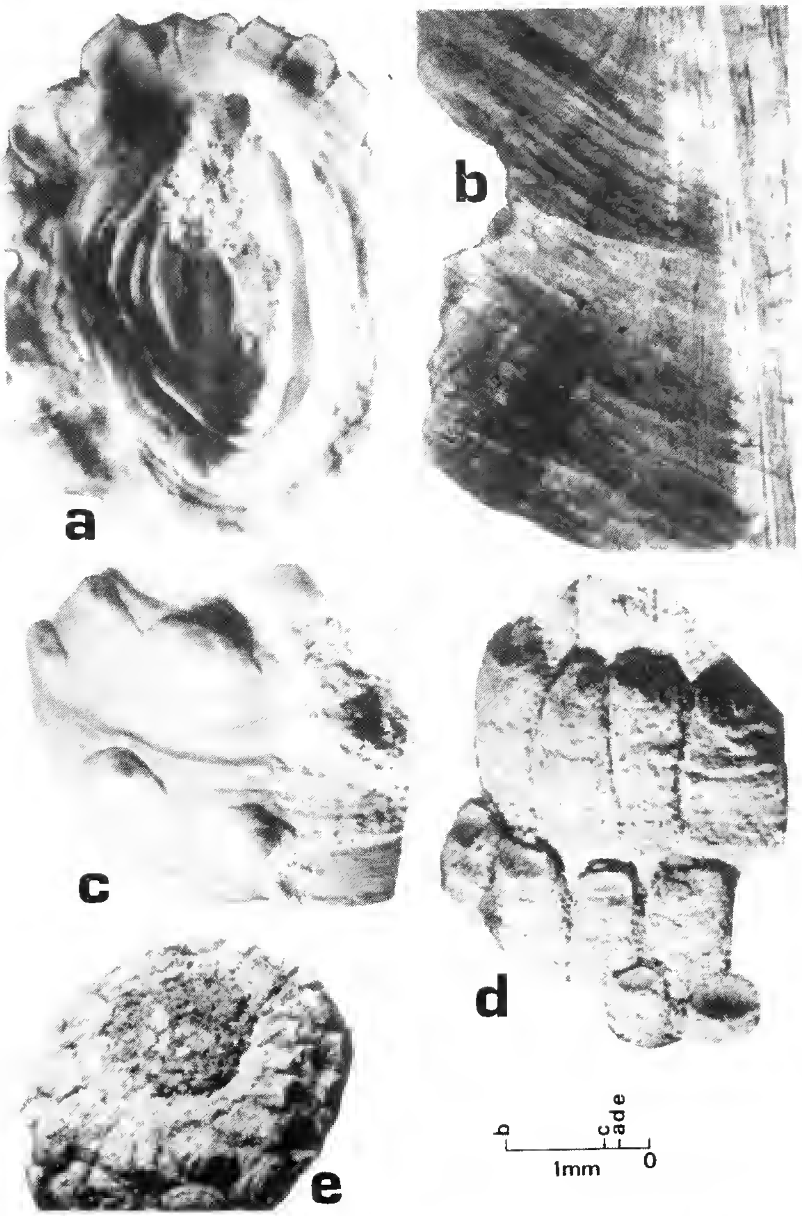

Figure 4 Morphology of *Waiparaconus* imbrications. **a:** apex of specimen **G071a** from the Gingin Chalk, Dandaragan, Western Australia. Santonian. **b:** Longitudinal section through **77.3532b,** from Kaynaba Homestead, Dandaragan, Western Australia. Santonian. **c:** detail of imbrications on **G071a,** showing proposed attachment sites for rachi; note that the distal part of imbrications may be reflexed. **d,e:** Portion of stalk from **G050a,** showing decortication of, and pressure solution effects on, the imbrications. **e:** apical region of **G050b**, showing development of new imbrications. Both G050a and G050b from Middle Waipara Gorge, Canterbury, New Zealand. Landenian.

Analysis

"Model 1" is supported by thin section analysis of material from New Zealand and Western Australia. Conic growth lines pass through imbrications, and thus represent the main structural element. This interpretation appears consistent with the Antarctic specimens, where although imbrications appear to retain much greater integrity, growth lines clearly pass through them to the more solid inner structure (Figure 4).

Genus *Waiparaconus* Buckeridge, 1983

Waiparaconus Buckeridge, 1983: 116.

Waiparaconus, Seilacher and Seilacher-Drexler, 1986:79

Diagnosis and Distribution

As for family.

Composition

At present a monospecific genus: *Waiparaconus zelandicus* (Withers). Type locality: Waipara River, North Canterbury, New Zealand. *W. zelandicus* is selected as type by precedence, being the first form described by Withers (1951).

Waiparaconus zelandicus (Withers, 1951)

Figures 1, 4a-e, 5a-h, 6a-f

Euscalpellum zelandicum Withers, 1951: 155-157, Pl.11, figs 1-3, Pl.12 fig. 1.

Euscalpellum antarcticum Withers, 1951: 157-158, Pl.12, figs 2-4.

Euscalpellum crassissimum Withers, 1951: 161-162, Pl.14, figs 1-5.

"Cirripede peduncle" Glaessner, 1956: 33, figs. 2a-2d.

Waiparaconus zelandicus (Withers), Buckeridge, 1983: 116, Pl.13a-f.

Diagnosis

Stalks massive, arcuate; imbrications with a single terminal tubercle; interior with longitudinal grooves, produced by fusion/partial fusion of adjacent imbrications.

Distribution

Late Cretaceous to Palaeocene, ?Upper Eocene; austral.

Discussion

Three distinct morphotypes of *Waiparaconus zelandicus* exist, and these have previously been recognised as different species (Withers, 1951). Distinction was made on the basis of the imbrications, i.e. whether they were completely or partially fused, and/or were narrow or broad. Material examined from Australia by Buckeridge (1983), and further specimens collected by Zinsmeister from Seymour Island, have shown the distinctions between the different forms to be less clear than originally thought, with a continuous sequence now being discernible: from a form with adjacent imbrications being weakly fused to one in which fusion (and subsequent calcite deposition) almost obliterates traces of older imbrications (Table 1). Rather than representing an

Table 1 Distribution of *Waiparaconus zelandicus* with known ranges in imbrication morphology from each region. The Antarctic (Seymour Island) material (Figures 5a-f, 6e,h) shows by far the greatest morphological variation, and if the new material from this location, and that from Australia had been available to Buckeridge (1983) and perhaps to Withers (1951), it is unlikely that specific separation would have been mentioned.

location	imbricating scales	age
Australia	moderately narrow; almost completely fused into the stalk, suture lines very fine, traceable for short distances; apex wide.	Santonian
Antarctica	moderately narrow; partially or almost completely fused into the stalk, sutures traceable for almost entire length; apex narrow to wide.	Campanian - Maastrichtian
New Zealand	moderately narrow; completely fused into the stalk, sutures traceable for very short distances only; apex narrow or wide.	Landenian
South America	broad; incompletely fused into stalk, nature of apex unknown.	Bartonian

evolutionary change, it is suggested that these differences would better be interpreted as reflecting variations in environmental conditions.

The Seymour Island material includes a stalk with the greatest known diameter (Figure 5a-c). In this specimen, the number of imbrications increases in proportion to the diameter: in early stages up to twenty imbrications appear in cross-section, this number increasing to over fifty with a doubling of the diameter. This type of growth, with the insertion of "secondary imbrications", is analogous to septa addition in anthozoans but is not a characteristic of the lepadomorph cirripedes. Withers (1951) discussed the similarity of this material to the Eocene lepadomorph *Euscalpellum eocenense* (Meyer), a peduncle of which (No. Z. 672) from the Cook Mountain Formation, Mississippi, was examined. *E. eocenense* peduncular scales are more discrete than *Waiparaconus* imbrications, they possess no terminal tubercles and their growth lines can be traced between adjacent scales. The growth lines do not arc inwards, but run parallel to the side of the peduncle, as would be anticipated if growth had occurred from the base. More importantly, the scales in *E. eocenense* are oriented in precisely the opposite direction to the imbrications of *Waiparaconus*, i.e. the peduncle increases in diameter from the base to the capitular end, with all scales erect.

Note: Other cirripede remains (capitular valves) that occur in the Cook Mountain Formation, are not intimately associated with this material. In light of this, it remains to be confirmed that the valves and the peduncle attributed to *E. eocenense* are of the same taxon.

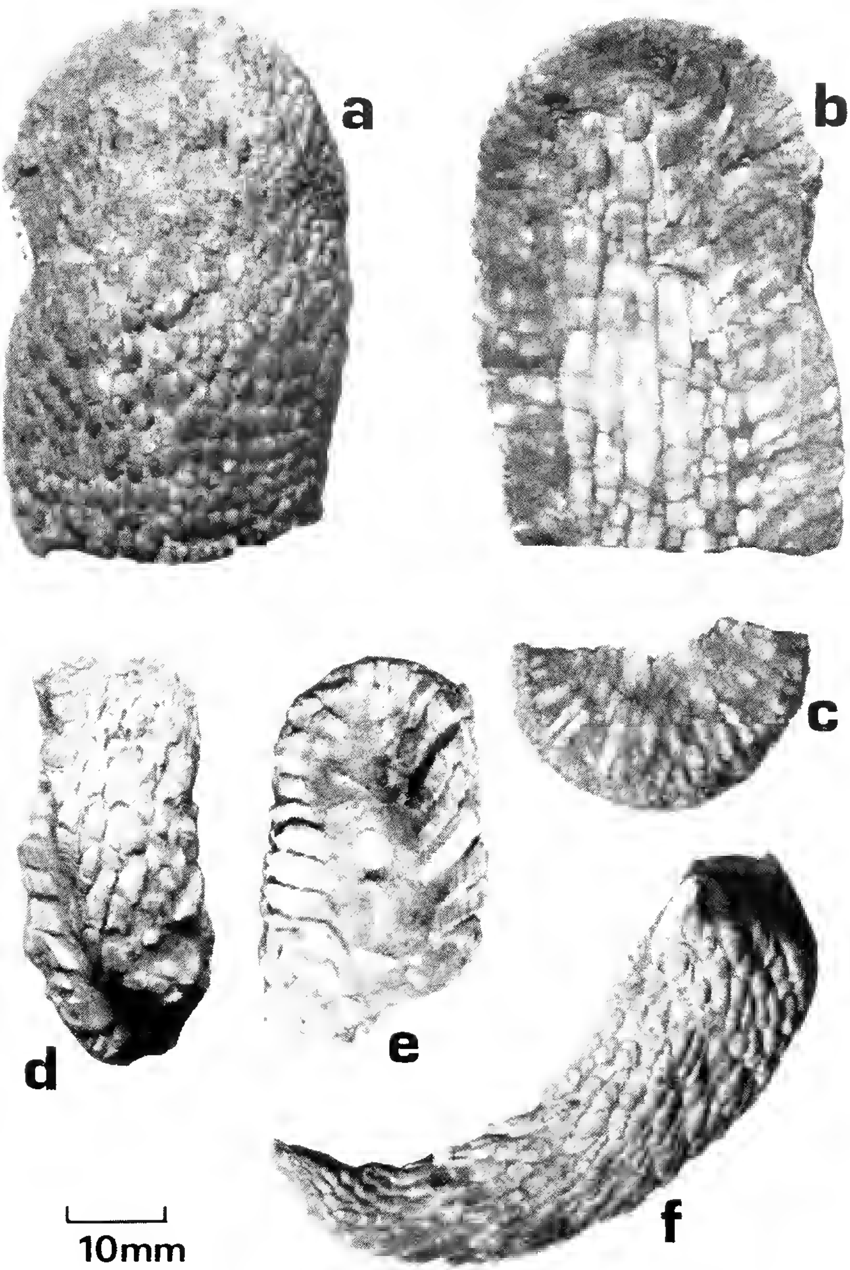

Figure 5 Antarctic *Waiparaconus*. **a,b,c:** external view, longitudinal section and cross section of specimen **1115**, Dagger Peak, Seymour Island, Campanian-Maastrichtian. **f:** Specimen **508** from same locality. **d,e:** Specimen **In 43813.** Stalk showing weakly cemented imbrications with external view, (d) and longitudinal section (e). From slope between Dagger Peak and Comb Ridge, Seymour Island, Campanian-Maastrichtian. Note: This specimen was initially figured as the holotype of *Euscalpellum antarcticum* Withers, in Withers (1951).

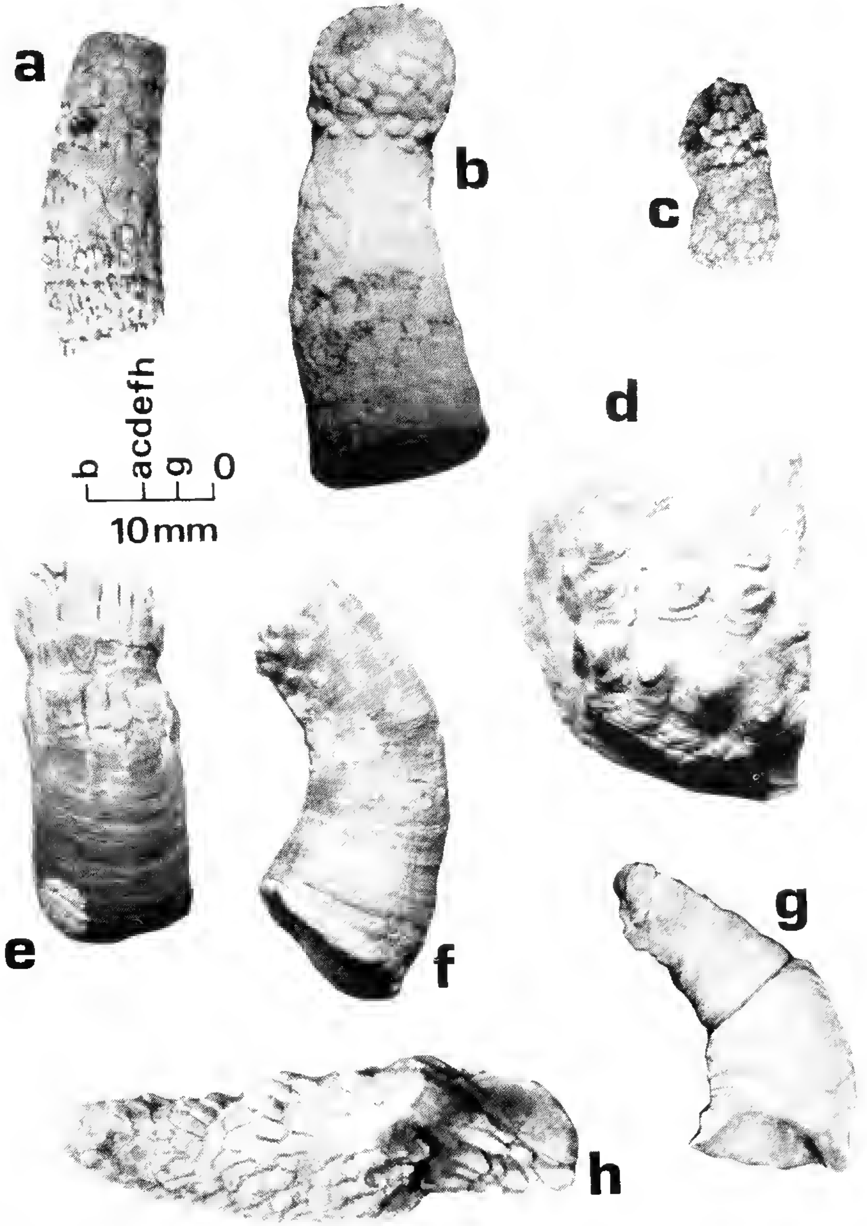

Figure 6 *Waiparaconus* stalk variation. a: Specimen **G050a**; **b:** Specimen **G050b**; **c:** Specimen **G050c** both from Middle Waipara Gorge, New Zealand. Landenian. **d:** Large "globular" specimen, **AR 2095** from Old Claverley Stream, Canterbury, New Zealand. ?Maastrichtian. **e,h:** Seymour Island material from Dagger Peak, **82a** showing extensive (e), and **82b,** partial fusion (h), of imbrications. Campanian-Maastrichtian. **g:** Large specimen with distally expanded base and almost complete fusion of imbrications. **77.3532a**, from Kaynaba, Dandaragan, Western Australia. Santonian. **h:** Well fused specimen with weakly expanded distal portion. **G070a** from Gingin Chalk, Dandaragan, Western Australia. Santonian.

Repositories

Material referred to in this paper was sourced from the following institutions: The Natural History Museum, London, for all specimen numbers prefixed by **In**; the Western Australian Museum, Perth for specimen numbers with no prefix, but typically **77.3532a**; the New Zealand Institute of Geological and Nuclear Sciences for specimen numbers prefixed by **AR**; specimens from the William J Zinsmeister Collection have three or two digits with no prefix, e.g. **1115**, and these are all held by Professor V. A. Zullo, University of North Carolina. All other material, prefixed by **G** is held by the author at Carrington Polytechnic.

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A new species of the *Glaphyromorphus isolepis* Species Group (Lacertilia; Scincidae) from Sumba Island, Indonesia

K.P. Aplin*, R.A. How* and Boeadi#

Abstract

The new species *Glaphyrmorphus butlerorum* is described from one locality in East Sumba, Indonesia. It differs from syntopic *G. emigrans* in body proportions and in details of scalation.

Introduction

In a recent paper on the *Glaphyromorphus isolepis* Species Group, Greer (1990) recognized six species including three from islands of the Lesser Sundas (Nusa Tenggara), Indonesia. Two of the Indonesian species, the recently described *G. timorensis* Greer, 1990 and *G. antoniorum* (Smith, 1926), are found only on Timor. By contrast, *G. emigrans* (Lidth de Jeude, 1896) is widely distributed in the region, with records as far west as Komodo and as far east as Teun (see Figure 1).

Here we describe a fourth species of this complex, collected in 1989 during the course of a vertebrate faunal survey of East Sumba. This fieldwork represents one part of a wider biogeographic and systematic survey of Nusa Tenggara, being undertaken by the Western Australian Museum in collaboration with the Museum Zoologicum Bogoriense.

Systematics

Glaphyromorphus butlerorum sp. nov.

Figures 2, 3

Holotype

R101829, in Western Australian Museum, adult female, collected by R.A. How, D.J. Kitchener, N. Cooper, A. Suyanto and J. Dell at Ngallu, East Sumba, in 10°06′30″S and 120°41′30″E, on 8th June 1989.

Paratypes

R101908 and R101860, adult females, data as for holotype.

Diagnosis

A small, relatively short-limbed member of the *Glaphyromorphus isolepis* Species Group (*sensu* Greer 1990), differing from all other members of this group in the following combination of characters: upper labials 6, paravertebral scales 59-61, and

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Museum Zoologicum Boogoriense, LIPI, Jl Raya Juana 18, Bogor 16122, Indonesia.

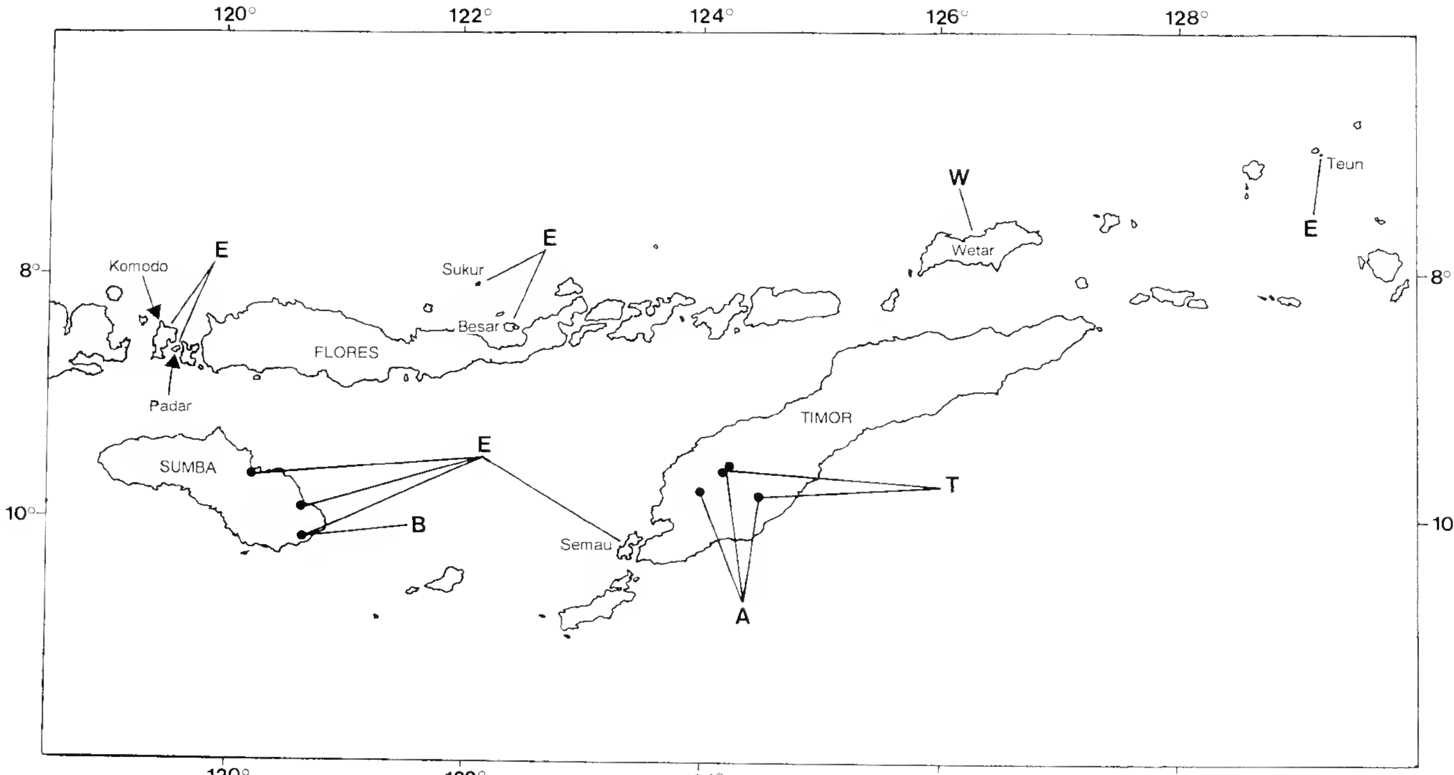

Figure 1 Map of the eastern portion of Nusa Tenggara showing collection localities of five taxa of the *Glaphyromorphus isolepis* Species Group. **B**: *G. butlerorum*; **E**: *G. emigrans emigrans* (including "*mertensi*"); **W**: *G. e. wetariensis*; **A**: *G. antoniorum*; **T**: *G. timorensis* [the record for Teun is based on Auffenberg (1980); his source is not stated].

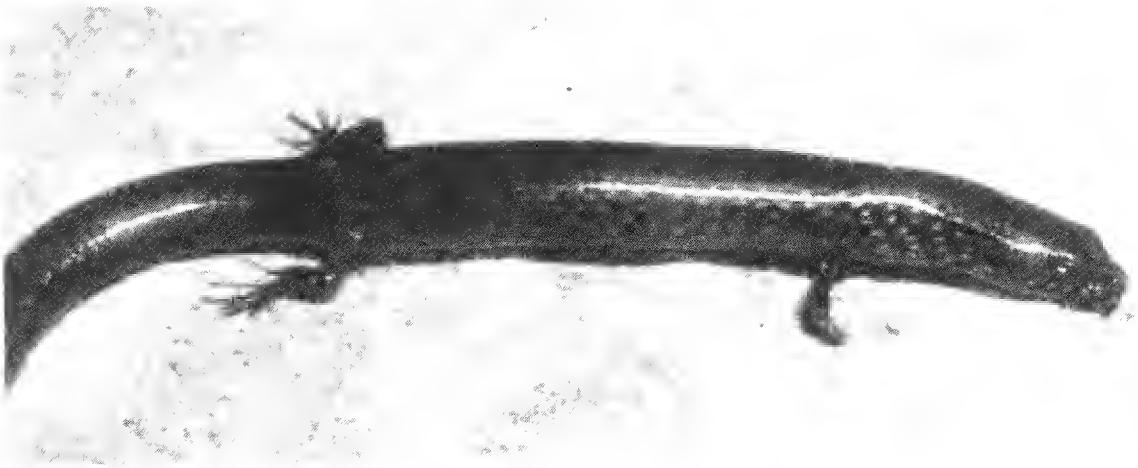

Figure 2 Holotype of *G. butlerorum* photographed in life by N.A. Cooper.

hind limbs 19.6-24.0% of SVL. It further differs from syntopic *G. emigrans* in its relatively shorter fore-limbs (15.2-18% of SVL v. >20%), lower subdigital lamellar counts (15-17 v. 18-21 on pedal digit IV; 8-9 v. 11-12 on manal digit III), and usually lower supraciliary count (6-7 v. 7-9).

Description

A small, indistinctly patterned, brown skink, with non-overlapping pentadactyl limbs, and relatively short fingers and toes.

Snout-vent length (SVL) to 50mm; tail evidently as long or longer than body (all specimens have partially regenerated tails); fore-limbs 15.2-18.0% of SVL; hind-limbs 19.6-24.0% of SVL; subdigital lamellae of third (longest) finger 8 (N=1) or 9(2), of fourth finger 7(1) or 8(2), of fourth toe 15, 16 or 17; with distinct keel on all pedal lamellae, and on distal lamellae of fingers; paravertebral scale count 59, 60 or 61; paravertebral scales not enlarged; inner preanals greatly enlarged, overlapping and almost covering outer preanals.

Rostral in broad contact with frontonasal, contact with first supralabial at level of anterior margin of nostril; supranasals absent; frontonasals separate, each prefrontal smaller than frontonasal; frontal approximately 1.7 times as long as wide; supraoculars usually 4 on each side, first two in contact with frontal (3 on each side in R101829, due to fusion of supraoculars 2 and 3); frontoparietals and interparietal distinct, subequal; parietals in broad contact behind interparietal; nuchals 0-3 on each side.

Nostril situated in lower half of nasal; loreals 2, posterior one slightly larger but not higher than anterior; preoculars 2, lower larger than upper and in series with loreals; supracilliaries usually 7: first to third large and contacting first suprocular; fourth and fifth low and contacting second and third suprocular respectively; sixth and seventh large, latter wedging between last supraocular and upper pretemporal (supracilliaries 6 on one side of R101860 due to fusion of second and third scales of typical pattern); subocular scales in complete series: presuboculars 2, posterior larger and wedging deeply

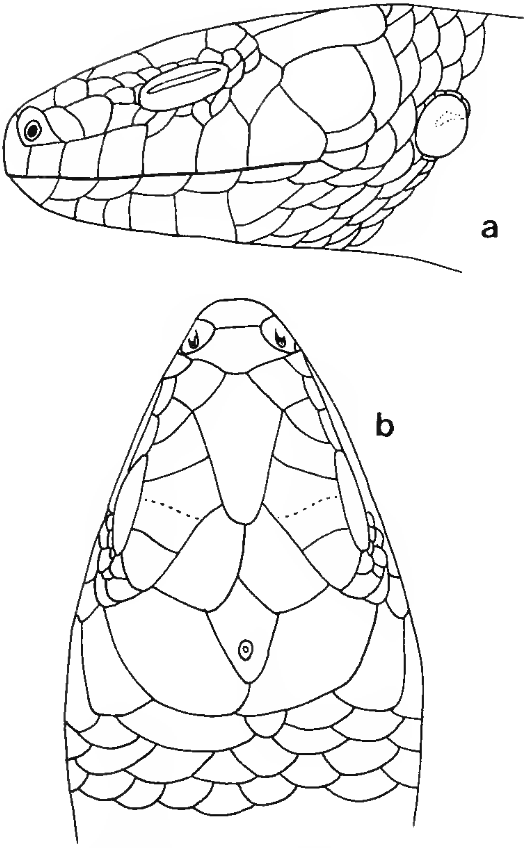

Figure 3 Head scalation of the holotype of *G. butlerorum* in a) lateral and b) dorsal views. The large, second supraocular of this specimen represents an abnormal condition resulting from fusion of the second and third supraoculars; the location of this suture in other specimens of the species is indicated by the dashed lines. Detail of palpebral scalation is not shown.

between supralabials 3 and 4; suboculars small, distinguishable from palpebral scales only in presence of pigment; postsuboculars 2, anterior one larger and wedging deeply between supralabials 4 and 5; pretemporals 2, upper larger than lower; single primary temporal; secondary temporals 2, upper overlapping lower; supralabials 6, fourth beneath eye, posterior 3 larger than anterior 3; postsupralabials 2.

Mental large, opposes rostral and first supralabial on each side; infralabials usually 5 on each side, but unilaterally reduced to 4 on two specimens; postmental contacts first infralabials only, followed by two rows of enlarged chin shields.

Auricular fossa approximately one half of area of orbital fossa, vertically ovate, without auricular lobules; tympanum deeply recessed in fossa.

Eyelid moveable; with row of 5 enlarged, semi-transparant scales.

Osteology. Palate (exposed by dissection of R101908) lacking pterygoid teeth; palatal rami of pterygoids in broad medial contact, excluded from infraorbital vacuity by process of ectopterygoid.

Colour. Pattern (based on R101829 and R101908) indistinct except on head. In preservative ground colour of dorsum brown; body forward of axilla and head dashed with dark brown, arranged in irregular rows; lateral surface dark brown spotted with white, grading evenly into brown of dorsum and immaculate white of venter. Head with dark brown lateral stripe, runs from above ear, through eye, to nostril; supra- and infra-labial scales dark brown, each scale with a central white spot; posterior border of postmental and chin shields dark brown; gular region with dark longitudinal bars (well-developed on R101908; indistinct on R101829). Dorsum of tail as for body; lateral surface with distinct dorso-lateral (dark brown flecked with white, approximately $1^1/_3$ scale width) and lateral (dark brown, less than 1 scale width) stripes, separated by pallid zone; ventral surface white with 3 rows of transverse, posteriorly concave, brown dashes. R101860 is paler brown and is less prominently marked.

Details of holotype (R 101829). SVL 50mm; tail 61mm of which 26mm is regeneration; head width 5.8mm; forelimb 8mm; hindlimb 12mm; scales at midbody 27; subdigital lamellae of third finger 8, of fourth finger 7, of fourth toe 15; paravertebral scales 61; supraciliaries 7 on both sides; nuchals 1/0; infralabials 5 on both sides.

Distribution and habitat. Known only from the type locality on Sumba, where it is syntopic with *G. emigrans*. All known specimens of *G. butlerorum* were purchased from local collectors, hence precise habitat data are not available. The landforms around Ngallu consist of a low escarpment of Tertiary limestone, incised by a major and several minor drainage systems. Immediately surrounding the village were gardens of banana and coconut on shallow soils interspersed with limestone outcrops. The river valley supported dense litter to 30 cm under moist evergreen forest.

Local collectors reported catching *G. butlerorum* and *G. emigrans* in rainforest litter. *Emoia similis, Lamprolepis smaragdina* and *Sphenomorphus florensis* were also obtained in this habitat.

Each of the three known specimens have well-differentiated but quiescent ovaries. This finding is consistent with data for other Nusa Tenggaran *Glaphyromorphus*, among which reproduction is strongly seasonal, with vitellogensis occuring in the late dry to early wet season (i.e., October-December; Greer 1990).

Etymology

After W.H. and M. Butler whose continuing financial support of natural science fieldwork in the Western Australian Museum helped make possible the herpetological survey of Sumba Island, Indonesia.

Remarks

The generic name *Glaphyromorphus* Wells and Wellington, 1983 is available under the recent Decision of the International Commission of Zoological Nomenclature (1991:337-8). The name is used in the revised sense of Greer (1989, 1990).

Placement of the new species in Greer's *Glaphyromorphus isolepis* Species Group is supported by the absence of auricular lobules, details of palatal osteology, the presence of five (or fewer) infralabials, the relative shortness of the limbs, and by the overall

Figure 4 A *Glaphyromorphus emigrans* (R101859) from Ngallu, East Sumba photographed in life by N.A. Cooper.

similarity in body form and head scalation between *G. butlerorum* and such taxa as *G. emigrans* and *G. antoniorum.*

Two names have been applied previously to *Glaphyromorphus* from Sumba: *Lygosoma emigrans* Lidth de Jeude, 1895, and *Lygosoma everetti* Boulenger, 1897 (the latter described without reference to the former). These taxa were regarded as conspecific by de Rooij (1915) and Forcart (1953), and more recently by Greer (1990) who examined relevant type material. Our comparative material includes thirteen specimens of a *Glaphyromorphus* from Sumba which agree closely with *emigrans* as described by Lidth de Jeude, Boulenger (as *everetti*) and de Rooij (see 'Other material examined'; and Figure 4).

The specific distinction of *G. butlerorum* from syntopic *G. emigrans* is readily apparent from meristic data (see Table 1): *G. butlerorum* shows consistently lower paravertebral, supralabial and subdigital lamellar counts than *G. emigrans. Glaphyromorphus butlerorum* is also less prominently patterned than *G. emigrans*, the primary difference being the presence of a distinct dorsolateral stripe in the latter species (compare Figures 2 and 4). The presence of two distinct species in the Ngallu sample is further substantiated by the absence of shared alleles (i.e., "fixed" genetic differences *sensu* Richardson *et al.* 1986) at the Acon-1, Adh and Mpi loci (S.C. Donnellan pers. comm.).

Other taxa which warrant comparison are *G. emigrans wetariensis* Mertens, 1928, from Wetar Island, *G. antoniorum* Smith, 1927 and *G. timorensis* Greer, 1990 from

Table 1 Summary meristic data for various Indonesian *Glaphyromorphus* species, subspecies and populations. Data for *G. butlerorum*, *G. emigrans* (Sumba), *G. antoniorum* and *G. timorensis* pertain to specimens listed in 'Other material examined'. Data for *G. emigrans* (Komodo) are from Auffenberg (1980) and for *G. e. wetariensis* are from Dunn (1927) and Mertens (1928). Key to variables: SVL = snout-vent length; FL = forlimb length; HL = hindlimb length; MBS = mid-body scale rows; PV = paravertebral scales; SL = supralabial scales; SC = suprciliary scales; LT4 = lamellae under fourth toe; LF3 = lamellae under third finger.

	G. butlerorum (N=3)	*G. emigrans* (Sumba: N=13)	*G. emigrans* (Komodo: N=23)	*G. e. wetariensis* (N=1-13)	*G. antoniorum* (N=156-158; 11 for PV)	*G. timorensis* (N=14)
Max. SVL	50	54	65	46	67	93
FL (as % SVL)	15.2-18.0	20.3-30.3	—	21.7	16.4-28.9	18.3-25.6
HL (as % SVL)	19.6-24.0	29.2-39.4	—	31.5	29.8-35.7	26.5-36.1
MBS	26-28	25-27	26-30	26-30	29-33	35-37
PV	59-61	67-75	—	—	67-80	79-86
UL	6	6-7	—	—	7	7
SC	6-7	7-9	—	—	6-9	7-9
LT4	15-17	18-21	17-21	17-21	15-21	17-22
LF3	8-9	11-12	—	—	8-11	10-11

Timor, and "*Sphenomorphus*" *mertensi* Darevsky, 1964 from Padar. Judging from data presented by Dunn (1927) and Mertens (1928), *G. e.wetariensis* differs from *G. butlerorum* in having relatively longer limbs, higher subdigital lamellar counts for the fourth toe (see Table 1), and in being more strongly patterned. Of the Timorese taxa, *G. timorensis* is not only considerably larger than *G. butlerorum*, but also shows numerous meristic differences (see Table 1). *Glaphyromorphus antoniorum* is similar to *G. butlerorum* in overall size and limb proportions, but differs from the new species in having higher midbody, paravertebral, subdigital lamellar, supralabial and supraciliary scale counts (see Table 1). Both of the Timorese taxa are also more strongly patterned than *G. butlerorum*. "*Sphenomorphus*" *mertensi* from Padar is regarded by Auffenberg (1980) as conspecific with "*Sphenomorphus*" *emigrans*, which he records from adjacent Komodo Island. Meristic data provided by Auffenberg (1980) for the Komodo population show slightly higher midbody and subdigital lamellar counts than found in typical *G. emigrans*, moreover his description suggests other morphological differences (e.g., the presence of auricular lobules in "*S*" *mertensi*). While "*S*" *mertensi* (Padar, Komodo) may yet prove to be distinct from typical *G. emigrans* (Sumba etc.), there appears to be no special resemblance between "*S*" *mertensi* and the new species described herein.

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Other material examined

Glaphyromorphus emigrans: W.A.Museum (R) 101841, 101859, 101861-2, 101894-902.

Glaphyromorphus antoniorum: W.A.Museum — 158 specimens including (R) 106417-27, 106429-51, 106456-67.

Glaphyromorphus timorensis: W.A.Museum (R) 106449, 106457, 106466-7, 106495-6, 106498-9, 106605, 106675, 107400, 107402-3, 107406.

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A new species of blindsnake, genus *Ramphotyphlops* (Typhlopidae, Squamata), from northwestern Western Australia, with a redescription of *R. hamatus*, Storr 1981

K.P. Aplin* and S.C. Donnellan†

Abstract

Ramphotyphlops pilbarensis sp. nov. is described from scattered localities in arid northwestern Western Australia. The species is morphologically most similar to *R. hamatus*, with which it was previously confused, and to *R. endoterus*, but differs from these taxa in various meristic and qualitative scalation features. Genetic data suggest a distant relationship amongst the three species. The importance of accounting for sexual dimorphism in typhlopid systematics is emphasized.

Introduction

Blindsnakes of the family Typhlopidae are one of the least studied components of the Australian herpetofauna. The last comprehensive revision of the group was by Waite (1918), who recognised a total of nineteen species. Since that time, additional species have been described by Kinghorn (1929, 1942), Loveridge (1945), Robb (1972) and Storr (1981, 1983, 1984), the latter describing nine new taxa from western and central Australia. Currently a total of thirty one species is recognised (Cogger 1986).

Typhlopid snakes are remarkably uniform in body form and scalation, and thus present relatively few characters of systematic value. For these reasons, the true number of species may be seriously underestimated by morphological criteria alone. Recently, we undertook an electrophoretic study designed to test for sibling species in the widespread but variable "species" *Ramphotyphlops australis* (Gray, 1845). The results of this study (to be published separately) not only confirmed the presence of at least two species within "*australis*", but also revealed *R. hamatus* Storr, 1981, for which several specimens were included as one of several outgroups, to comprise two, genetically very distinct taxa. Subsequent examination of voucher material confirmed the presence of two, morphologically distinct species within *R. hamatus*, one of which is described as new in this paper. Four specimens fo the new species (those pre R80000) were included by Storr (1981) among the paratype series of *R. hamatus*. The composite nature of Storr's description, together with the presence of hitherto undescribed sexual

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dimorphism in this (and other) typhlopid species, warrants its redescription. The new species is compared in detail with each of *R. hamatus* and *R. endoterus* Waite, 1918.

Methods

Individual typhlopid body scales are more easily distinguished along the pigmented, dorsal surface than along the unpigmented venter and for this reason, vertebral scale counts (from immediately behind the frontal to a point opposite the vent) were taken in preference to the more traditional ventral counts. Where both counts are available (the latter from Storr's unpublished data sheets), the vertebral and ventral counts typically differ by ± 5-10, which is consistent with the combined repeatability of the two measurements. Subcaudal counts are taken ventrally and do not include the terminal, spine-bearing scale. Body diameter is the average of body width and depth, measured at or near midbody. The sex of all specimens was determined by examination of the reproductive tract; meristic and mensural data are presented separately for each sex and for a combined sample which includes those animals with indistinct or damaged gonads. Specimens in the collection of the Western Australian Museum are indicated by an R prefix; those in the South Australian Museum are prefixed with SAMR.

Allozyme electrophoresis of liver homogenates was performed on "Cellogel" (Chemetron, Milan) according to the methods of Richardson *et al.* (1986). The enzymes examined are listed at the end of the paper with their Enzyme Commission numbers and abbreviations.

Systematics

Ramphotyphlops pilbarensis **sp. nov.**

Figures 1,2

Holotype

R90864 in the Western Australian Museum, adult male, pit-trapped on 26 September 1988 by J. Dell at Site WS2, Woodstock Station, Pilbara region in 21°36′42″S 118°57′20″E. Liver sample preserved in -80°C ultrafreeze at W.A. Museum.

Paratypes

R10897 (M) Muccan HS; R13055 (M), R13056, R73521, R90643 (F), R90864 (M) Woodstock Station; R83772 (F) 25 km WNW Balfour Downs; R108813 (M) 20 km E South Hedland.

Diagnosis

A moderately large, moderately elongate blindsnake with prominent beaked snout, 22 midbody scale rows and nasal cleft intersecting preocular. Distinguishable from other *Ramphotyphlops* with 22 midbody scale rows as follows: from *R. hamatus* by more numerous vertebrals (♀ > 400 v. < 400; ♂ usually > 380 v. usually < 380), relations of nasal cleft (from second supralabial in *R. hamatus*) and more anteriorly placed nostril; from *R. australis* (sensu Storr 1981) by more prominently beaked snout, relations of nasal cleft (from second supralabial in *R. australis*) and more numerous vertebrals (*australis* ♀ < 365; ♂ < 330); from *R. endoterus* by longer snout, more elliptical rostral, more anteriorly placed nostril and less numerous vertebrals (*endoterus* ♀ > 426; ♂ >

Figure 1 A male *Ramphotyphlops pilbarensis* from 20 km east of South Hedland (WAM R108813), photographed in life by B. Maryan.

416). Distinguishable from the superficially similar *R. unguirostris* in having fewer midbody scale rows (22 v. 24) and in the relations of the nasal cleft (to first supralabial in *R. unguirostris*).

Description

SVL: ♀ 312-362 (N=2, X=337±35.4) ♂ 225-260 (4, 239±15.2) all specimens 110-362 (N=8). Tail: ♀ 7.7-8.8 (2, 8.3±0.8) ♂ 8.9-9.7 (4, 9.3±0.4). Tail as % of total length: ♀ 2.37-2.41 (2, 2.4±0.02) ♂ 3.6-3.8 (4, 3.8±0.1); Diameter: ♀ 6.4-7.0 (2, 6.7±0.4) ♂ 5.1-5.7 (4, 5.3±0.3). Number of times diameter repeated in total length: ♀ 45.7-57.9 (2, 51.8±8.7) ♂ 42.3-50.4 (4, 46.6±3.6).

Head moderately elongate and moderately depressed. Rostral "beak" prominent, rounded in dorsal outline, with slight to moderate bilateral indentations on each side of rostral scale; extended backward by low ridge to near posterior margin of preocular; margin of beak acute but usually lacking a distinct "cutting edge" or any ventral emargination. Nostrils inferior, situated about 3/4 way from eye to tip of snout; shielded above by posterolateral continuation of rostral beak. Eyes moderately large and distinct.

Rostral (from above) elliptical, longer than wide, about 2/3 as wide as snout, and extending back about 4/5 way to eyes; rostral margins on undersurface of snout converging to rear; lingual groove weakly developed. Nasals narrowly to widely separated behind rostral; nasal cleft crosses preocular/nasal suture well above level of supralabials, then runs to second supralabial; not continued beyond nostril. Preocular

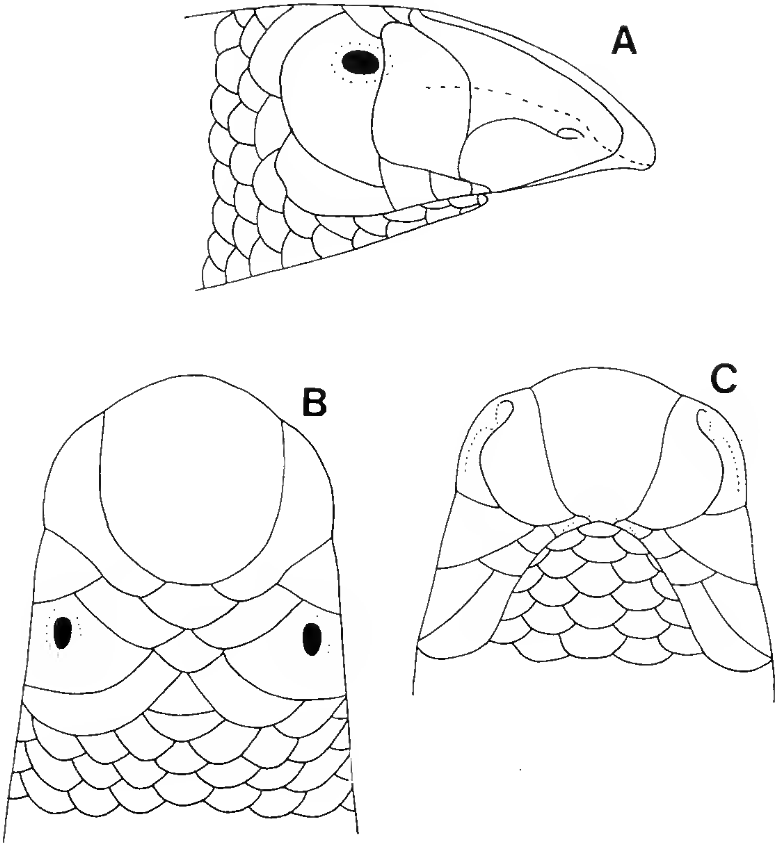

Figure 2 Head scalation of the holotype of *Ramphotyphlops pilbarensis* in A, lateral, B, dorsal and C, ventral views.

narrow, less than half width of ocular. Prefrontal larger than frontal, these scales in narrow contact; frontal slightly smaller than interparietal. Supraoculars subequal to prefrontal, narrowly excluded from median contact. Scales of first postocular row usually fused into elongate "nuchals" of 2-4 scale rows width. Supralabials 4, increasing in size from first to last; first contacts rostral and nasal; second abuts nasal and preocular; third is deeply wedged between preocular and ocular. Mental no larger than postmental scales; infralabials 3, third covered by last supralabial.

Scales rows 22 at midbody (N=8) and on neck (8). Vertebrals: ♀ 400-425 (2; 412.5±17.7); ♂ 372-391 (4, 384.0±8.3); all specimens 363-425 (8). Subcaudals: ♀ 15-16 (2; 15.5±0.7); ♂ 17-22 (4; 20.0±2.5); all specimens 15-22 (N=8).

Colour (in preservative) of dorsal and upper lateral surfaces pale purplish-brown; of lower surface (9-11 scale rows wide) cream; boundary between these zones usually diffuse, owing to presence of some partially pigmented scales, but jagged and sharp in some areas of most specimens. Snout pale, with diffuse pigmentation.

Tongue (protruding on R10897) bifid for 1.4 mm; with 2-3 lateral papillae just proximal to furcation.

Inverted hemipenis (as revealed by dissection of R10897) helically coiled, with 3 complete turns. Noninversible portion of hemipenis extremely elongate, 'flagellum'-like, protuding from cloacal aperture in R90864.

Retrocloacal sacs (sensu McDowell 1974) of males very elongate, extending forward 15.7 mm (a total of 29 scales) from the vent in R90864.

Individual and ontogenetic variation.

In R83772 the rostral beak bears a sharp cutting edge; this is interrupted at the level of each rostral/nasal suture, and lacks any distinct emargination. In the two immature specimens (R13056 and R73521) the rostral beak is less prominent and less acutely angled than in adults. Immature pattern as for adults but dorsum paler.

Details of holotype.

SVL: 232 mm; Tail: 9.1 mm; Vertebrals: 372; Subcaudals: 19; Diameter: 5.7 mm.

Distribution and habitat

Known from scattered localities in the catchments of the Yule and de Grey Rivers, northwestern Western Australia; from Woodstock Station in the northeast Pilbara, north to Muccan on the De Grey River, and southeast to Balfour Downs on the southern margin of the Great Sandy Desert (see Figure 2).

Detailed habitat data are available for two specimens (R90643 and R90864), both pit-trapped at How *et al.*'s (1991) Site WS2 on Woodstock Station. This site is described as follows: "*Acacia pyrifolia*, 2-3 m tall, 3% canopy cover, *Hakea suberea*, 2-3 m tall, <0.5% canopy cover and *Acacia* sp. 2-3m tall, <0.5% canopy cover over *Triodia* spp.(2) *c.* 0.5m tall, 80% canopy cover. Soil coarse sandy loam with granite bedrock at 30-40 cm. Site was burnt in January 1990." Site WS2 was further characterized by an abundance of meat ant (*Iridomyrmex*) nests (J.Dell, *pers.comm.*).

Etymology

After the region in which it occurs, and with the aim of drawing attention to the largely unheralded level of faunistic endemism of the Pilbara region.

Ramphotyphlops hamatus, Storr 1981

Figure 4

Material

Specimens marked with asterisk were included in electrophoretic study: sex indeterminate unless stated.

R81525 (F) White Cliffs Homestead; R56072 (F), R58925 (F), R69572 (F) Marandoo; R67920 (F), R66323 (M); R66322 (M), R67919 (F) 31-36 km SE Mt Meharry; R92998 (M) 6 km WSW Mt Newman; R26304 (F) Newman; R13359 Jiggalong; R15113 (M) Ullawarra Station; R34570 50 km E Carnarvon; R37049 (M) Callagiddy Station; R62373 (M) Mt Narryer Station; R82734 19 km N Nerren Nerren HS; R62870 (M) 21 km SSE Mt Keith; R69294 (M), R69329, R69306 (M), R74795 (M), R69226 (F), R69242 (F) 9.5-12.5 km SSE Banjawarn; R62871 (F) 10km NW Erlistoun; R69193 (F) 18.5 km ENE Yuinmery HS; R97337 (F) Mullewa; R1733 (M) Newmarracarra via Geraldton; R32368 Geraldton; R28312 (F) Canna; R34684 (F) 7 km E Oudabunna HS; R13686 (F) Morawa; R12653 (F) Paynes Find; R72900 (M) 2.5 km N Mt. Linden; R45699 (F) Three Springs; R24789 (F) Caron; R73357 (F) 11.5 km WNW Mt Manning Range;

SAMR29495* (F) Leonora; R10044 (F) Pithara; R24984 (F) Mollerin; R7025 Boulder; R21568 (F) Merredin; R97470* (M) 9.5 km NE Kellerberin.

Description

SVL: ♀ 85-377 (23, 253.3±61.8) ♂ 110-273 (15, 214.9±51.2) all specimens 85-377 (44). Tail: ♀ 2.6-8.8 (23, 8.2±1.6) ♂ 4.5-11.0 (15, 7.9±2.1). Tail as % of total length: ♀ 1.7-3.2 (23, 2.4±0.4) ♂ 2.3-4.1 (15, 3.6±0.5); Diameter: ♀ 2.3-7.8 (23, 5.6±1.3) ♂ 2.4-6.9 (15, 4.8±1.3). Number of times diameter repeated in total length: ♀ 28.7-58.7 (23, 46.6±6.9) ♂ 38.1-57.8 (15, 47.3±5.9).

Head moderately elongate, not markedly depressed (see Figure 4). Rostral beak prominent, rounded in dorsal outline, with slight to very slight indentations at lateral margins of rostral; extended backward by low ridge to near posterior margin of preocular; margin of beak acute, that portion of beak on rostral scale with a distinct, emarginated cutting edge. Nostrils inferior, situated about 2/3 way from eye to tip of snout; shielded above by posterolateral continuation of rostral beak. Eyes moderately large and distinct.

Rostral (from above) subovate, slightly longer than wide, about 3/4 as wide as snout, and extending back 4/5 way to eye; lateral margins of rostral on undersurface of snout convergent to rear; rostral without lingual groove. Nasals narrowly to widely separated behind rostral; nasal cleft passes well forward of preocular/nasal suture, usually runs to second supralabial near contact with first supralabial (occasionally to the inter-labial suture); not continued beyond nostril. Preocular about 2/3 width of ocular. Prefrontal larger than frontal, these scales in narrow contact; frontal smaller than interparietal. Supraoculars subequal to prefrontal, narrowly excluded from median contact. "Nuchals" usually one per side. Supralabials four, morphology as in *R. pilbarensis*. Mental larger than postmental scales; infralabial row as in *R. pilbarensis*.

Scales rows 22 (N=46) at midbody and on neck (N=10). Vertebrals: ♀ 343-396 (23; 370.4±16.2); ♂ 330-367 (15; 350.3±10.0); all specimens 330-396 (N=44). Subcaudals: ♀ 12-16 (23; 13.3±1.2); ♂ 12-18 (15; 15.8±1.7); all specimens 12-18 (44).

Dorsal and upper lateral surfaces (in preservative) pale to dark purplish-brown; lower surfaces cream, usually 9-11 scale rows in width (but as few as 3 in some specimens); primary boundary usually jagged and sharp, owing to bordering scales being either wholly dark or immaculate; most specimens with some outlying, all dark scales. Snout variably pale or dark.

Immature specimens with paler upper colouration but with same basic patterning as adults.

Tongue (protruding on R69329, R12653) bifid for 1.5 mm; with 2-3 lateral papillae just proximal to furcation.

Inverted hemipenis (as revealed by dissection of R72900) helically coiled, with 3 turns; apical, noninversible "flagellum" elongate.

No trace of retrocloacal sacs in two adult males examined (R72900 and SAMR29495), despite presence of sperm in efferent ducts.

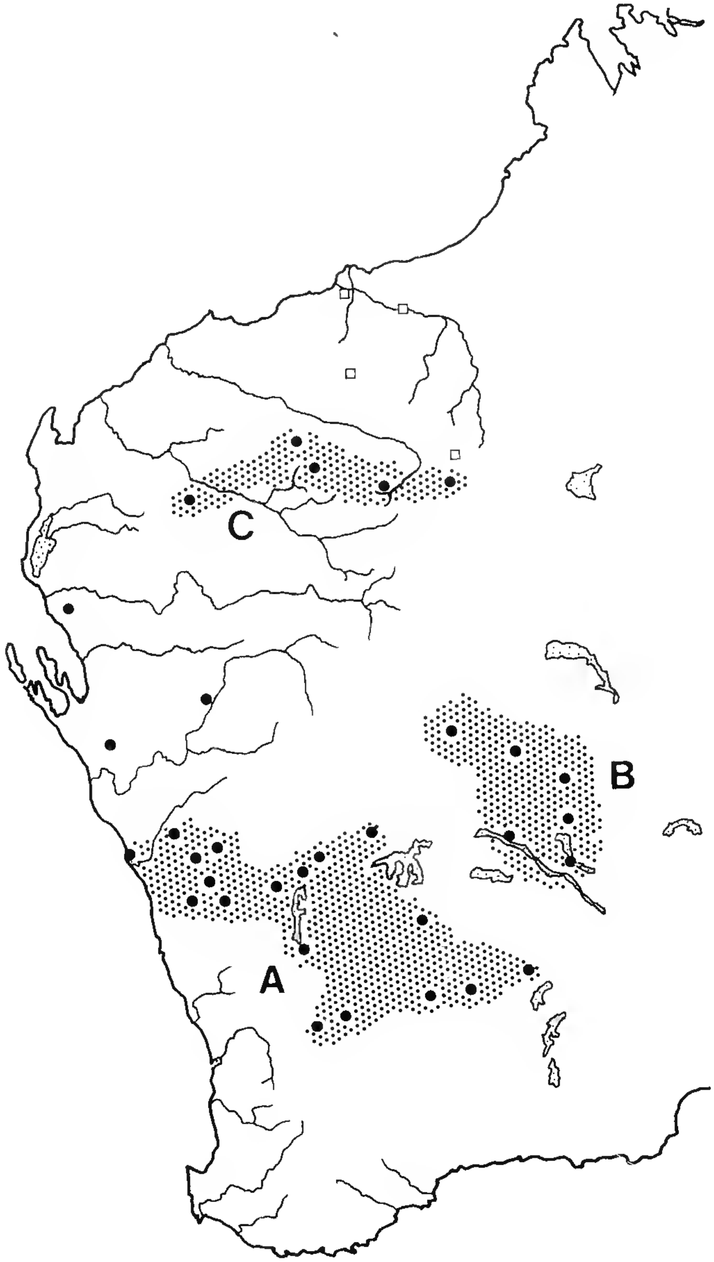

Figure 3 Map of Western Australia showing specimen locations for *Ramphotyphlops pilbarensis* (□) and *Ramphotyphlops hamatus* (●). For analysis of geographic variation, the sample of *R. hamatus* is arbitrarily divided into three geographic regions: A, "Southwestern"; B, "Eastern"; and C, "Northern".

Distribution and geographic variation

Widespread through southern arid and semi-arid regions of Western Australia, from various localities in the Hamersley Range south to Kellerberrin in the Wheatbelt and Woolgangie in the southern Goldfields (see Figure 3). The easternmost records are from the Laverton district in the eastern Goldfields. With the exception of one specimen (R34570) from Grey's Plains (southeast of Carnarvon), all specimens are from localities above 200 m in elevation.

Specimens from the eastern and northern part of the range are longer on average and have higher vertebral scale counts than those from the southwestern region. Using the arbitrary geographic groupings shown on Figure 3, vertebral counts of female *R. hamatus* are 343-375 (N=13) for area A, 374-383 (4) for Area B, and 383-396 (5) for area C. Males show similar though less pronounced trends. There are no obvious trends in either subcaudal counts, diameter or tail length.

With the presently available material, it is unclear whether these geographic differences are representative of gradual clines or of abrupt shifts in population meristics. In either case, it is clear from the limited genetic data (see below) that *R. hamatus* from Kellerberrin (in area A) and from Leonora (in area B) are genetically very similar. For this reason, we are relatively confident that *R. hamatus* as currently comprised represents a single species with at best, weakly differentiated regional populations.

Habitat

Habitat notes are available for 12 specimens scattered throughout the species range; it has been collected in "mallee woodland over spinifex (e.g., R67920, R66322)", in "mid-dense mulga woodland" (R66323), in "samphire" (R74795) and in "bowgada and minner-richie (*Acacia* spp.) at the foot of a breakaway" (R96639). Three specimens were located under rocks; one was dug from an abandoned ant nest.

Electrophoretic distinction between *R. pilbarensis, R. hamatus* and *R. endoterus*

Only a small number of specimens were available for electrophoretic analysis, two of *R. pilbarensis* from Woodstock Station, one of *R. hamatus* from each of Kellerberrin and Leonora, and one of *R. endoterus* from Yulara in South Australia. Table 1 shows the allelic profiles of the these samples for 35 presumptive gene loci.

Ramphotyphlops pilbarensis and *R. hamatus* have fixed differences (i.e., they fail to share alleles) at 12 loci: *Est-1, Est-2, Got-1, Hbdh, Mdh-1, Np, Ntak, PepA, Pgam, Pgk, Pgm-2* and *Sordh.* This amounts to 35% fixed difference overall between the allopatric samples.

Ramphotyphlops pilbarensis and *R. endoterus* have fixed differences at 11 loci (31% of loci scored): *Acon-2, Adh, Gdh, Got-1, Gpi, Hbdh, Mdh-1, Np, Ntak, PepA* and *Pgam.*

The degree of genetic differentiation among these species exceeds that usually found among widely separated populations of a single biological species (Avise 1975; Richardson *et al.* 1986). However, in the absence of sympatric comparisons, the genetic

Table 1 Allele frequencies, expressed as a percentage, in four populations of *Ramphotyphlops*. Alleles are designated alphabetically, with *a* being the most cathodally migrating allele. Where enzymes are encoded by more than one locus, the loci are designated numerically in order of increasing electrophoretic mobility. Where allele frequencies are not given, the frequency is 100%. Sample sizes are given in brackets at the head of each column. Population 1 is *R. pilbarensis* from Woodstock Reserve, W.A.; population 2 is *R. hamatus* from Kellereberin, W.A.; population 3 is *R. hamatus* from Leonora, W.A.; population 4 is *R. endoterus* from Kulnara, S.A. The following 21 loci were invariant among the listed populations: *Acon-1, Acp, Enol, Fum, Gapd, Gda, Glo, Got-2, Gpi, Lap, Ldh-1, Mdh-2, Mpi, Ndpk-1, Ndpk-2, Pk, Pgm-1, Sod* and *Tpi.*

	POPULATION			
LOCUS	1 (2)	2 (1)	3 (1)	4 (1)
Acon-2	a	a	a	b
Ada	b	b	b	b(50) a(50)
Adh	b	b(50) a(50)	b(50) a(50)	b
Est-1	a	b	b	a
Est-2	b	a	a	b
Fdpase	a	b	a	a
Gdh	a	a	a	b
Got-1	b	a	a	b
Gpi	b	b	b	a
Hbdh	a	b	b	c
Mdh-1	a	b	b	b
Np	a	b	b	b
Ntak	a	b	b	b
Pep-A	a	d(50) c(50)	d	b
Pgam	b(75) a(25)	c	c	c
Pgk	c(25) b(75)	a	a	b
Pgm-2	d(25) c(50) b(25)	a	a	b
Sordh	b	a	a	c(50) b(50)

data are merely suggestive and would not constitute sufficient grounds for the recognition of a new species.

A phylogenetic analysis undertaken as part of a wider allozyme electrophoretic study (incorporating several populations of *R. australis* and *R. bituberculatus*; the latter employed as an outgroup) suggests that *R. hamatus* as formerly construed is polyphyletic; i.e. each of *R. hamatus* and *R. pilbarensis* are most closely related to part of *R. australis* as it is currently construed (Aplin and Donnellan in prep.). Interestingly, these data also hint at special cladistic affinity between *R. endoterus* and *R. hamatus*.

The two populations of *R. hamatus* have a single fixed difference at the *Fdpase* locus. This may be indicative of a low level of genetic differentiation between the Wheatbelt and the Eastern Goldfields populations of *R. hamatus*, or may it be due to the small sample sizes, one in each case. Additional sampling is required to clarify this point.

Summary of morphological differences between *R. pilbarensis, R. hamatus* and *R. endoterus*

Ramphotyphlops pilbarensis is most readily confused with each of *R. hamatus* and *R. endoterus*. All three are moderately elongate snakes with 22 scales at midbody and a pronounced rostral beak. Nevertheless, each is readily identified by a combination of meristic and discrete characters.

Ramphotyphlops pilbarensis differs most strikingly from *R. hamatus* in the relations of the nasal cleft: this intersects the preocular/nasal suture in *R. pilbarensis* yet passes well forward of this suture in *R. hamatus* (compare Figures 1 and 3). Other differences include the more anterior placement of the nostril in *R. pilbarensis*, the more acutely pointed (from above) snout of *R. hamatus*, and the presence of a distinct emargination of the rostral beak in *R. hamatus* alone. The two species are closely similar in snout-vent length and body proportions, with females substantially longer and stouter than males in both *R. hamatus* and *R. pilbarensis*. Females of each species likewise show no difference in tail length, however the tail of male *R. pilbarensis* appears to be slightly longer on average than that of male *R. hamatus*.

Vertebral and subcaudal counts also show strong sexual dimorphism in each of the two species. In this case however, there is also a clear separation **between** the species **for each sex**, *R. pilbarensis* with higher vertebral and subcaudal counts than *R. hamatus*. Given that the two species do not differ in absolute size, the body scales of *R. pilbarensis* are thus relatively foreshortened, resulting in a greater number of scale whorls for a given length of snake. Unfortunately, the degree of difference is not sufficient to make this a viable means of identification, there being only 20-30 additional whorls in a snake of 200-300 mm SVL (i.e., one extra whorl per cm).

Ramphotyphlops pilbarensis and *R. endoterus* are similar in many respects including the relations of the nasal cleft (contacting the preocular in both species), the absence of any emargination around the rostral beak, and overall size and proportions. *Ramphotyphlops endoterus* differs from *R. pilbarensis* in having a relatively shorter snout, a more nearly ovate rostral shield (as viewed from above; see Figure 24 in Waite 1918), higher vertebral counts (♀ 436-447 v. 400-425; ♂ 416-445 v. 372-387; values for *R. endoterus* from unpublished observations on material in W.A. and S.A. Museums), and lower subcaudal counts (♀ 10-16 v. 15-16; ♂ 15-18 v. 19-22).

The hemipenis of *R. endoterus* (based on R17782 and R22096) is essentially similar to that of the other species, having a long apical flagellum and three helical coils in the inverted condition. Male *R. endoterus* appear to lack retrocloacal sacs. In this regard it is similar to *R. hamatus* and differs from *R. pilbarensis*.

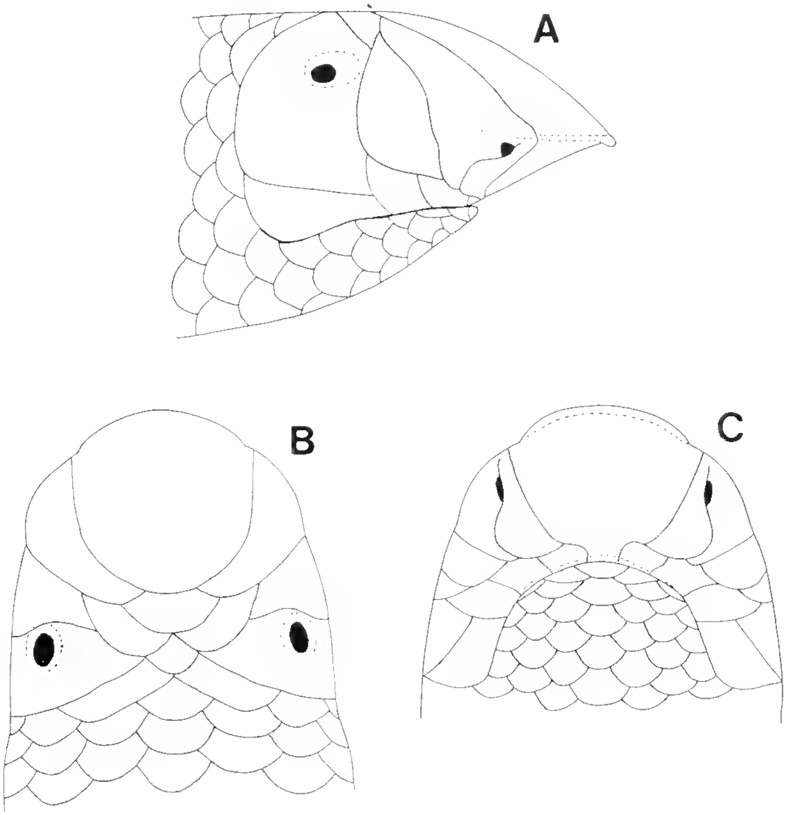

Figure 4 Head scalation of the holotype of *Ramphotyphlops hamatus* in A, lateral, B, dorsal and C, ventral views.

Discussion

The presence in the new species of both a helically coiled hemipenis bearing a long, noninversible portion, and well-developed retrocloacal sacs support its inclusion within *Ramphotyphlops* as defined by Robb (1966; see also McDowell 1974, as *Typhlina*). More suprising is the finding that retrocloacal sacs are absent in at least some individuals of the species *hamatus* and *endoterus*, this despite the presence in both of a hemipenis of the *Ramphotyphlops* type. Since retrocloacal sacs are widely distributed among Australo-papuan typhlopids (Robb 1966; McDowell 1974) their absence in the latter two species, if confirmed, is most likely due to secondary loss. However, much additional work on the reproductive anatomy of these taxa is required before any firm conclusions should be drawn.

The present study raises a number of additional points of general relevance to the systematics of Australian typhlopid snakes. The first is that the level of meristic variation in species of *Ramphotyphlops* has been overestimated in earlier studies, owing to the presence of significant sexual dimorphism, the presence of some composite taxa, and the presence of significant geographic variation in some values. In the case of *R. hamatus*, Storr reports a combined sex, species-wide range of 338-394 for ventrals and 11-22 for subcaudals. Our data indicate that males of this species have significantly narrower ranges for both vertebrals (330-367) and subcaudals (12-18), while females show a narrower range for subcaudals (12-16) but an equivalently wider range for vertebrals (343-396). As indicated above, female vertebral counts show marked geographic variation and actual populational ranges may be considerably narrower; viz. ranges of 343-375 (N=13), 374-383 (4) and 383-396 (5) for the southwestern, eastern and northern regions respectively. Clearly then, analyses based on known-sex samples should yield better taxonomic discrimination among species of *Ramphotyphlops*, particularly where comparisons are between geographically restricted samples.

A high level of sexual dimorphism was recorded by Laurent (1964) and Roux-Esteve in African typhlopids (*Typhlops* and *Rhinotyphlops*) and is evident in meristic data supplied by McDowell (1974) for various Indonesian and Melanesian typhlopids (*Typhlops* and *Ramphotyphlops*). From our ongoing studies of Australian *Ramphotyphlops*, we can confirm the presence of marked dimorphism in at least 6 species (*hamatus, pilbarensis, pinguis, australis sensu* lato; the latter taxon probably a composite of 3 species). We suggest that marked sexual dimorphism will be a major component of meristic variation in many if not all Australian typhlopids, and urge that all future taxonomic work on the group be based on "known sex" comparisons.

A second general point concerns the taxonomic utility of certain features which have in the past been used to distinguish between species of *Ramphotyphlops*. Tail length and body diameter are two characters which feature in many of the original descriptions of Australian typhlopids and in Boulenger's (1893) key to "*Typhlops*". Tail length is often referred to either in relation to overall body length or in relation to tail breadth. As shown in this study, tail length is both absolutely and relatively longer in male than in female *Ramphotyphlops*, presumably as a means of accomodating the elongate hemipenes. Moreover, because males are actually smaller overall, this translates into an even greater dimorphism in relative length. The length to width ratio is also affected in the same way as males have a longer tail but are narrower bodied (and tailed) overall. Body diameter is often cited in relation to body length (i.e. the diameter goes 30-40 times in the total length). Although in *R. hamatus* diameter is also sexually dimorphic when taken as an absolute, this is offset by the greater length of females. Hence the ratio of body length to body diameter appears not to differ significantly between the sexes.

One character which appears to have been downplayed by recent workers is the relations of the nasal cleft. This character features prominently in Boulenger's key to the blindsnakes of the world, and provides the first triplet in Waite's (1918) key to Australian typhlopids. Cogger (1986 and earlier editions), however, cautioned against strong reliance on this character for identification, and suggested that it "is much more variable than has generally been conceded". Storr (1981) employed the relations of the nasal cleft as a terminal key character, but noted variation in this character in three taxa: *R. australis, R. hamatus* and *R. grypus.* Interestingly enough, two of these taxa are now known to be composites, and at least in the latter case, the differing relations of the nasal cleft actually represents the single most effective means of distinguishing *R. pilbarensis* from *R. hamatus.* This is not to say that this character is invariant or that it will always reliably discriminate between species, but rather that the level of variability of any given characters can only be determined in the context of a well-resolved taxonomy based on other characters. In the case of anatomically conservative groups such as typhlopid snakes, biochemical techniques including allozyme electrophoresis hold great potential for the initial discrimination of morphologically cryptic species.

Acknowledgements

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APPENDIX I

Proteins examined, Enzyme Commission numbers, and Abbreviations

Aconite hydratase (ACON, E.C. 4.2.1.3), acid phosphatase (ACP, E.C. 3.1.3.2) alcohol dehydrogenase (ADH, E.C. 1.1.1.1), enolase (ENOL, E.C. 4.2.1.11), esterase (EST, E.C. 3.1.1.1), fructose-diphosphotase (FDPASE, E.C. 3.1.3.11), fumarate hydratase (FUM, E.C. 4.2.1.2), glyceraldehyde-phosphate dehydrogenase (GAPD, E.C. 1.2.1.2), guanine deaminase (GDA, E.C. 3.5.4.3), glutamate dehydrogenase (GDH, E.C. 1.4.1.2), lactoylglutathione lyase (GLO, E.C. 4.4.1.5), aspartate aminotransferase (GOT, E.C. 2.6.1.1), glucose phosphate isomerase (GPI, E.C. 5.3.1.9), 3-hydroxybutyrate dehydrogenase (HBDH, E.C. 1.1.1.30), lucine amino peptidase (LAP, E.C. 3.4.11.1), lactate dehydrogenase (LDH, E.C. 1.1.1.27), malate dehydrogenase (MDH, E.C. 1.1.1.37), mannosephosphate isomerase (MPI, E.C. 5.3.1.8), Nucleoside diphosphate kinase (NDPK, E.C. 2.7.4.6), purine-nucleoside phosphorylase (NP, E.C. 2.4.2.1.), Nucleoside-triphosphate adenylate kinase (NTAK, E.C. 2.7.4.10), Peptidase A (PEPA, E.C. 3.4.-.-), phosphgycerate mutase (PGAM, E.C. 2.7.5.3), phosphgycerate kinase (PGK, E.C. 2.7.2.3), pyruvate kinase (PK, E.C. 2.7.1.40), phosphoglucomutase (PGM, E.C. 2.7.2.3), superoxide dismutase (SOD, E.C. 1.15.1.1), L-iditol dehydrogenase (SORDH, E.C. 1.1.1.14), triose-phosphate isomerase (TPI, E.C. 5.3.1.1).

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Two new genera of terrestrial isopods (Crustacea: Isopoda: Oniscidea) from north-western Western Australia

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Abstract

Oniscidea collected from the Kimberley region and Barrow Island, Western Australia belong to the families Ligiidae, Olibrinidae, Philosciidae and Armadillidae. The family Olibrinidae is recorded for the first time from Australia. Two new genera of Armadillidae, *Kimberleydillo* gen. nov. and *Barrowdillo* gen. nov., and two new species, *Kimberleydillo waldockae* sp. nov. and *Barrowdillo pseudopyrgoniscus* sp. nov., are described.

Introduction

This publication deals with the specimens of terrestrial isopods collected during the months of August and September 1991 from cave and non-cave habitats by Ms J.M. Waldock and Dr W.F. Humphreys from Barrow Island. Specimens prefixed WAM are lodged in the Western Australian Museum, those prefixed DH are in the personal collection of the author.

Systematics

Family Ligiidae Brandt and Ratzeburg, 1831

Genus *Ligia* Fabricius, 1798

Ligia exotica Roux, 1828

Ligia exotica Roux, 1828, pl.13, fig.9; Roman, 1977: 119, figs 6-7.

Megaligia exotica Verhoeff, 1926: 348; Van Name, 1936: 48.

Material examined

Barrow Island, Wapet camp, 20°50′8″S, 115°25′0″E, beach beneath stones, 6 September 1991, W.F. Humphreys and B. Vine, (WAM 126-91), female.

Remarks

This cosmopolitan species is the most widely distributed in the world, except Europe. In Australia, in spite of the fact that most records of *Ligia* have been assigned (Green 1962: 83) to *Ligia australiensis* Dana, 1853, it seems that this species is limited to the south-eastern and southern coasts of Australia from New South Wales to South Australia and in Tasmania (Green 1974: 238). The other records should be assigned to *Ligia exotica*.

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Family Olibrinidae Budde-Lund, 1913

Genus *Olibrinus* Budde-Lund, 1913

Olibrinus sp.

Material examined

Barrow Island, Wapet camp, 20°50′8″S, 115°25′0″E, beach beneath stones, 6 September 1991, W.F. Humphreys and B. Vine, WAM 127-91, 1 ovigerous female.

Diagnosis

This species is elongated, with long antenna, the flagellum of which is multiarticulate. The pleon is narrower than the peraeon. Frontal line is absent, but a supra-antennal line is present. Pleopod exopodites 1 and 2 without respiratory area.

Description

Small elongated animal of 5.2 mm x 1.6 mm. The colour whitish to the naked eye, but magnified (x18), a thin network of pale brown is apparent, thicker on cephalon. A brown spot present on the ventral face of the meros on every peraeopod. Eyes reduced, each with five ommatidia embedded in a black pigmentary spot. Pleon narrow with apex of epimera visible from above. Pleotelson triangular and wider than long. Uropods with long protopodites; insertion of endopodite on projection of the bottom of the protopodite.

Remarks

This is the first record of the family Olibrinidae in Australia. Roman (1977) gave an account of the different species of *Olibrinus* with their distribution. This was discussed again by Taiti and Ferrara (1991) who placed the Japanese genus *Marinoniscus* as a synonym of *Olibrinus*. Six of the ten described species come from the shores of the Indian Ocean; the three remaining species are from Japan and one from Hawaiian Islands. The Barrow Island specimen may well be of an undescribed species but, an adequate description cannot be presented from a single female specimen.

Family Philosciidae Vandel, 1952

Genus *Laevophiloscia* Wahrberg, 1922

Laevophiloscia yalgoonensis Wahrberg, 1922

Philoscia (Laevophiloscia) yalgoonensis Wahrberg, 1922: 130.

Laevophiloscia yalgoonensis Vandel, 1973: 90.

Material examined

Barrow Island, Western Australia. Cave B1, W.F. Humphreys and B. Vine, 5 September 1991, WAM 111-91, 4 males and WAM 112-91, 5 females; W.F. Humphreys and B. Vine, 6 September 1991, WAM 114-91, 1 female; W.F. Humphreys and B. Vine, 10 September 1991, WAM 121-91, 1 male and 2 females; W.F. Humphreys and B. Vine, 10 September 1991, WAM 122-91, 1 male; W.F. Humphreys and B. Vine, WAM 123-91, 4 males and 5 females; W.F. Humphreys and B. Vine, 12 September 1991, WAM 124-91, 1 male. Cave B3, W.F. Humphreys and B. Vine, 12 September 1991, WAM 125-91, 1 male and 1 female.

Remarks

This species was redescribed by Vandel (1973). It is common in Western Australia, being found both epigean and in caves. It is probably a recent entry into caves as specimens living in caves hardly differ from outside forms.

Family Armadillidae Brandt and Ratzeburg, 1831

Genus *Kimberleydillo* gen.nov.

Type species

Kimberleydillo waldockae sp. nov., herein designated.

Diagnosis

Unable to conglobate with dorsal surface not strongly but regularly curved, suggesting *Cylisticus* habit; neither schisma nor peraeon ventral lobes. Flagellum of antenna 2-jointed. Five pairs of pseudotracheae and uropod protopodite flattened and situated between sides of telson and epimera of pleon segment 5. Telson with trapezoidal proximal part and subrectangular distal part; apex slightly rounded.

Remarks

The fact that this genus is unable to conglobate and all the interlocking structures are absent, places this genus in the subfamily Australiodillinae Vandel, 1973 with the genera *Australiodillo* Verhoeff, 1926 and *Neodillo* Dalens, 1990. *Kimberleydillo* is, however, distinct from these genera by the dorsal surface being regularly curved, while the margins are more or less extended horizontally in *Australiodillo* and *Neodillo*. In addition the pleotelson is indented in *Australiodillo* and entire in *Kimberleydillo*. The antennulae seem four jointed in *Neodillo* and three jointed in *Kimberleydillo*. The reduced pigmentation, the translucence of tegument and the lengthening of the antenna seem to be steps towards troglomorphy.

Kimberleydillo waldockae sp.nov.

Figures 1-9

Holotype

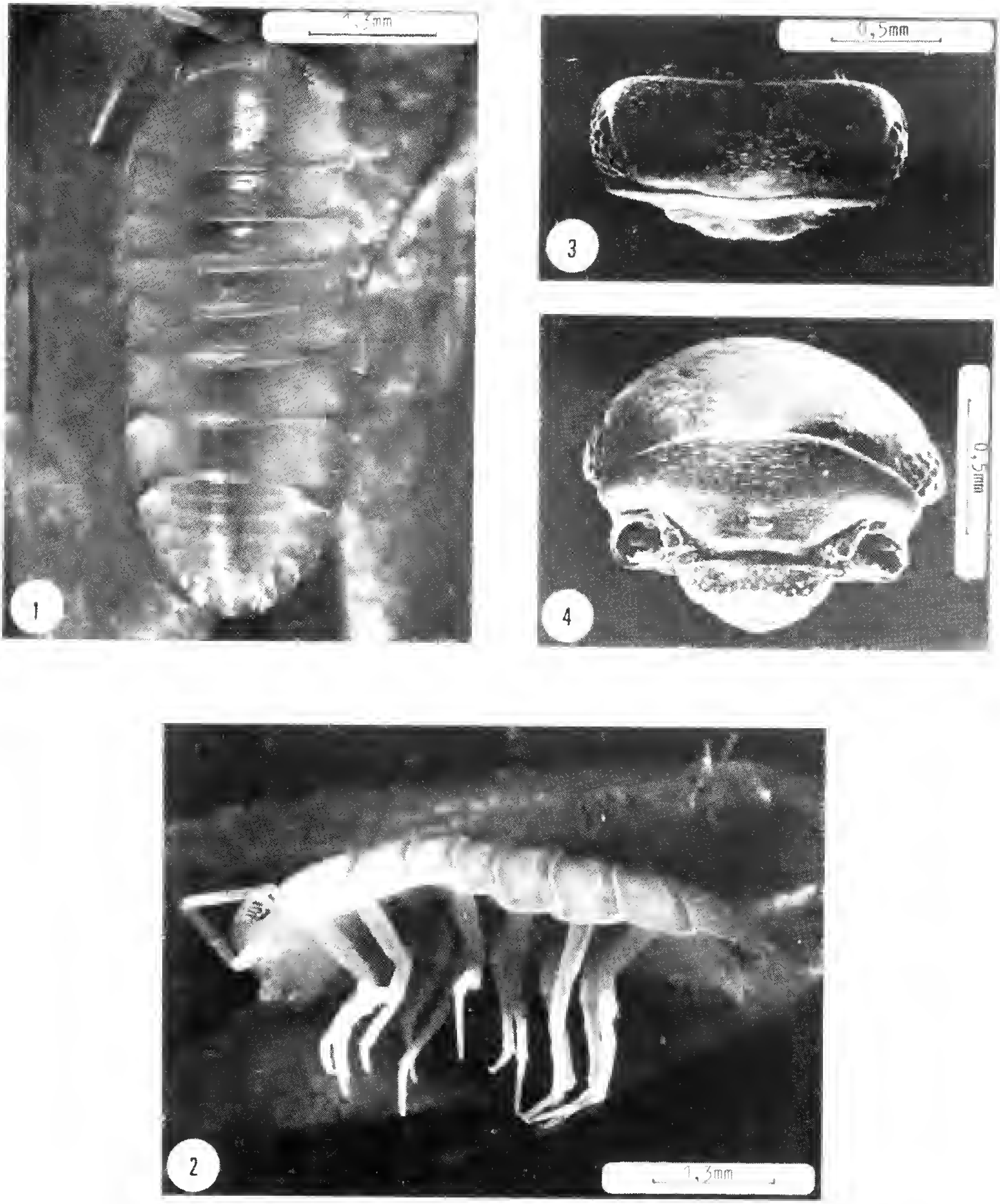
Tunnel Creek, 17°37′S, 125°09′E, Kimberley, Western Australia, dark zone on calcite extrusion; Ms J.M. Waldock, 11 August 1991, WAM 128-91, female.

Paratypes

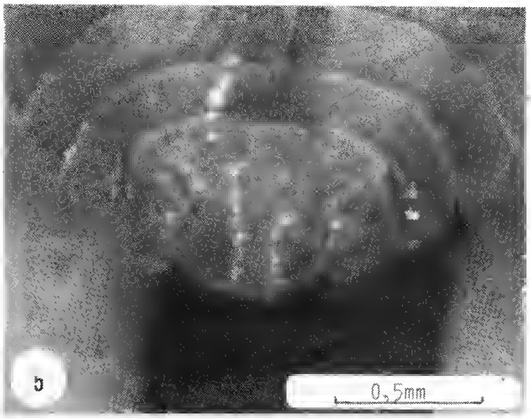
Tunnel Creek, Kimberley, Western Australia, dark zone on calcite extrusion; Ms J.M. Waldock, 11 August 1991, WAM 129-91, 1 male and WAM 130-91, 1 female, DH: 1 female.

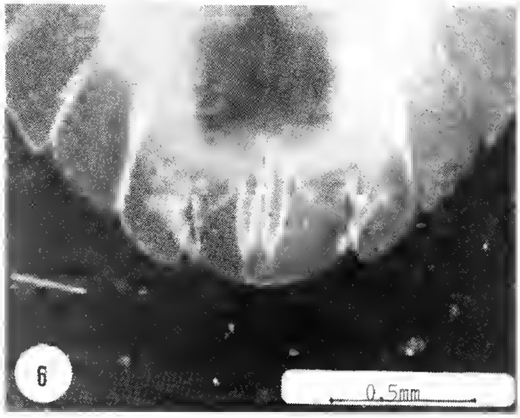
Diagnosis

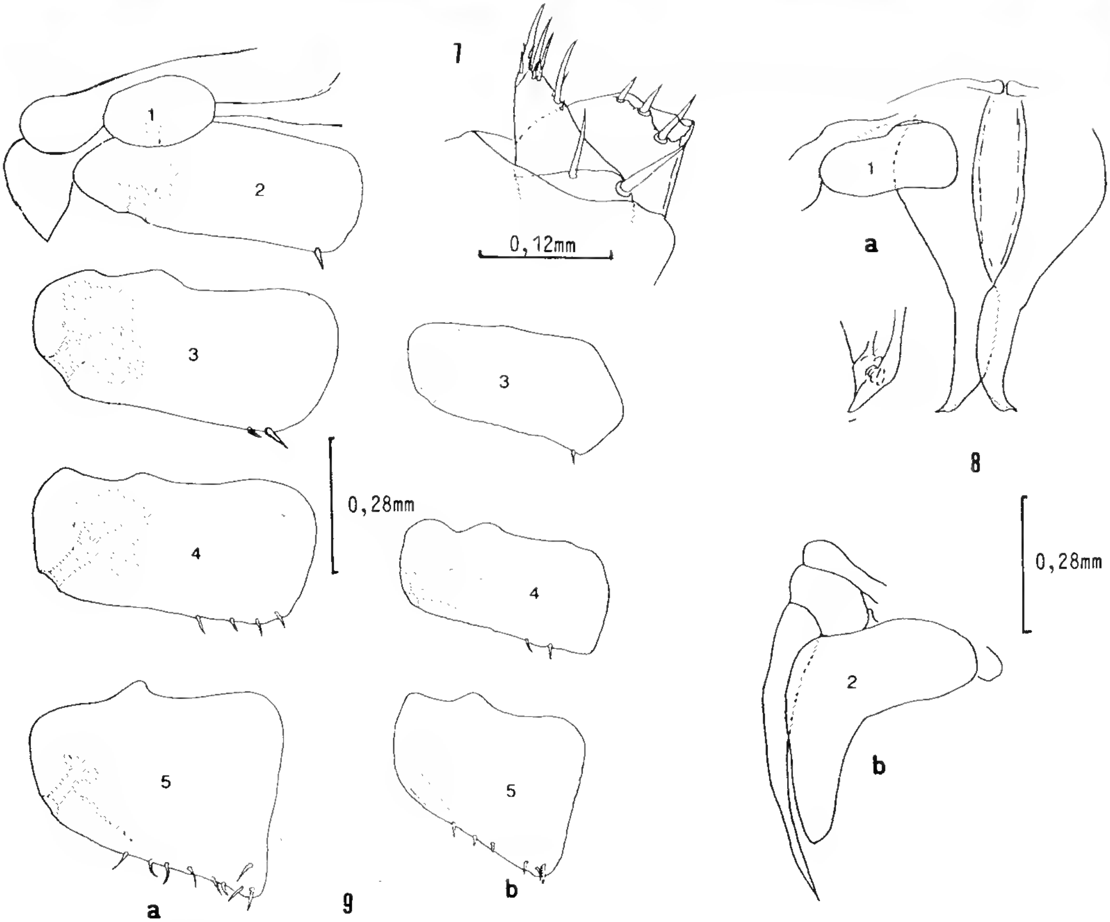
Lateral parts of posterior margin of peraeon segments sinuated but gradually less from anterior to posterior segments. Telson with apex not indented.



Figures 1-4 *Kimberleydillo waldockae* sp.nov., 1, whole animal in dorsal view; 2, whole animal in lateral view; 3, cephalon in dorsal view (S.E.M.); 4, cephalon in frontal view (S.E.M.).







Figures 5-9 *Kimberleydillo waldockae* sp. nov., 5, pleotelson in dorsal view; 6, pleotelson in ventral view; 7, right maxilliped; 8, first (8a) and second (8b) male pleopods; 9, female (9a) and male (9b) exopods of pleopods.

Description

Small, the holotype, which is the largest specimen, is 5.9 mm x 2.6 mm; the smallest, the male, is 3.8 mm x 1.5 mm. On a greyish and more or less translucent background a brown-grey network stands out clearly when magnified (x18), more dense on the posterior margin of each peraeon segment.

Black eyes each with 13 to 16 ommatidia. Frontal line uninterrupted and straight, protruding slightly above the vertex. Face smooth, slightly convex, without outline of shield. Posterior margins of peraeon segments I-II distinctly sinuated. Lateral margins of peraeon segment I thin. No interlocking structures. Lateral margins of pleon segment 5 slightly divergent. Tegument smooth. A1 3-jointed with distal article slender bearing 4 to 5 aesthetascs toward apex. A2 with 2-jointed flagellum, the distal segment being twice as long as the first. Total length of the antennae / total length of body = 0.80. Md with simple molar penicil. Mx1 with apparently only 9 teeth; penicils of the inner branch spindle-shape elongated. Peraeopods long and slender. Uropod with long exopodite. Five pairs of pseudotracheae with an invagination on every one of the pleopod exopodites. The female has the first pleopod exopodite reduced to the respiratory area; the exopodites progressively increase in size from the first to the fifth.

Distribution

Known only from the dark zone of a cave.

Derivation of name

The generic name alludes to the type locality, the epithet honours Ms J.M. Waldock, the collector.

Genus *Barrowdillo* gen.nov.

Type species

Barrowdillo pseudopyrgoniscus sp. nov., herein designated.

Diagnosis

Endoantennal conglobation. Epimera horizontal. Flagellum of antenna 2-jointed. Schisma absent on the peraeon epimeron I. Four pairs of pseudotracheae. Only four pleopod exopodites (1st-4th) are visible and interdependent among themselves. Uropod protopodite flattened and acute. Pleotelson hour-glass-shaped.

Remarks

The structure of the pleopod exopodites which are found in this genus are, among all Oniscidea, only known in the sub-family Buddelundiinae Verhoeff, 1926. Until now, this subfamily was represented only by the single genus *Buddelundia* Michaelsen, 1912. The ornamentation and, above all, the epimera extending horizontally and the absence of a schisma in peraeon epimeron I distinguish the new genus *Barrowdillo* from *Buddelundia*. The lack of a schisma, the high frontal lamina and the sharply protopodite of uropods seem to be primitive characters for an Armadillidae, but spherical conglobation, ornementation and reduction of endopodites and exopodites of uropods are synapomorphies.

Barrowdillo pseudopyrgoniscus sp.nov.

Figures 10-20

Holotype

Barrow Island, Western Australia; cave B3, 20°48′1″S, 115°21′7″E, W.F. Humphreys and B. Vine, 4 September 1991, WAM 108-91, male.

Paratypes

Barrow Island, Western Australia; cave B3, W.F. Humphreys and B. Vine, 4 September 1991, WAM 109-91, 1 female; DH, 1 female; W.F. Humphreys and B. Vine, 7 September 1991, WAM 116-91, 1 male and WAM 117-91, 1 female; cave B2, W.F. Humphreys and B. Vine, 7 September 1991, WAM 119-91 and 120-91, 2 females; DH, 1 male.

Diagnosis

Dorsum with distinct ornamentation. Lateral margins of the body parallel; spherical conglobation. Frontal lamina straight, without medial incision and raised well above the vertex. Interlocking structures on the seven peraeopod segments.

Description

Holotype specimen 9.6 mm x 4.8 mm. Dorsal surface convex but the epimera of peraeon and pleon, and the telson are splayed out horizontally. Cephalon, peraeon, pleon and pleotelson with developed tubercles arranged in alternate rows (3 on the cephalon, 3 on the protergite and 4 on metatergite of the first pereon, 3 on the next peraeon segments, 1 on pleon segments 3-5 and 3 tubercles on the pleotelson).

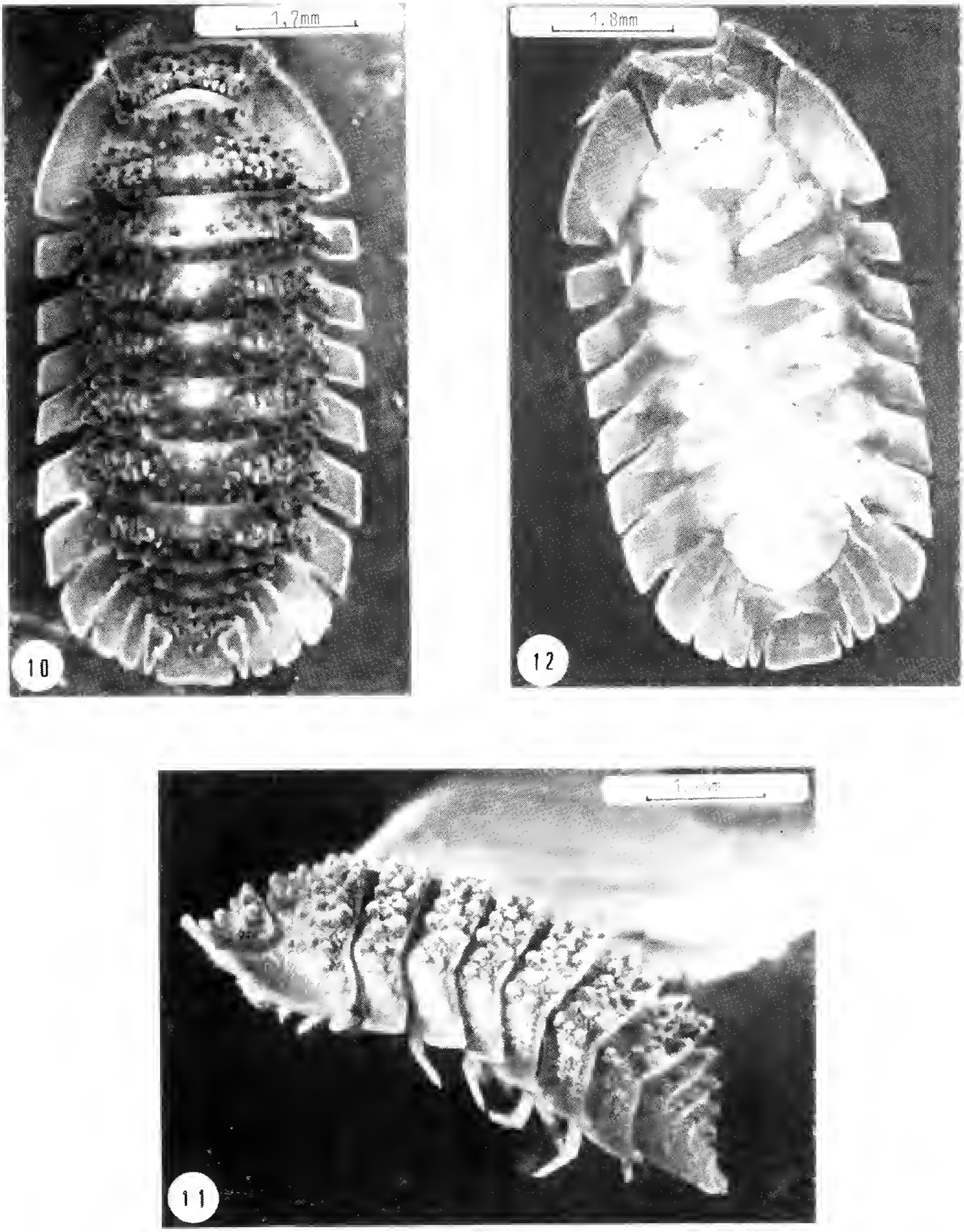
Cephalon with frontal lamina protruding above the vertex. Black and small prominent eyes each with 12-13 ommatidia, not joined. Peraeon segment I with an endolobe on the internal face of epimeron. On the same face of peraeon segment II a tooth shaped internal lobe. On third and fourth peraeon segments the interlocking structures are inconspicuous, better marked from V to VII segments, but missing on pleon segments. A1 3-jointed with 6-7 aesthetascs subapically situated. Short and stocky antenna, with 2-jointed flagellum, the distal article being three times length of the first. Mandible with simple molar penicil, and a wisp of six or seven small penicils between lamina mobilis and molar penicil. Maxillula with inner branch rounded at the apex, bearing 2 long penicils, outer branch with 4+6 teeth. Maxilliped with stout thorn on the endite. Peraeopods with reduced dactylos. Uropod with protopodite becoming sharp at the apex, with reduced endopodite and minute exopodite. Second pleopods of male with endopodites curved distally.

Distribution

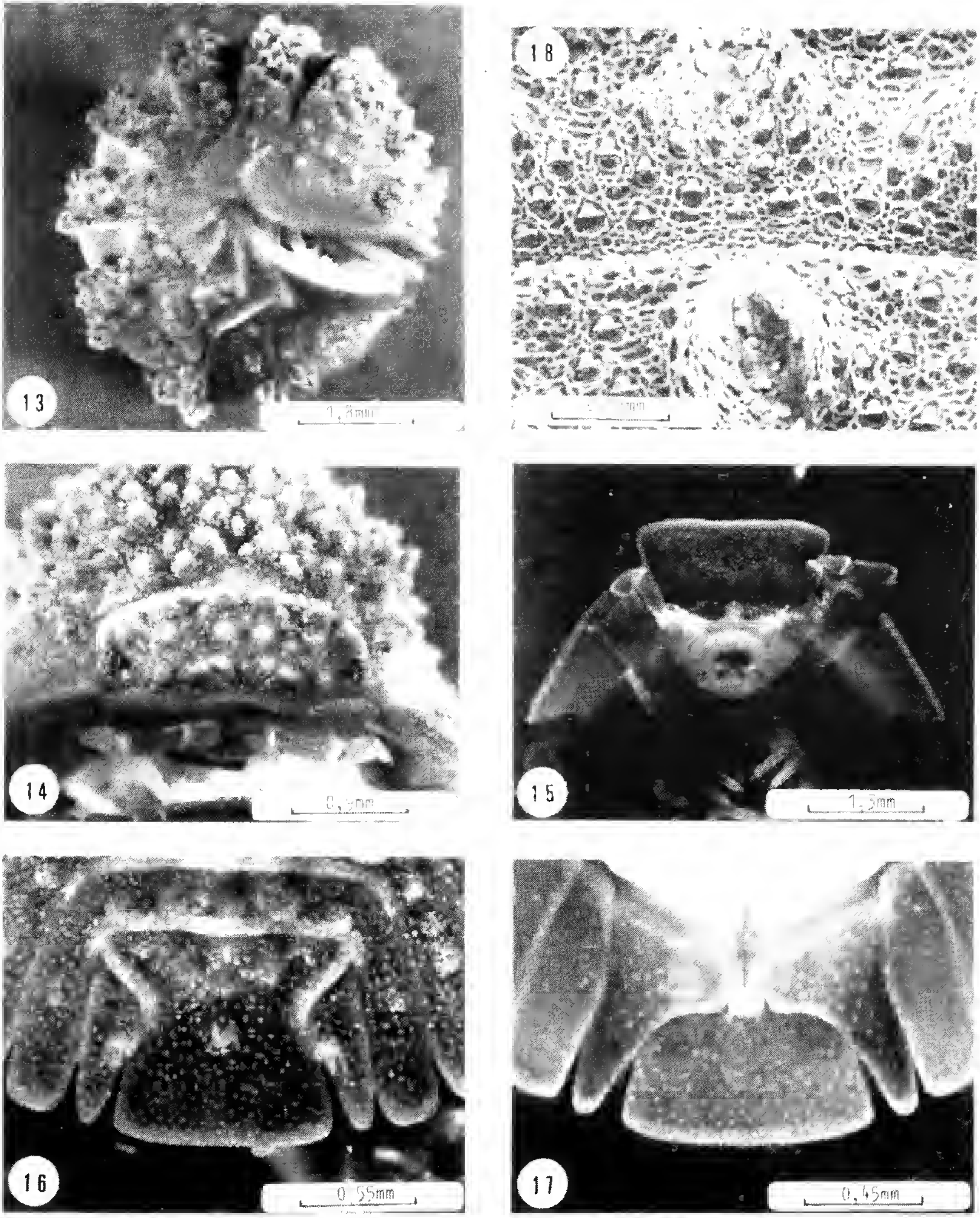
This species is known only from two caves in Barrow Island, but it is not a troglobite and probably also lives outside caves.

Derivation of name

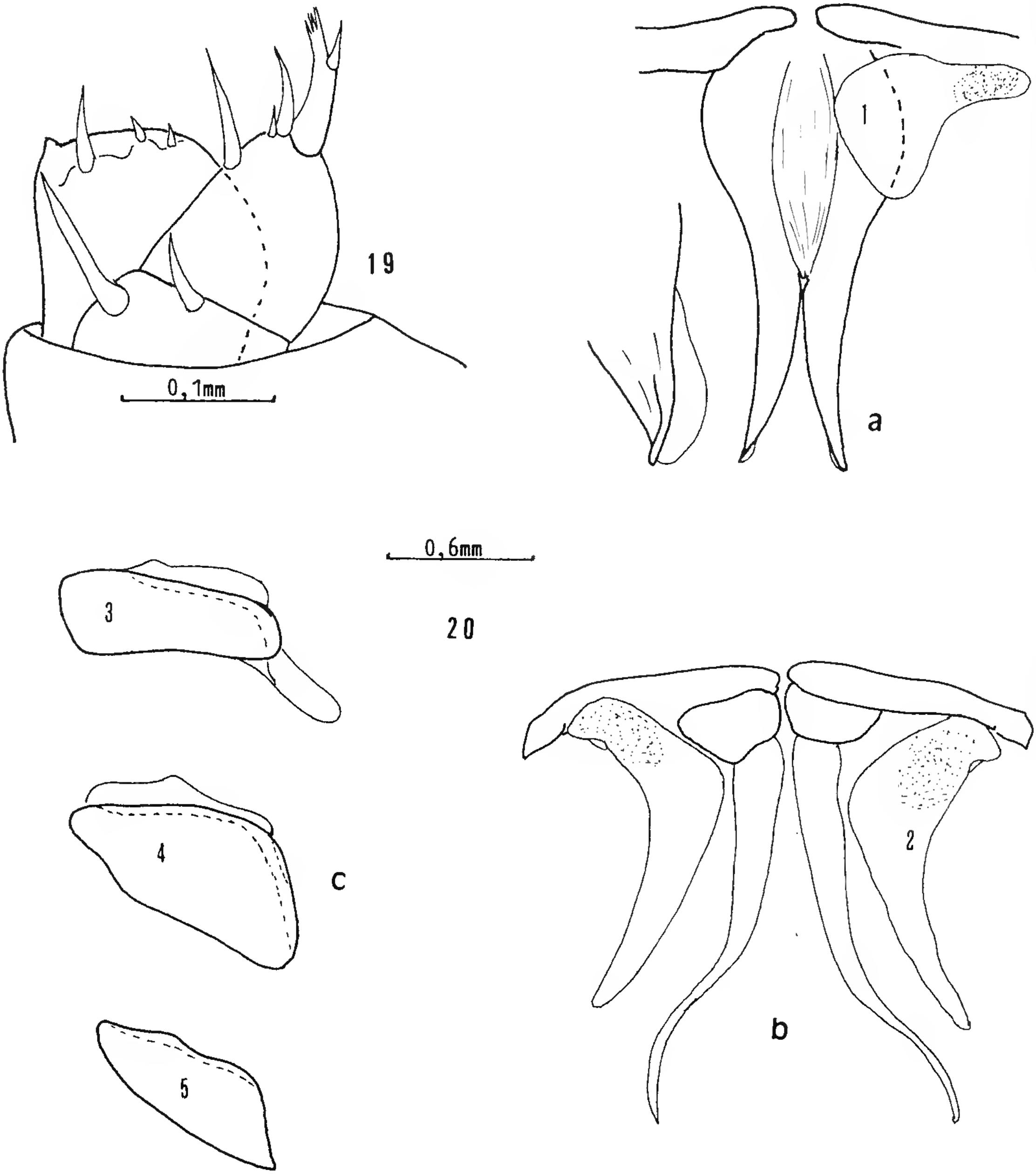
The name of the genus is derived from its place of discovery and the name of the species in an allusion to *Pyrgoniscus* which is similar in appearance.



Figures 10-12 *Barrowdillo pseudopyrgoniscus* sp.nov., 10, whole animal in dorsal view; 11, whole animal in lateral view; 12, whole animal in ventral view.



Figures 13-18 *Barrowdillo pseudopyrgoniscus* sp.nov., 13, whole animal rolled in lateral view; 14, cephalon in dorsal view; 15, cephalon in frontal view; 16, telson in dorsal view; 17, telson in ventral view; 18, dorsal tegumentary surface of the third pleonite (S.E.M.).



Figures 19-20 *Barrowdillo pseudopyrgoniscus* sp. nov., 19, left maxilliped; 20, first (20a) and second (20b) male pleopods, and exopods (20c) of third, fourth and fifth pleopods; the fifth male exopod is not visible on the whole animal, being completely covered and hidden by the fourth.

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Fish fauna of seagrass beds in south Sulawesi, Indonesia

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Abstract

The composition of the fish communities associated with two different seagrass habitats in South Sulawesi (Indonesia) was studied by making representative collections with the chemical ichthyocide rotenone. A coastal seagrass bed on an intertidal mudbank and a seagrass meadow on a shallow reef flat of a coral island had different fish communities. Both habitats were equally rich in species (26 and 27 species respectively). The coastal seagrass fish community was dominated by estuarine-dependent species, whereas reef-dependent fish species dominated in the meadow on the reef flat. Only a few species could be regarded as specific to the seagrass habitat. Potential significance of the seagrass habitats as nursery areas for fishes was indicated by the numbers of juveniles of several species, including some of economic importance.

Introduction

Seagrass beds are widely distributed in the tropical Indo-Pacific region. They often occur adjacent to coral reefs and mangrove forests. The importance of seagrass meadows as habitat for fishes and decapod crustaceans is well documented (Bell and Harmelin-Vivien 1982,1983; Blaber *et al.* 1989; Parrish 1989; Sogard and Able 1991). Several authors reported significantly higher faunal densities in seagrass beds relative to unvegetated sand or mud substrates (see review by Orth *et al.* 1984). The physical nature of the seagrass canopy is thought to play a major role, potentially influencing available shelter, food and protection from predators (Heck and Orth 1980; Leber 1985; Stoner and Lewis 1985). The importance of seagrass beds as a nursery habitat for juvenile fishes and crustaceans, including several of economic importance, is also widely acknowledged (Pollard 1984; Bell and Pollard 1989; Heck and Weinstein 1989; Chester and Thayer 1990; Orth and Van Montfrans 1990).

Little is known of the composition of the seagrass-associated fish communities in Indonesia. Hutomo and Martosewojo (1977) reported on the fishes associated with seagrass beds from Burung Island (Pari Island, Seribu Islands, Java). Martosewojo (1989) documented fish communities of reef flat, reef edge and pelagic habitats in the Flores Sea, which included several stations in seagrass beds. The present study documents the species composition of fish communities associated with two contrasting seagrass habitats in South Sulawesi, Indonesia. Some preliminary observations on habitat specificity are discussed.

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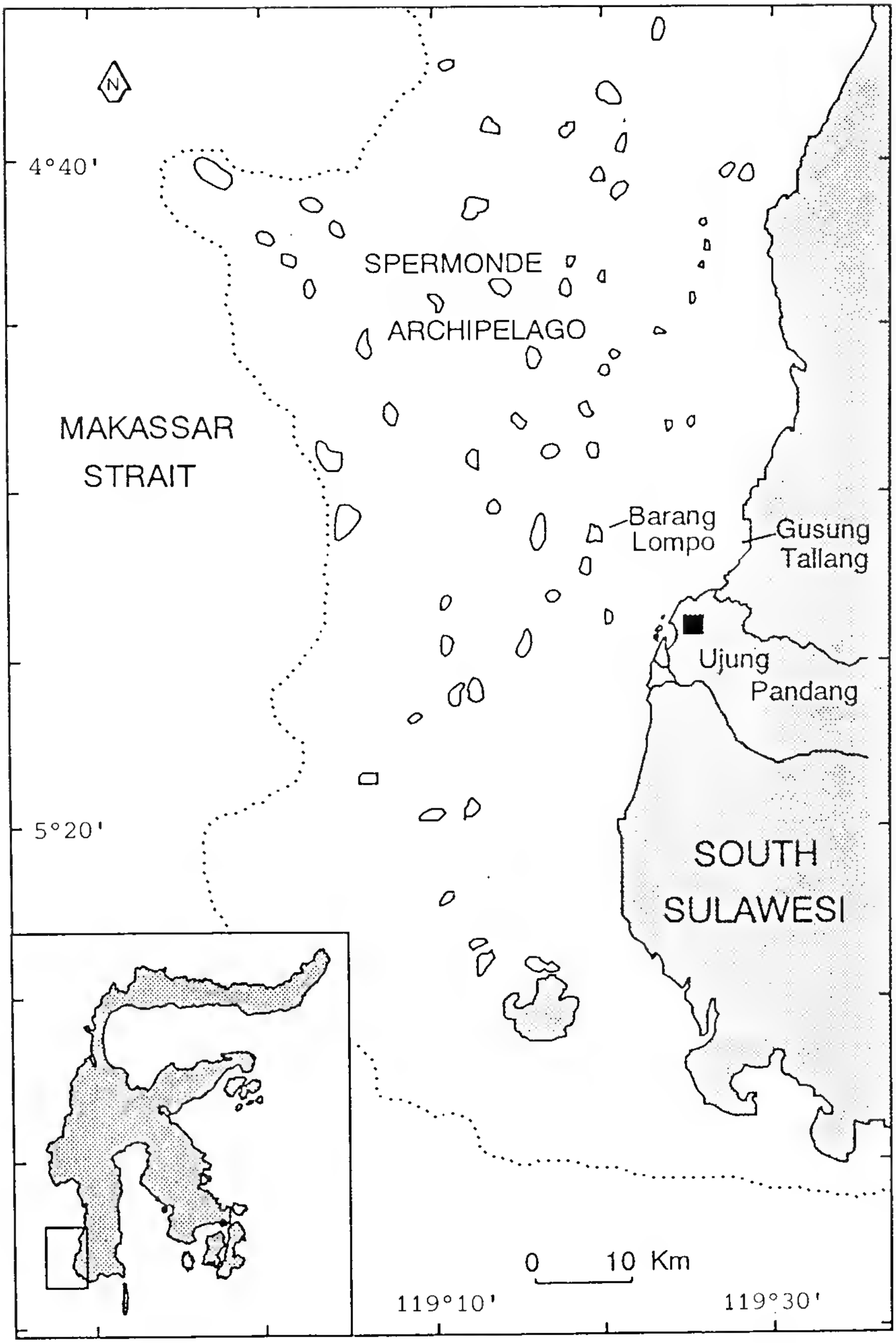

Figure 1 Map of the study area, showing the locations mentioned in the text (dotted line is approximate edge of continental shelf).

Materials and Methods

Study area

The study was undertaken at two sites in South Sulawesi, Indonesia, representing different seagrass habitats (Figure 1). These sites have been subject of a detailed study of biological and physical parameters, which will be published elsewhere (Erftemeijer, in prep.).

1. Barang Lompo (5° 03′S, 119° 20′E), a coral reef island in the Spermonde Archipelago, located c. 14 km from the coast, has an extensive shallow reef flat of approximately 100 ha covered by carbonate sands. Mixed seagrass beds dominated by *Thalassia hemprichii* and *Enhalus acoroides*, with smaller patches of *Halophila ovalis, Halodule uninervis,* and *Cymodocea rotundata,* cover over 50 ha of this reef flat. Several blow-outs and open sand areas occur in these beds. Isolated sea anemones and small coral patches are also scattered over the reef flat. Rich coral growth, however, is limited to the reef edge and slopes. The water at this site has a very low turbidity, and is characteristic in composition to that of tropical oceanic waters.

2. Gusung Tallang (5° 04′S, 119° 27′E) is an intertidal area along the South Sulawesi west coast, located c. 0.5 km north of the mouth of the Tallo River. The substrate is dominated by sandy mud, protected from waves and currents by a long and narrow sandbar in the north, running perpendicular to the coast. On this muddy sand, a monospecific seagrass meadow occurs of *Enhalus acoroides*, covering an estimated 40 ha. This area is bordered by a narrow strip of mangrove forest backed by extensive brackish water fishponds. The water at Gusung Tallang is characterized by a high concentration of phytoplankton and suspended organic material, resulting in poor visibility.

Methods

Representative collections were made of the fish communities in the seagrass beds at each locality, by utilizing the chemical ichthyocide rotenone. Approximately 0.5-0.8 kg of powder was used for each station, which was conducted during neap low tide (minimal current velocity). The effective sample area was about 50 x 50 m, to some extent affected by wind-driven currents. Stunned fishes were collected with small handnets. Special effort was made to pick up all specimens to obtain data on relative abundance of the different species. Fishes were preserved in 10% seawater formalin. Most species were identified by the second author (G.R. Allen) at the Western Australian Museum. Certain problematical gobiids were identified by Helen K. Larson (Northern Territory Museum, Darwin). Identification was aided by photographs taken of specimens while fresh. All material was deposited at the Western Australian Museum, Perth (WAM). Data on habitat specificity are largely based on the long experience in ichthyological surveys in this region by the second author (G.R. Allen).

Table 1 List of fishes collected in seagrass beds. Phylogenetic order of families follows the classification of Nelson (1984) with slight modification. (BL = Barang Lompo, 31-I-1992; GT = Gusung Tallang, 13-VIII-1991). Figures refer to the total number of specimens in the sample. Species marked with an x were often observed in the seagrass beds while snorkeling, but did not occur in the samples.

Family and species name	BL	GT
Ophichthidae		
Muraenichthys macropterus Bleeker, 1857	-	7
Ophichthus apicalis (Bennett, 1830)	-	1
Clupeidae		
Spratelloides delicatulus (Bennett, 1831)	3	-
Spratelloides gracilis (Temminck and Schlegel, 1846)	>100	-
Engraulididae		
Stolephorus sp.	-	9
Plotosidae		
Plotosus canius Hamilton, 1822	-	7
Plotosus lineatus (Thunberg, 1787)	-	9
Synodontidae		
Saurida gracilis (Quoy and Gaimard, 1824)	1	-
Hemiramphidae		
Hyporhamphus dussumieri (Valenciennes, 1846)	2	-
Athcrinidae		
Hypoatherina sp.	-	8
Syngnathidae		
Microphis brachyurus (Bleeker, 1853)	-	4
Syngnathid sp.	-	1
Scorpaenidae		
Dendrochirus zebra (Cuvier, 1929)	2	-
Paracentropogon leucoprosopon (Bleeker, 1856)	-	1
Platycephalidae		
Platycephalus isacanthus (Cuvicr, 1829)	-	5
Chandidae		
Ambassis nalua (Hamilton, 1822)	-	>50
Serranidae		
Centrogenys vaigiensis (Quoy and Gaimard, 1824)	2	-
Epinephelus coioides (Hamilton, 1922)	-	1
Pseudochromidae		
Pseudochromis fuscus Müller and Troschel, 1849	1	-
Terapontidae		
Pelates quadrilineatus (Bloch, 1760)	-	13
Apogonidae		
Apogon melas Bleeker, 1848	3	-
Cheilodipterus quinquelineatus Cuvier, 1828	3	-
Foa brachygramma (Jenkins, 1902)	-	3
Sillaginidae		
Sillago sihama (Forsskål, 1775)	-	2

Table 1 (cont.)

Family and species name	BL	GT
Leiognathidae		
Leiognathus brevirostris (?) (Valenciennes, 1835)	-	1
Gerreidae		
Gerres filamentosus Cuvier, 1829	-	3
Nemipteridae		
Pentapodus trivittatus (Cuvier, 1830)	5	-
Pomacentridae		
Amphiprion ocellaris Cuvier, 1830	1	-
Dischistodus chrysopoecilus (Schlegel and Müller, 1839)	2	-
Dischistodus perspicillatus (Cuvier, 1930)	3	-
Pomacentrus tripunctatus Cuvier, 1830	2	-
Labridae		
Cheilinus chlorurus (Bloch, 1791)	2	-
Cheilio inermis (Forsskål, 1775)	x	-
Halichoeres chloropterus (Bloch, 1791)	3	-
Novaculichthys macrolepidotus (Bloch, 1791)	2	-
Blenniidae		
Petroscirtes variabilis Cantor, 1850	x	-
Eleotrididae		
Butis amboinensis (Bleeker, 1853)	-	13
Gobiidae		
Acentrogobius caninus (Valenciennes, 1837)	-	4
Amblyeleotris sp.	x	-
Amblygobius bynoensis (Richardson, 1844)	4	-
Cryptocentrus sp.	x	-
Drombus sp.	-	11
Glossogobius biocellatus (Valenciennes, 1837)	-	5
Myersina macrostoma Herre, 1931	-	1
Valenciennea sexguttata (Valenciennes, 1837)	1	-
Siganidae		
Siganus canaliculatus (Park, 1797)	1	-
Siganus javus (Linnaeus, 1766)	-	20
Siganus virgatus (Valenciennes, 1835)	1	-
Bothidae		
Pseudorhombus neglectus Bleeker, 1866	-	1
Cynoglossidae		
Cynoglossus kopsi (?) (Bleeker, 1851)	-	11
Monocanthidae		
Acreichthys tomentosus (Linnaeus, 1758)	2	-
Tetraodontidae		
Arothron manilensis (de Proce, 1822)	-	11
Arothron mappa (Lesson, 1830)	1	-
Total number of species:	27	26

Results

A total of 49 fish species were collected in seagrass beds in South Sulawesi. Visual observations (snorkeling) added 4 additional species to the list at Barang Lompo (reef flat), which were considered to be characteristic of the seagrass beds at this site, but which did not occur in the samples. No species was common to both habitats (Table 1). The total number of species was nearly equal at the two sites (27 and 26 species respectively).

Of the fishes collected during this survey, only a few can be regarded as typical for seagrass habitats. The majority of fishes collected at Gusung Tallang are species known to be characteristic of estuarine habitats and brackish waters. With exception of the cardinalfish *Foa brachygramma* (a species typical of sheltered places in seagrass beds such as underneath logs or in empty shells), none of the species found in the seagrass beds at this site are confined to this habitat.

At least three species collected in the seagrass beds at Barang Lompo may be considered typical of this habitat and are rarely encountered in other habitats, i.e. the leatherjacket *Acreichthys tomentosus*, the green weed wrasse *Novaculichthys macrolepidotus* (also found in meadows of the weed *Sargassum*), and the false scorpionfish *Centrogenys vaigiensis* (preferably with some hard substratum around). Some other species that were collected at this site are typical weed species (not necessarily seagrass), including the green-spotted wrasse *Halichoeres chloropterus* and the cigar wrasse *Cheilio inermis* (not in samples, but frequently observed while snorkeling).

The majority of the fishes collected at Barang Lompo are species characteristic of the reef flat environment (regardless of the presence of seagrasses), notably the yellow-banded threadfin bream *Pentapodus trivittatus*, the white-patch damsel *Dischistodus chrysopoecilus*, the three-spot damsel *Pomacentrus tripunctatus*, and the tropical garfish *Hyporhamphus dussumieri*. Others are confined to sandy environments (not necessarily reefflats), such as the striped catfish *Plotosus lineatus*, the six-spot goby *Valenciennea sexguttata*, the byno goby *Amblygobius bynoensis*, white damsel *Dischistodus perspicillatus*, the slender grinner *Saurida gracilis* and shrimp gobies (*Amblyeleotris* sp. and *Cryptocentrus* sp.). In addition, the false clownfish *Amphiprion ocellaris* is the only anemonefish that occurs in shallow seagrass beds, in association with its host anemone *Stichodactyla gigantea*; however these species also occur in deeper waters (Allen 1980). The remaining fishes collected at this location are typical reef species that occasionally visit the seagrass beds, or species that occur in a wide range of habitats.

Some of the species collected (or observed) in the seagrass meadows at Barang Lompo, display camouflage colour patterns clearly adapted to seagrass (or weeds in general): *Acreichthys tomentosus*, *Novaculichthys macrolepidotus*, *Halichoeres chloropterus*, *Cheilio inermis* (green initial phase), and *Petroscirtes variabilis*.

Shrimp gobies were abundant in seagrass beds at Barang Lompo, but were not retrieved in the samples. Visual observations indicated that at least two genera were represented (*Cryptocentrus* and *Amblyeleotris*) but no positive identifications were made to species level. These gobies live in symbiosis with burrowing alpheid shrimps *Alpheus* spp. (Karplus 1987). Withdrawal in the burrows during sampling probably explains their absence in the rotenone collections. Their density at this site was estimated at 4-5 individuals per m^2 (visual observations).

The majority (15 species) of fish individuals collected at Gusung Tallang were juveniles or subadults. Species of which more than 10 juveniles occurred in the samples, included *Butis amboinensis*, *Siganus javus*, *Pelates quadrilineatus*, *Arothron manilensis*, and *Stolephorus* sp.. At Barang Lompo, a much smaller proportion (6 species) of the total catch consisted of juveniles. They included *Arothron mappa*, *Plotosus lineatus*, *Cheilinus chlorurus*, *Apogon melas*, *Spratelloides delicatulus*, and *S. gracilis*. With the exception of the two species of clupeids (*Spratelloides* species), which occur in a variety of shallow-water habitats, these are typical reef species.

Visual observations and sampling data indicate that siganids (rabbitfishes) are among the most dominant fishes utilizing the seagrass habitat. Rabbitfishes are economically important food fishes in many parts of Indonesia (Polunin 1983). They are herbivores that generally occur in shallow waters, usually encountered in pairs or small schools (Woodland 1990). We have observed them to forage on seagrass leaves with attached epiphytes.

Discussion

The present study identified 53 species associated with seagrass habitats in South Sulawesi. They belonged to 29 different families, which included 8 of 10 families reported as dominant in Australian seagrass beds (Pollard 1984).

The two contrasting seagrass habitats investigated had no single fish species in common. The seagrass associated fish community at the coastal site (Gusung Tallang) was dominated by estuarine and brackish water fish species, practically none of which are considered specific to the seagrass habitat. The fish community of the seagrass meadows at the coral island Barang Lompo consisted mainly of species characteristic of coral reef environments, a few of which can be regarded as specific for the seagrass beds.

Although only a few fish species are typically confined to seagrass meadows, this habitat is important to many others by providing shelter and food resources. The majority of the fishes collected at Gusung Tallang and a substantial proportion of those caught at Barang Lompo were juveniles, which might indicate that the beds were being used as a nursery habitat. Some of these species are of economic importance as food fishes, notably the siganids, clupeids and engraulids (Polunin 1983). The utilization of seagrass beds as nursery grounds appears to be based on their provision of both adequate shelter from predators and an abundant food source, particularly in the form of small epibenthic crustaceans (Pollard 1984; Parrish 1989). Hutomo and Martosewojo (1977) collected 78 fish species associated with seagrass beds at Pari Islands (Java) by repeatedly using a beach seine-net, and reported on some seasonal variations in their abundance. They noted a community composition similar to that recorded in the present study, with cardinalfishes, wrasses, siganids, monocle-breams, silver-biddies and leatherjackets among the dominant groups.

Hutchins (1990 a,b) collected 56 fish species in seagrass beds at Shark Bay (Western Australia, 25°-27°S, 113°-114°E) by box-trawling. He found no significant differences in species composition of the fish community between *Amphibolis* and *Posidonia* meadows in the same area. Both Hutchins (1990 a,b) and Hutomo and Martosewojo (1977) found evidence of utilization of seagrass beds by fishes as a nursery ground. Although the sampling methodology differed between these two surveys and also from the present study, the results are well comparable. Future sampling with different techniques might reveal additional species, notably when carried out during different months of the year and also during the night. Several fish species are known to migrate between reefs and seagrass beds for nocturnal foraging or shelter (Parrish 1989). .Recent work by Black *et al.* (1990), who performed beach seining in intertidal *Amphibolis* seagrass beds in Shark Bay, indicated significant differences in species diversity and abundance of fishes between seagrass beds and adjacent sand flats, between day and night, and between February (winter) and June (summer).

In accordance with available literature, our data confirm that the fish communities of seagrass meadows mainly consist of 'estuarine-dependent' fishes in coastal areas and of 'reef-dependent' fishes at coral islands. Seagrass vegetation rarely functions as a specific habitat type to which certain fishes are restricted, but it may greatly increase the habitat variability in these systems. One of the most important functions of seagrass beds in relation to fishes, is their role as a nursery area (Pollard 1984). The meadows may intercept large numbers of recruits that apparently profit from the abundant food supply and the shelter from predators.

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A new *Amegilla* (Hymenoptera: Anthophoridae) from Western Australia

Robert W. Brooks*

Abstract

Amegilla paracalva sp. nov. is described here in response to studies of Houston (1991). It belongs to the subgenus *Asaropoda* which is endemic to the Australian region (not Tasmania or New Zealand). Descriptive morphology follows that of Brooks (1988).

Amegilla (Asaropoda) paracalva sp. nov.

Figures 1-6

Holotype

Male: *Western Australia,* 16 km WSW of Lyons River Homestead, (24°38'S, 115°20'E), 30 August-1 September 1980, C.A. Howard and T.F. Houston collection numbers 344-27, reared from brood cell. Became adult 5 September 1983. Western Australian Museum Collection (WAMC) 90/879.

Paratypes

Allotype with same data but collection number 344-14/ex: nest burrow in breakaway hollow, WAMC 90/880; 2 female paratypes with same data except first specimen with collection number 344-27, ex: nest in clay flat, WAMC 91/179 and second reared from cell taken from ground nest, pupated prior to 12 October 1981, adult by 6 November 1981, WAMC 91/180. Holotype, allotype and one paratype at the Western Australian Museum, Perth and one paratype at the Snow Entomological Museum, Lawrence, Kansas.

Diagnosis

Body covered with buff to light orange hair; integumental facial marks cream-coloured (Figures 1,2); male genitalia and metasomal stema as Figures 3-6.

Amegilla (Asaropoda) paracalva sp. nov. can be separated from *A. calva* and *A. preissi* in that it has white to cream-coloured integumental facial marks while those of the latter two are lemon yellow. Also in male *A. paracalva* the apicomedian emargination of S5 is much wider than deep, the base of the emargination is rounded the sides being at a 90° angle and S6 is apicomedially emarginate. S5 of *A. calva* and *A. preissi* has an apicomedian emargination about as wide as deep, emargination basally angulate not rounded with the sides about 60° and S6 is apically simple to very slightly emarginate. *A. calva* and *A. preissi* are restricted to New South Wales and Queensland, *A. paracalva* to Western Australia.

Description

Male (holotype)

Body length about 15 mm; forewing length about 10 mm. Inner orbits parallel; shortest distance between eyes 0.83 frontal length of eye; head wider than long; clypeal

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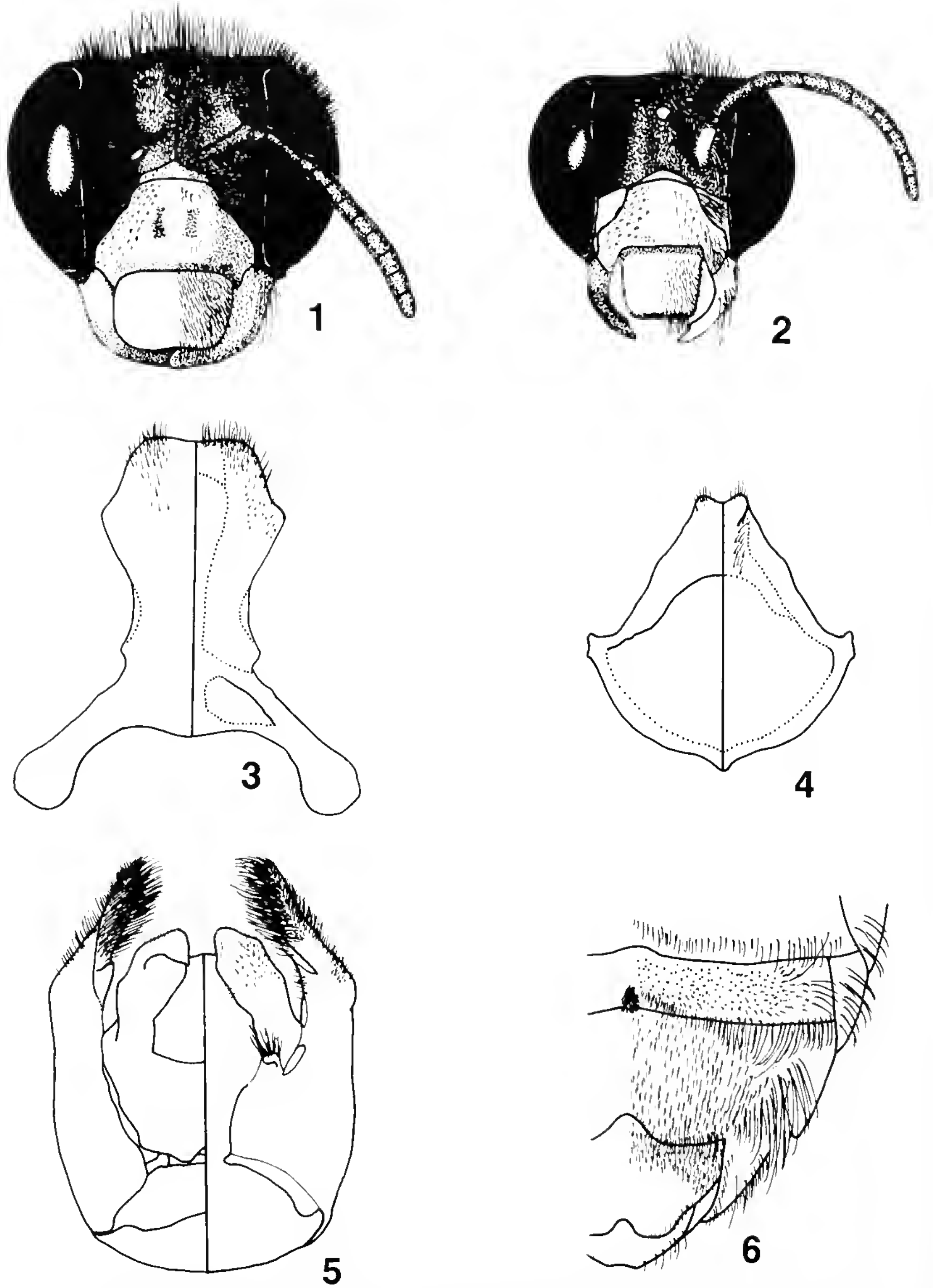

Figures 1-6 *Amegilla paracalva* sp. nov.; 1, female face; 2, male face; 3-5, male S7, S8 and genital capsule, left side is dorsal, right is ventral; 6, male S5-7, ventral view.

protuberance in profile 0.67 eye width; mandible with weak subapical tooth; flagellomere 1 equal to combined lengths of next 1.5 flagellomeres and 0.68 as long as scape (excluding basal bulb); flagellomere 2 equal to 0.77 length of flagellomere 3; flagellomeres 3-10 gradually increasing in length; last flagellomere subequal to length of flagellomere 1; distance between posterior ocelli 1.1 occllocular distance; distance from median ocellus to posterior ocellus equal to 0.68 ocellocular distance. Marginal cell length equal to 0.82 distance from apex of cell to wing tip; cu-v of hind wing about equal to length of second abcissa of M+Cu; jugal lobe about half as long as vannal lobe. S5 and S6 with narrow apicomedian cmargination (Figure 6); S7, S8 and genital capsule as in Figures 3-5.

Pubescence. Head with pale buff hair, lighter on lower half; scutum with light orange-brown and scattered black hairs; metanotum and scutellum with light orange-brown hair, rest of thorax with pale hair; foreleg with pale hair on outer surface, dark orange-brown hair on inner surfaces of tibia and tarsus; midtibia pale with mixture of dark and pale hair on tarsus and all dark on innter tarsal surface; hindleg pale only on outer surface of femur and tibia, rest dark. Metasomal terga with appressed orange-brown hair that is lighter and longer laterally but with a few dark hairs laterally on T6 and dark dense pile apicolaterally on T7; S1-5 with pale apical fringes which are longer laterally; S4 with apicomedian patch of black apically directed bristles (Figure 6); S6 with basal band of pale hair.

Colouration. Black except integumental facial marks, mandibular base, labrum, clypeus, paraocular and supraclypeal areas and anterior portion of scape cream coloured as in Figure 2; apical half of mandible, maxilla, glossa, tegula, legs, apices of metasomal sterna and terga reddish-brown.

Punctation. Punctures on clypeus 0.5-1.0 puncture-widths apart, rather dull basally to shiny apically; rest of punctation typical of *Amegilla.*

Female

Body length 16 mm, forewing length 13 mm. Agrees with description of male except for sex-limited characters including facial marks (Figure 1) and as follows: flagellomere 1 equal to combined length of next 2.7 flagellomeres, about as long as scape (excluding basal bulb) and 1.7 as long as last flagellomere; distance between posterior ocelli about equal to ocellocular distance, from median to posterior ocellus 0.64 ocellocular distance.

Pubescence. Outer posterior surface of foretarsus with long curved dark hairs; inner surface of midleg with dark hair; anterior and posterior surfaces of midfemur pale; outer surface of midtibia pale with dark band on apicoposterior surface; midtarsus with scattered white hairs on anterior surface and white posterior band; inner surfaces of hindleg black, out surfaces white except anterior edge of tarsus black; metasomal terga with scattered inclined dark hairs, T5 with apicomedian tuft of dark hair; T6 all black; metasomal sterna with long dark hairs medially, pale hairs laterally.

Remarks

Amegilla paracalva sp. nov. is most closely related to *Amegilla calva* (Rayment) and *A. preissi* (Cockerell). Among *Asaropoda* these three species are uniquely characterized by hair pale to gray evenly covering thoracic and metasomal areas; midtibial spur strongly hooked apically and S6 of female simple without U-shaped carina delimiting median area.

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Guide to Authors

Subject Matter:

Reviews, observations and results of research into all branches of natural science and human studies will be considered for publication. However, emphasis is placed on studies pertaining to Western Australia. Full length papers should not normally exceed 30 typed pages. Short communications should not normally exceed three typed pages and this category of paper is intended to accommodate observations, results or new records of *significance*, that otherwise might not get into the literature, or for which there is a particular urgency for publication. All material must be original and not have been published elsewhere.

Presentation:

Authors are advised to follow the layout and style in the most recent issue of the *Rec. West. Aust. Mus.* including headings, tables, illustrations and references.

The title should be concise, informative and contain key words necessary for retrieval by modern searching techniques. Names of new taxa must not be included. An abridged title (not exceeding 50 letter spaces) should be included for use as a running head..

An abstract must be given in full length papers but not short communications, summarizing the scope of the work and principal findings. It should normally not exceed 2% of the paper and should be suitable for reprinting in reference periodicals. Contrary to Recommendation 23 of the International Code of Zoological Nomenclature it may include names of new taxa.

Footnotes are to be avoided, except in papers dealing with historical subjects.

The International System of units should be used.

Numbers should be spelled out from one to nine in descriptive text; figures used for 10 or more. For associated groups, figures should be used consistently, e.g. 5 to 10, not five to 10.

Spelling should follow the *Concise Oxford Dictionary*.

Systematic papers must conform with the International Code of Botanical and Zoological Nomenclature and, as far as possible, with their recommendations.

Synonymies should be given in the short form (taxon, author, date, page) and the full reference cited at the end of the paper.

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The original and two copies of manuscripts and figures should be submitted to the Editorial Committee, c/-Publications Department, Western Australian Museum, Francis Street, Perth, Western Australia 6000. They must be in double-spaced typescript on A4 sheets. All margins should be at least 30 mm wide. Tables plus headings and legends to illustrations should be typed on separate pages. The desired position for insertion of tables and illustrations in the text should be indicated in pencil. Tables should be numbered consecutively, have headings which make them understandable without reference to the text, and be referred to in the text.

High quality illustrations are required to size (13.5 cm x 18 cm) or no larger than 32 cm x 40 cm with sans serif lettering suitable for reduction to size. Photographs must be good quality black and white prints, 13 cm x 18 cm (5 inches x 7 inches). If scale line and lettering are required on photographs *do not* place directly on to print. They should be positioned on a clear paper or film overlay. Scale must be indicated on illustrations. All maps, line drawings, photographs and graphs, should be numbered in sequence and referred to as Figure/s in the text and captions. Each must have a brief, fully explanatory caption. On acceptance an IBM compatible disk containing all corrections should be sent with amended manuscript. The disk should be marked with programme (e.g. Wordperfect, Windows, etc) and exact catchline used.

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Papers and short communications are reviewed by at least two referees and acceptance or rejection is then decided by an editorial committee.

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The senior author will receive fifty free offprints of the paper. Additional offprints can be ordered at page proof stage.

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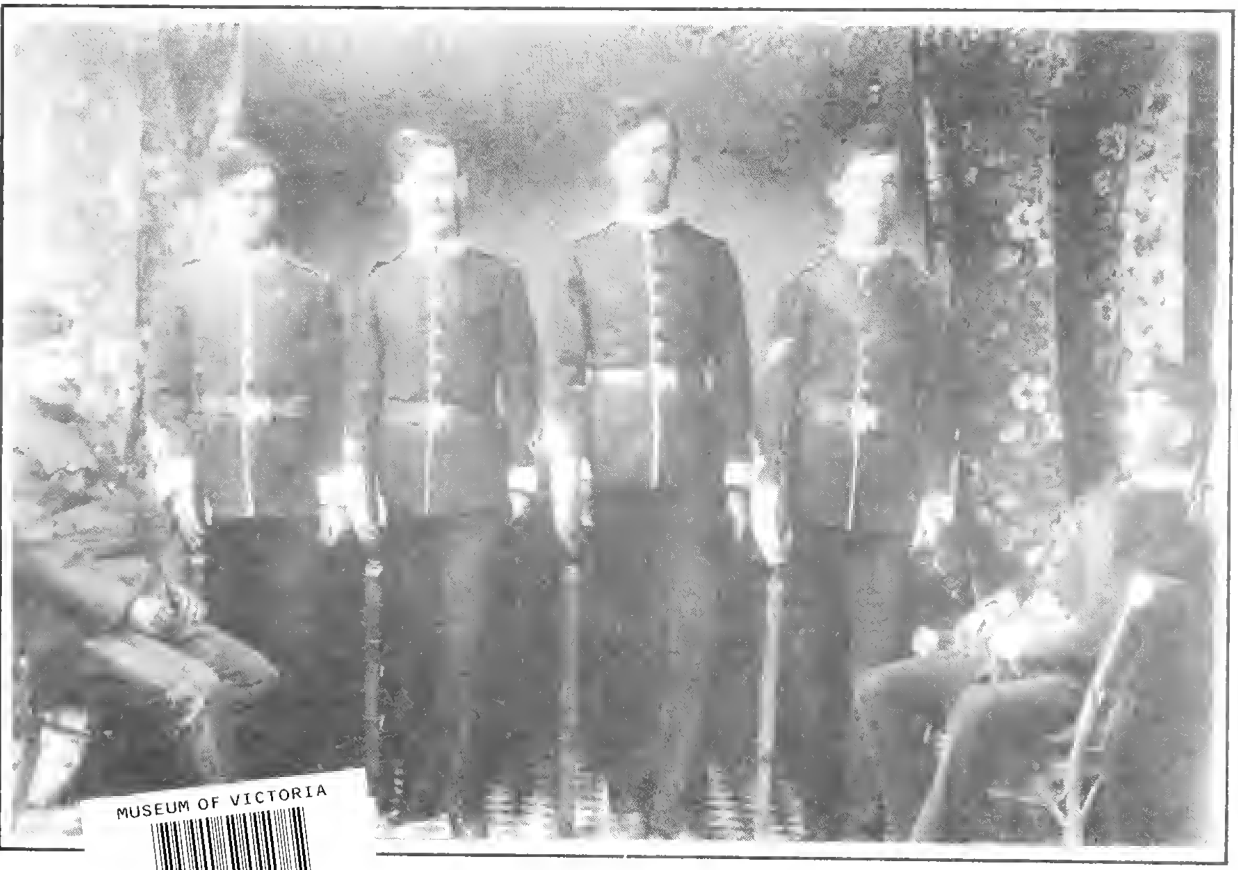

RECORDS of the Western Australian Museum

Volume 16, Part 3.
1993

Editors:
Kenneth J. McNamara
Mark S. Harvey

Cover: Four members of the Geraldton Rifle Volunteers armed with the Martini-Enfield Rifle Mark I Modified, W.A. Pattern and the Pattern 1888 Sword Bayonet. (Courtesy of the Geraldton Historical Society. Battye Library 2302B.)

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THE MARTINI-ENFIELD RIFLE IN WESTERN AUSTRALIA

PART I

The Western Australian Pattern Martini-Enfield

George B. Trotter*

ABSTRACT

Three distinct groups of .303 inch Martini-Enfield rifles are located and described. They are identified as being fitted with a nose cap which allows the fixing of the Pattern 1888 Sword Bayonet, rather than the usual Pattern 1895 Socket Bayonet. They are thought to be unique among Martini-Enfield variants issued in Australia. The rifles are tentativety named as follows. Group one, M-E Mark I Modified, W.A. Pattern, Group two, M-E Mark II Modified, W.A. Pattern and Group three, Unofficial Conversion M-E Mark I, Modified, W.A. Pattern.

INTRODUCTION

The Martini-Henry rifle, after trials began in 1871, became the principal arm of the British Army from 1874-1889. It was a large, robust breech loading single shot rifle taking a .450 inch black powder cartridge. The Martini-Henry was made in six Marks.[1] The first three, Mk I (1871-76), Mk II (1877-79) and Mk III (1879-89), were issued in the Australian colonies. Due to experimentation and improvements in ammunition, a new "small bore" cartridge of .303 inch was perfected in 1888 and adopted for use in the new Lee-Metford bolt action magazine repeating rifle approved for issue to the British Army in that year. This new cartridge still utilized black powder as the propellant. At this time a new bayonet was also approved, it was for the new Lee-Metford rifle and was designated the Pattern 1888 sword bayonet.

British arms establishments immediately geared up for the production of this new arm and ammunition. It was soon found that it would be advantageous to convert the single shot Martini-Henry to use the same cartridge as the new magazine rifle also, as it would be some time before sufficient quantities of the new magazine rifles could be produced to entirely re-equip the Army. These conversions would be produced in sufficient numbers to arm the British colonies and territories overseas and the various volunteer units at home, until they too could be issued with the new arm.

The first conversions of Martini-Henrys to the new cartridge were the Mk V (one only) and Mk VI in 1889, which in 1891, following British Military nomenclature practice, were designated the Martini-Metford Mk I and II. (The body of the rifle was designed by F. von Martini and the barrel for the new .303 inch cartridge was designed by W.E. Metford, hence the name Martini-Metford).

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[1] Temple, B.A. and Skennerton, I.D. "Treatise on the British Military Martini", Vol 1 (1983) Vol 2 (1989). Privately Published, Qld. These volumes are recommended as an exhaustive reference on the history of the Martini rifles. Please refer to them for technical details and dates of rifles mentioned in the introduction. Reference is made to these volumes again in this paper.

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The Martini-Metford Mk I was fitted with a two piece nose cap/bayonet boss designed by John Rigby. This nose cap was identical to the new Lee-Metford magazine rifle nose cap and took the new Pattern 1888 sword bayonet thereby providing a cheaper standby arm that utilized the standard British service cartridge and bayonet. It was at this time, 1891-92, that a new smokeless propellant, cordite, was developed, and the new .303 inch cartridge was immediately adapted to utilize the new product, necessitating a change in the sighting of the rifle. Western Australia in 1893 ordered a quantity of arms similar to the Martini-Metfords Mark I, but the W.A. order stipulated sighting for black powder. Because of minor changes specified by the W.A. Government and the fact that these rifles were new-made rather than conversions they were designated Martini-Metford Rifle Mk I Modified (W.A. Pattern).

Soon after the advent of the cordite propellent it was discovered that the higher pressures and hotter gases quickly eroded the throat of the cartridge chamber, which rendered the barrel inaccurate and shortened barrel life. To remedy this problem, a new improved rifling was designed in 1895 at the Royal Small Arms Factory (RSAF) at Enfield. Subsequently, the new conversions of Martinis to utilise the .303 inch cordite cartridge were fitted with Enfield barrels and were designated Martini-Enfields Mk I and II in rifle form and Mk I, II and III in carbine form. It is the Martini-Enfield Rifles Mk I and II, modified for W.A. which are the subject of this study.

Abbreviations which may be found in the text are as follows:

M-E = Martini-Enfield; M-H = Martini-Henry; Mk = Mark; ML-E = Magazine Lee-Enfield; Pat. '88 = Pattern 1888; RSAF = Royal Small Arms Factories.

NOTE: The various firearms described in this paper belong to private collections in Western Australia and the eastern states except for one M-E Mk I, (W.A.1043D), which is from the W.A. Army Museum collection, item 082.90

THE .303 MARTINI-ENFIELD RIFLE MARKS I & II SEALED PATTERN

The Royal Small Arms Factory (RSAF) at Enfield, following established practice, would, once a rifle had been developed, tested and determined to be capable of fulfilling the purpose to which it was intended to be put, was "sealed". That is, the perfected prototype was literally labelled and sealed with red sealing wax and kept in the Pattern Room at Enfield as the pattern to govern all subsequent production of that arm. The Martini-Enfield Rifles Mk I (M-E I) and Mk II (M-E II)

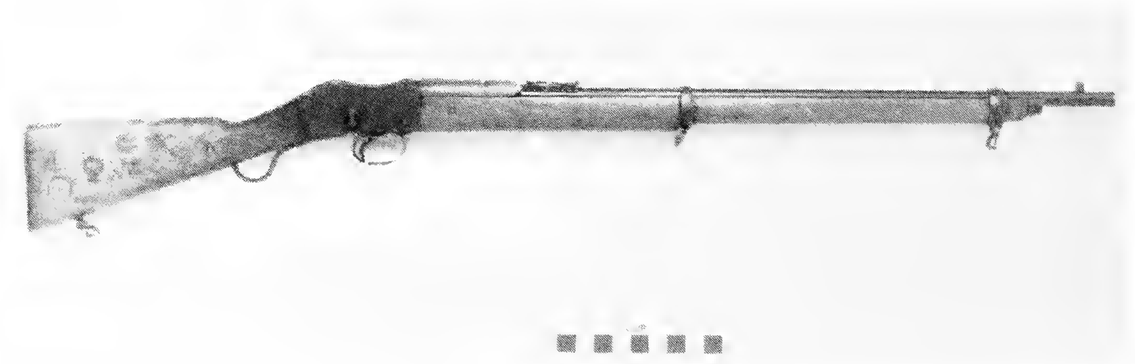

Figure 1 Sealed Pattern .303 inch Martini-Enfield Rifle Mark II. Except for the differences noted in the introduction, this is essentially the same rifle as the Mark I. It is illustrated to show the nose cap, the major difference between the Sealed Pattern and the Modified W.A. Pattern (Figure 3) (Photo D. Elford, W.A.M.)

(Figure 1) were sealed in this way. The salient features of these two arms which were converted from the Martini-Henry Rifle Mk III (M-H III) and Mk II (M-H II) respectively are as follows, and indicate the changes made to the original M-H II and M-H III parts.

Essentially, an existing M-H III was taken from a rack (some were made from new components) and converted to a M-E I by alterations to the following parts of the original arm.

Barrel:	three inches (75mm) shorter and slimmer in profile.
Upper Band:	(at muzzle), had the bayonet bar ground off and had the barrel arch reduced in diameter to fit the new slimmer barrel by having a sleeve brazed into place.
Breech Block:	a new breech face block was dovetailed into place. This new breech face had a smaller diameter firing pin hole and a finer firing pin point.
Body:	was reduced in height at the breech, to facilitate the lower sights required for the new cartridge. This height reduction is 2 mm.
Butt:	was stamped with the respective Mark number, I or II in Roman numerals, and fitted with a brass marking disc.
Clearing Rod:	of a new approved pattern was fitted in the existing slot under the fore-end.
Fore-end Wood:	was shortened, re-profiled for the upper band and had a thin wooden liner glued into the original barrel channel to accept the new slimmer barrel.
Nose Cap:	already quite small, was reduced even more and re-profiled to fit the new barrel.
Sling Swivel:	was removed from the upper band and replaced with a piling swivel. The sling swivel was relocated to the lower band. The trigger guard sling swivel was removed and a new swivel installed on the butt.
Bayonet:	the bayonet intended for this arm was the Pattern 1895 triangular socket bayonet (most of them converted from the Pattern 1876 M-H Rifle bayonet).
Sights:	were graduated to 1800 yards for Cordite ammunition.

The difference between the M-E I and the M-E II depended on which original M-H rifle was chosen as the basis of conversion. The difference between the two Marks was that the M-E I had its fore-end held firmly into the body of the rifle by a metal hook, inletted into the underside of the wooden fore-end, which engaged a socket in the front of the body. It also had a small cocking indicator (the tear drop shaped protrusion on the right side of the body). The M-E I nock's form (the large diameter section of the barrel nearest the body which contained the firing chamber), was about 10 mm shorter than the M-E II. The M-E II differed from the previously mentioned M-E I in that the fore-end was attached by a steel pin which entered the side of the fore-end near the body and penetrated a hole in a lug projecting from the underside of the barrel. The ends of the steel pin can be seen from either side of the rifle. The cocking indicator is also considerably larger than that of the M-E I. The nock's form of the M-E II is about 10 mm longer than the M-E I. Both Marks are fitted with a wooden handguard secured by a spring clip which covers the nock's form of the barrel. The respective fore-ends will not interchange. The M-E I was approved on 4 October 1895 and introduced on 1 February 1896, a total of 48,610 were converted until production ceased in 1903. The M-E II was approved on 11 February 1896 and introduced on 1 April 1896, a total of 40,023 were converted including 7,000 by a private contractor. The year of conversion is stamped on the left side of the body (Figure 2) while the original date of manufacture of the Martini-Henry remains on the right side. The left hand side mark "M.E. 303/I" or "II" will confirm the external features of the particular Mark of rifle. In the case of the modified variant produced for

Figure 2 The Martini-Enfield Mark I conversion details found on the left side of the body. The royal cypher of Queen Victoria, the place and date of conversion, the steel batch mark and the Mark, in this case Martini-Enfield .303 inch Mark I. Note also the various proof and armourer's marks and the twin opposing broad arrows denoting sale or surplus. (Photo D. Elford, W.A.M.)

W.A., the author has adopted the term Modified W.A. Pattern. Strictly speaking they are not a Pattern, but a modification of the Sealed Pattern, but to differentiate this W.A. type from all other variants the term W.A. Pattern has been used.

THE MARTINI-ENFIELDS, W.A. PATTERN

The first specimen of the M-E Modified, W.A. pattern, was noted by the author in 1985, it was a Mark I. This specimen (Figure 3) conformed in all respects to the Sealed Pattern of M-E I (See Figure1) as illustrated in *A Treatise on the British Military Martini* except in one very important feature. The nose cap (Figure 4) of the specimen was the newer Rigby one piece nose cap/bayonet boss now used on the Magazine Lee-Enfield repeating rifle introduced in 1895. As the Magazine Lee-Enfield rifle took the Pattern 1888 sword bayonet, it was therefore obvious that this Martini-Enfield Mark I was also fitted to take the Pattern 1888 bayonet. The butt had been stamped WA/40/D indicating W.A. ownership. It being a solitary specimen with no reference information being available at the time it was impossible to determine whether the arm was "correct". An identical rifle was seen illustrated in a Cobb & Co. militaria catalogue of the late 1980's[2], but as no details were retained in the Cobb & Co records concerning this arm, no comparison could be made. Although encouraging, the Cobb & Co. illustration provided no additional information other than

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[2] Cobb & Co. Pty. Ltd. Catalogue. Surrey Hills, Victoria (n.d.) p.30.

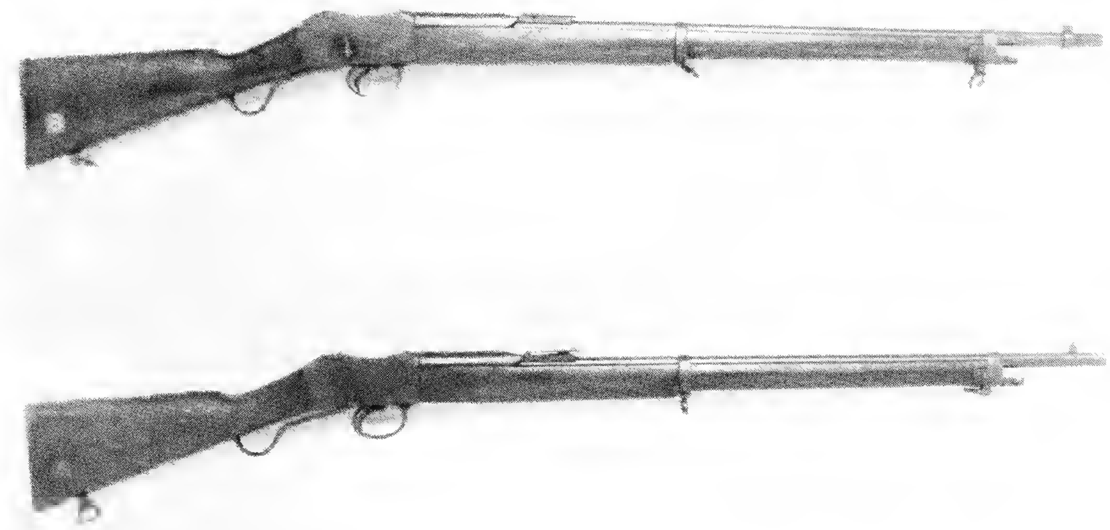

Figure 3 Martini-Enfield Rifles Mark I Modified, W.A. Pattern. The upper rifle is WA/40/D and the lower is WA/1043/D. Note the Rigby pattern nose cap/bayonet boss, which is the feature of the W.A. Pattern. The fore sight of the upper rifle has been lost and replaced by a bush blacksmith. (Photo D.Elford, W.A.M.)

confirmation that WA/40/D was not an isolated specimen. The specimen was therefore merely noted for future attention.

In 1991, Mr Malcolm Higham, a volunteer worker, reported an unusual M-E I in the W.A. Army Museum collection. This new specimen also had the nose cap to take the Pattern 1888 bayonet and the butt was stamped WA/1043/D. On comparing this butt marking with WA/40/D it was found that the same letter and numeral stamps had been used to mark both rifles (Figure 5). Both rifles conformed to each other in all conversion respects, even to the inspection stamps in the fore-end barrel channel and most importantly, the "J.A." inspection stamp stamped into the end of the fore-end wood under the nose cap (Figure 6), confirming that these two rifles had been converted and inspected by the same armoury and subsequently marked in W.A. at the same time and place. With uniformity such as this it seemed apparent that these rifles could be part of a group of rifles issued to W.A. Defence Force members and which were until now unknown to Australian collectors and arms researchers. It was at this time that Volume II of *A Treatise on British Military Martinis* was published and which provided the first information regarding this *modified* version of the M-E I Sealed Pattern.[3] The two specimens conformed to the description of the modified M-E I given in the *Treatise* and it was further stated that in 1898 RSAF Enfield, where these specimens were made, sent 200 M-E I rifles modified to take the Pattern 1888 bayonet to W.A. The *Treatise* however, did not publish a photograph of the M-E I Modified, as no specimens had ever been found. A photograph of a representative specimen made by the private British gun trade was substituted in *Treatise* instead. In one significant feature however the two specimens differed from the published details, which were taken from the RSAF Enfield production records and quoted in

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[3] *Ibid* pp. 417-419.

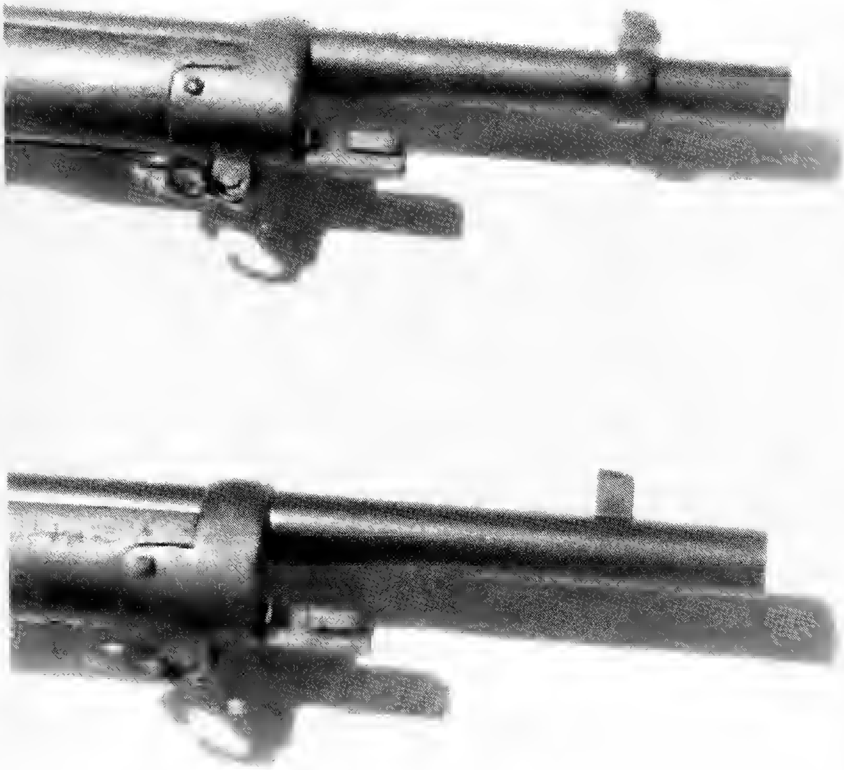

Figure 4 Detail of the nose cap/bayonet boss of the W.A. Pattern Mk I. It is this feature, a modification of the Sealed Pattern which makes the W.A. Pattern unique. The nose cap is also found on the early versions of the Lee magazine rifle. (Photo R. Stein)

Treatise. The RSAF records showed that the 200 M-E rifles sent to W.A. in 1898 had been sighted to 1600 yards for black powder. These two specimens are sighted to 1800 yards for cordite. The barrels are dated 1909 indicating that they are later replacements. Had they still retained their original barrels they would have been dated the same year as the conversion, 1896 and 1895 respectively.

A survey was undertaken to see if any additional specimens could be located in Australia. This was achieved by the publishing of two short illustrated articles by Mr. Higham seeking data on these WA marked arms in the *Journal of the W.A. Rifle Association*, September 1991 and the Australia-wide circulation *Australian Shooters Journal*, February 1992. Over the following weeks approximately thirty replies were received and passed on to the author, resulting in a total of five Martini-Enfields of the modified pattern being confirmed. At this point an anomaly arose, two of the five specimens were identified as M-E Mark II Modified, a Mark not mentioned at all in the *Treatise*. Although the Mk I and II are both Modified W.A. Pattern they differ from each other in the usual details of Mark as described in the introduction. In addition, a further two M-E Mark I rifles, unofficially converted, were located in Perth, making a total of seven specimens of M-E rifles, divided by their conversion characteristics into three distinct groups.

The details of the three M-E groups will now be described, beginning with the Mark I.

Figure 5 Butt markings of WA/1043/D, (Bottom) include the Enfield roundel, the Mark I and Class 1 marks and the surplus mark. The various cancelled marks and numbers are those of the original Martini-Henry from which this Martini-Enfield was converted. WA/40/D is the well worn butt at top. Close examination of these two specimens revealed that the letter and numeral punches used to mark them for W.A. service are identical (Photo R. Stein).

Table 1 Marks, numbers and pertinent features of the M-E I.

Butt Marks	Place/Date of Conversion	Serial Number	Barrel Number & Date	Provision for Clearing Rod in Nose Cap?	Nose Cap Insp. Stamp	Bayonet Type
WA/40/D	Enfield 1896	D 7261	B6460 1909	Yes	J.A.	Pat. '88
WA/ 1043/D	Enfield 1895	D 6321	B7379 1909	Yes	J.A.	Pat. '88
WAA/7	Enfield 1896	D 273	?3154 1910	Yes	J.A.	Pat. '88

Figure 6 The J.A. inspection mark which is found on many Sealed Pattern Martini-Enfield fore-end woods and on the W.A. Pattern Martini-Enfields examined. This mark confirms that both types of arms originated at RSAF Enfield. (Photo D. Elford, W.A.M.)

GROUP ONE: THE .303 INCH MARTINI-ENFIELD RIFLE MARK I MODIFIED, W.A. PATTERN

The discovery of the first two M-E Mark I specimens was supplemented by the confirmation of a third M-E Mark I as a result of the survey articles. The technical details of the three and their W.A. markings reinforced the possibility that these rifles were indeed part of a unique group of W.A. arms.

An inspection of the fore-end wood under the nose-cap on a number of "control" Sealed Pattern M-Es bearing Eastern States ownership marks, revealed that several of them also had the J.A. inspection stamp. This mark confirmed that the nose-cap modification was an official RSAF Enfield modification and eliminated the possibility that the specimens of Martini-Enfield Mk I and II located could have been modified locally. The nose caps, inspection markings, conversion characteristics and dates which appear on these three specimens conform to the known features of the RSAF modified conversions produced for W.A. in 1898.

These rifles conform to the description of how those sent to W.A. in 1898 should appear, except for the replacement cordite sighted barrels.

GROUP TWO: THE .303 INCH MARTINI-ENFIELD RIFLE MARK II MODIFIED, W.A. PATTERN

As already stated, the arms survey located two Martini-Enfield Mk II Modified with W.A. marks (Figure 7) and in addition a 1911 photograph of another (Figure 10). No record of the manufacture or shipment of these arms exists at RSAF Enfield, therefore, officially they do not exist. No

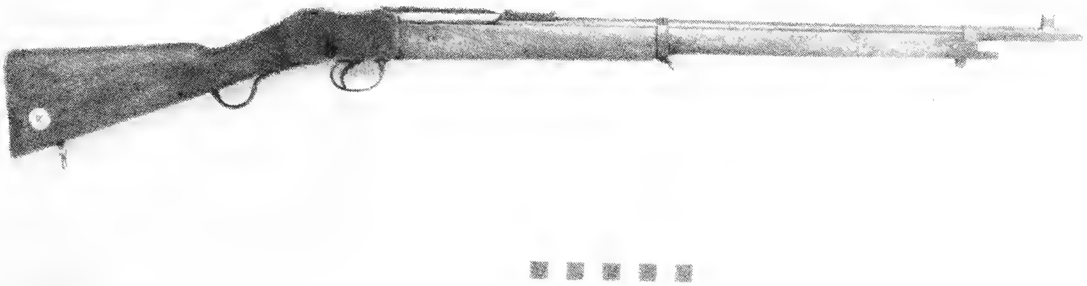

Figure 7 Martini-Enfield Rifle Mark II Modified, W.A. Pattern. The larger cocking indicator and fore-end attachment pin, which distinguishes this rifle from the Mark I are apparent. The spring steel fore sight protector is still present on this arm, while the piling swivel is missing from the nose cap. This arm is WA/34. (Photo D. Elford, W.A.M.)

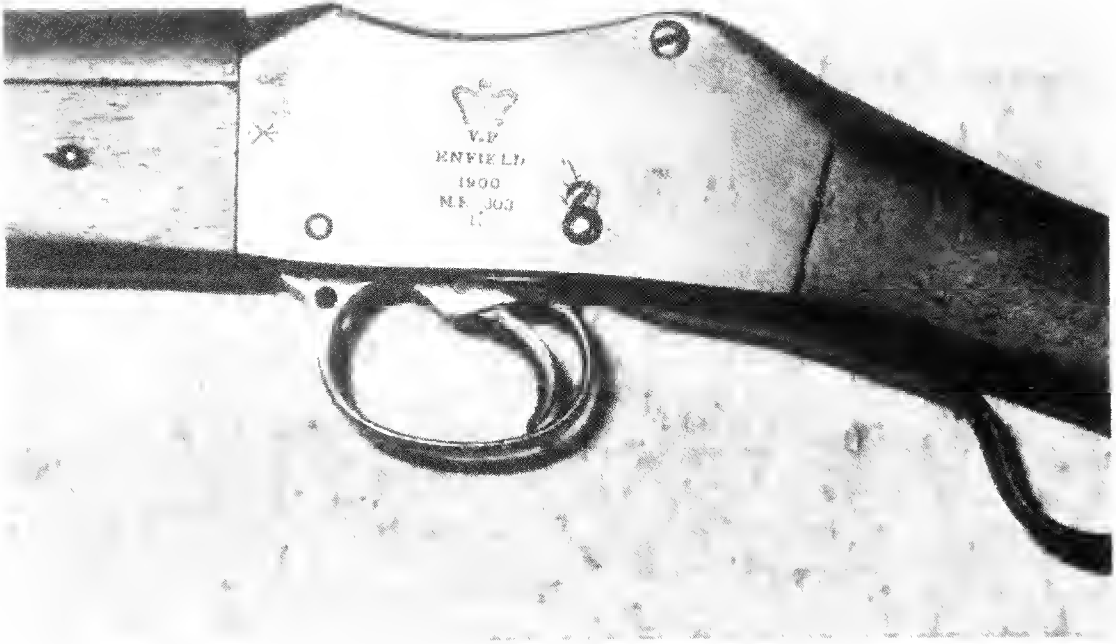

Figure 8 The conversion side of the W.A. Pattern Mark II. (Photo R. Stein)

Figure 9 Butt markings of the Mark II. W.A. is punched with different, larger letter punches which have also been noted on another Mark I W.A. Pattern butt. The Enfield roundel, Mark II stamp and surplus marks are also evident. (Photo R. Stein)

documentary evidence other than a contemporary photograph has been located which specifically refers to this Mark of M-E. The 1911 photograph and the arms themselves prove their contemporary existence in W.A. and their survival to the present, but confirmation of how they came into official W.A. hands and the archival proof of their conversion at Enfield is as yet undiscovered. A strong case is put in Part II however which tentatively identifies their origin and acquisition and can be taken to be, in the absence of that confirmation, the most probable explanation for their existence here.

Table 2 Marks, numbers and pertinent features of the M-E II.

Butt Marks	Place & Date of Manufacture	Serial Number	BarrelNumber & Date	Provisionfor clearing rod?	Nose Cap Insp. mark	Bayonet Type
WA 34	Enfield 1900	B4384	4384B1900	No	J.A.	Pat.'88
WA2(3?)	Enfield1900	A5424	5424B1900	No	E	Pat.'88
WA 750D	Contemporary Photograph taken in 1911			No		Pat.'88

The table shows that the major difference between these Mark IIs and the Mark Is previously discussed, apart from the Mark differences outlined in the introduction, is the absence of the bored-through clearing rod hole in the nose cap/bayonet boss. Clearing rods, originally provided for all .303 arms were found to be unnecessary and in May 1899 were declared obsolete.[4] Consequently these M-E IIs do not have the nose cap/bayonet boss bored through to accept a clearing rod. This

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[4] *Ibid.* Temple & Skennerton p 423.

Figure 10 This 1911 photograph depicts Patrol Leader A. Foster (age 14) who has just received his marksman's badge, earned with a Martini-Enfield Mark II Modified W.A. Pattern. Close examination of the butt in the original photograph reveals the markings WA/750/D, the Enfield roundel and the Mark II stamps. The butt also bears the surplus stamp. This butt marking conforms exactly to the Mark I numerical sequence of fig. 5 and appears to be struck with the same letter and numeral stamp. (Photo D. Elford from the collection of P. Hodgson)

type of nose cap is the correct one for the 1900 date of these rifles. The rifles also retain their original 1900 dated cordite sighted barrels. These specimens and the one in the photograph of 1911 (Figure 10) conform to what the modified version of a normal Sealed Pattern M-E II would look like if they existed. It is thought that this is a previously unrecorded variant of the Martini-Enfield group of rifles and as such is of considerable importance in the sphere of Martini military arms. The JA stamp on WA/34 and the use of the same letter and numeral stamp to mark WA/750/D (of the 1911 photograph) as were used to mark two of the 1898 order of Mark Is, establishes a common link between the two groups of specimens in terms of their common RSAF Enfield origin and their common W.A. issue.

GROUP THREE: THE UNOFFICIAL MARTINI-ENFIELD MARK I MODIFIED, W.A. PATTERN

Two M-E Is which were not official RSAF Enfield conversions were located by the survey. In addition a separate fore-end, complete with nose cap was also located. These two specimens are conversions of the .450 inch Martini-Henry Mark III to Martini-Enfield Mark I Modified, W.A. Pattern.

Table 3 Pertinent features of the Unofficial conversions of Martini-Henrys Mark III to Martini-Enfield Mk I Modified, W.A. Pattern.

ButtMarks	Placc/Date of Conversion	Original Date/Maker	BarrelNumber and Date	Clearing Rod Hole	Nose Cap Insp. Mark	Nose Cap Type	Bayonet Type
WADF 521	None	1885 BSA & M Co	5747 B'08, '09	Yes	Nil	Rigby Metford	P.'88
WADF 529	None	1885 BSA & M Co	V68295'14	Yes	Nil	Rigby Metford	P.'88
-	-	Fore-end only		Yes	Nil	Rigby Metford	P.'88

Except for the differing barrel dates, these two arms conform to each other in all respects. They have had the breech block face dovetailed and replaced with one with a smaller firing pin hole and a finer firing pin, also the "hump" at the breech on the front of the body has been reduced 2 mm in height as for an official RSAF conversion. The fore-end has the glued barrel liner to facilitate the slimmer barrel and bears Enfield inspection marks in the liner but does not have the "J.A." inspection stamp on the end of the wood under the nose cap. These arms (and the solitary fore-end) conform to the official Enfield RSAF converted Martini-Enfield Mark I Modified W.A. Pattern in all their features and dimensions, except in two important ways. They bear no conversion details or date on the left side of the body and the two-piece Rigby nose cap/bayonet boss is the earlier Martini-Metford type mentioned in the introduction, and which requires different machine profiling of the wooden fore-end tip. These two M-Es therefore do not conform in these two points to the specific characteristics of the Enfield converted specimen M-E Is and IIs. What is instantly recognisable however is that these arms in fact constitute a third distinct group or sub-group of W.A. marked W.A. Pattern arms.

CONCLUSION

It can be seen from the reference in the "A Treatise on the British Military Martini" detailing the 1898 production of this type of arm for W.A. that the first of these three groups of the WA Pattern variant (the Mark Is) are undoubtedly linked to that production. The second group (the Mark IIs) are, although not recorded in the *Treatise*, definitely linked by markings to both RSAF

Figure 11 Unofficial conversion of a W.A. marked Martini-Henry Mark III into a Martini-Enfield Mark I Modified, W.A. Pattern. The muzzle has been shortened at a later date and the rear sight replaced on this specimen. The nose cap is of the earlier bulky two piece Rigby pattern usually found fitted to Martini-Metfords and Lee-Metfords. The middle band and sling swivels are missing. The left hand conversion side of the body is unmarked on these arms. (Photo D. Elford, W.A.M.)

Figure 12 Butt markings of the Unofficial Conversion Martini-Enfield Mark I. WADF (in a circle) 521, with sale mark. The WADF stamp (W.A. Defence Force) was originally applied to the Martini-Henry rifle from which this specimen was converted. They were not re-marked at the time of their conversion. (Photo D. Elford, W.A.M.)

Enfield and W.A. The group three Unofficial Conversions appear to be a separate but conforming variant. The common functional link between the three groups of arms is the fitting of the Rigby one or two piece nose cap which allows the fixing of the Pattern 1888 bayonet, a definite connection with and a continuation of, the earlier 1893-95 procurement of 700 Martini-Metford Mark I (W.A. Pattern) rifles by W.A. which also fixed the Pattern 1888 bayonet.

An examination of archival records of the procurement of arms by colonial W.A. must be undertaken in order to establish whether W.A. did in fact order arms conforming to this pattern and whether the dates and circumstances of procurement conform to the dates and physical features of these W.A. Pattern Martini-Enfields.

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Special thanks are due to Malcolm Higham for publishing the survey articles and forwarding the data received. The author would have found it impossible to present this discussion were it not also for the support of the following individuals who went to considerable trouble to provide information on arms in their collections, and advice. I thank them all for their generosity. Barry Temple, Ian Skennerton, Herb. Woodend (RSAF, Enfield), Murray Rose, Noel Blakely, Warwick Murray, Jim Grant, Nathan Thompson, Phil Hodgson, Ross Sinclair, John Sweetman, Sgt. Alan Gronow (W.A. Police), W.A. Army Museum, Ron Cook, Kim Gray.

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THE MARTINI-ENFIELD RIFLE IN WESTERN AUSTRALIA
PART II

The Procurement of .303 inch calibre Martini Arms by Western Australia

George B. Trotter*

ABSTRACT

The procurement of .303 Martini arms by the colony of W.A. between 1893-1900 is traced using the available archival record. It is demonstrated that those procurements relating to Martini-Enfield rifles can be defined as three separate groups, viz, Group one, 200 M-E Is (1898), Group two, 200 M-Es (1900) and Group three, at least 251 Unofficial Conversion M-E Is (1899-1900). Archival evidence is presented which firmly establishes the historical link between the Group one and Group three arms described in Part I of this paper and W.A.s procurement program described in Part II. A reasonable hypothesis is presented to link the Group two M-E Mark IIs also described in Part I with 200 M-Es ordered in 1900 which are described in Part II.

Two earlier orders for .303 Martini-Metfords and a later order for .303 Lee-Speed Magazine rifles are also addressed to maintain the historical context and chronological continuity.

INTRODUCTION

In Part I of "The Martini-Enfield Rifle in Western Australia", three distinct groups of Martini-Enfield rifles were identified and described. These three groups of rifles, respectively the Martini-Enfield Mark I Modified, the Martini-Enfield Mark II Modified and the Unofficial Conversions Mark I Modified, are unique amongst M-E rifles in Australia. The modification which makes them unique consists of fitting the Rigby type nose cap which takes the Pattern 1888 sword bayonet. The fitting of Pattern 1888 bayonets to M-E rifles is a practise adopted by W.A. alone out of all the various recipients of M-E rifles known to date, throughout the British Empire between 1896-1903.

In order to link the three groups of Modified WA Pattern rifles to W.A. it has been necessary to examine the procurement of .303 inch Martini arms of various types by W.A. between the years 1893-1900. Regrettably, no original W.A. arms requisitions containing the details of the rifles ordered, such as their Mark, were found, similarly no W.A. Defence Force arms registers were located which would have confirmed the numbers, marking and issuing of the rifles within W.A. Gaps in the documentary records make it difficult to piece together an exact sequence of events, however, by consulting contemporary military records, government records, production records, treasury records, photographs and finally the arms themselves, it is felt a reasonably accurate historical connection can be established between the actual specimen arms and W.A.s ordering program.

Abbreviations which may be found in the text are as follows:

M-E = Martini-Enfield; M-H = Martini-Henry; M-M = Martini-Metford; Mk = Mark; ML-E

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= Magazine Lee-Enfield; Pat. '95 = Pattern 1895; Pat. '88 = Pattern 1888; RSAF = Royal Small Arms Factories; SMLE = Short, Magazine Lee-Enfield.

THE PROCUREMENT OF .303 INCH CALIBRE MARTINI ARMS BY W.A.

In 1889, the British Empire adopted the .303 calibre black powder cartridge and the .450 inch black powder Martini-Henry was converted to eventually become the .303 inch Martini-Metford Mark I and Mark II. South Australia, between 1890-1893 acquired by exchange some 500 M-M "hybrid" Mk I rifles with their own S.A. modifications. They had a steel trapdoor in the buttplate for an oil bottle and were sighted for cordite cartridges. Western Australia consequently decided to adopt a similar pattern themselves[1]. In an 1893 letter from the Colonial Secretary's Office in Perth to the W.A. Agent General in London, the Agent General was advised that W.A. had adopted the Martini-Metford[2], and an 1893-94 W.A. Treasury Public Accounts document gives the order date as 17.1.93.[3] Although no W.A. records were found which included the actual order, it is evident that an order was issued, as 700 Martini-Metfords Mark I Modified were ordered for W.A. from Birmingham Small Arms Co. on 12th April, 1894 for 62 shillings and 9 pence each, on War Office specification 57/20/8142.[4] The W.A. modifications included a brass trapdoor in the buttplate and black powder sighting to 1600 yards. These rifles took the Pattern 1888 sword bayonet. Evidently there was some delay in delivery as the W.A. Colonial Secretary wrote to the Agent-General in London twice in 1895 declaring his concern at their non-arrival.[5] They did however arrive between July and December in 1895 and appear for the first time in the W.A. Naval and Military Returns for that year.[6] In the Report of the W.A. Commandant of Local Forces for the year ending 30th June 1896 it is stated "during the past year seven hundred (700) Martini-Metford rifles have been received and taken on charge. It would be desirable to obtain 200 more".[7] These Martini-Metford Mark Is appear in numerous photographs of the 1895-1900 period. (Figures 1, 3).[8] The mention of the desirability of acquiring "200 more" Martini-Metfords evidently received a favourable response because a Royal Small Arms Factory (RSAF) Enfield production manuscript describes 200 Martin-Metford Mark II rifles as being produced "for West Australia" on Extension 782 of 30.4.97". They were sighted for black powder, and it was also noted that the rifle "Takes Sword bayonet Martini-Henry Rifle pattern 1887".[9] Again, no order from W.A. was found but a W.A. Treasury Public Accounts Report for 1897-98 shows a large expenditure for "Small Arms and their Maintenance" for that precise period indicating the arrival of the arms in 1898.[10] The M-M Mark IIs also appear in a number of photographs (Figure 4) taken in 1900. The photographs show these rifles in the hands of men of the Third and Fourth W.A. Contingents to South Africa[11] and the Naval and Military Returns for 1900 show a total of 891 Martini-Metfords on issue, indicating that the second lot of 200 Mark II rifles did in fact arrive.[12]

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[1] Temple B.A. and Skennerton I.D. "Treatise on the British Military Martini" Vol. 1 (1983) Vol 2 (1989). Privately Published Qld. Pp 387-395.

[2] Battye Library CSO Letter Register of 1893, 111/93 Number 969.

[3] Treasury Department Archives, Estimates of Public Accounts of the Government of W.A. 1893-94. (See Table 4).

[4] *Op.Cit.* Temple and Skennerton p.392. Although 1894 is given in this work, all specimens noted are dated 1895.

[5] Battye Library. CSO Letter Register of 1893, 11/93 1138, 111/93 1654.

[6] Battye Library. W.A. Naval and Military Estimates. Quoted in the W.A. Statistical Register for 1895.

[7] Battye Library. Quoted in Votes and Proceedings of WA Parliament 1896.

[8] Battye Library Photograph Collection (Figure 1) and Rae Bros (Eds) "How Westralia's Sons Served the Empire." Melbourne 1900. (Figure 3)

[9] RSAF Archives. Unsigned, undated manuscript of production (apparently compiled by an employee interested in the production details of the various rifles over the years).

[10] Treasury Department Archives. Estimates of Public Accounts of the Govt. of W.A. 1897-1898. (See Table 4).

[11] Rae Bros. (Eds.) "How Westralia's Sons Served the Empire" Melbourne 1900 pp 69-85.

[12] Battye Library. Quoted in W.A. Statistical Register for 1900.

An undated, unsourced list entitled "Issues of .303" Arms made to the Colonies since Introduction" shows W.A. receiving to May 1898, "900 Converted Rifles".[13]

In the same order, or at least arriving in the same year and making up the remainder of the large expenditure on Small Arms in the 1898 year, was a lot of 200 Martini-Enfield Mark I Modified, W.A. Pattern rifles. No W.A. order was found which identifies this lot of arms, but an exchange of correspondence between the British Colonial Secretary and the Governor of W.A. exists which addresses them. In response to the already quoted 1896 Report of the W.A. Commandant of Local Forces in which he states that "it would be desirable... to convert all the Martini-Henry rifles on charge to Martini-Enfield rifles (owing to an improvement in the rifling, the "Martini-Metford is now known as the "Martini-Enfield"), the British Government in a secret Defence Committee Colonial Office Despatch, made an offer on 27 August 1897 to *exchange* our old Martini-Henrys for the new Magazine Lee-Enfields or the newly converted M-Es. The British despatch containing the details of the offer was not located but the subsequent correspondence confirms that W.A. opted (probably on the grounds of cost) to accept the M-Es.

> "With regard to the recommendation contained in his report for 1895-65, that M-M rifles on charge should be converted to M-Es they would point out that the offer of HMG contained in the C.O. Despatch dated 27 August 1897 will enable this to be carried out under conditions advantageous to the colony. In considering the questions of re-armament it is desirable however that the Colonial Government should have in mind than an enemy attacking the colony will almost certainly be armed with magazine rifles. The M-E is only a single-loader, and troops carrying such rifles would be under a serious disadvantage in meeting the attack of an enemy using a superior weapon. The cost of the L-E is £4.6.1. If the colony are not at the present time however prepared to face the expense of arming its forces with magazine rifles it is to be hoped that the offer of the M-E rifles by HMG will be accepted, thus securing the advantage of the use of the same ammunition as that of the Army and Navy".[14]

The W.A. Martini-Henrys (presumed to be 200), were sent in late 1897 or early 1898 and exchanged for 200 M-E Is. W.A. however did not undertake a simple exchange of arms, instead it requested that the exchange M-E rifles be first modified to accept the Pattern 1888 sword bayonet so that these new M-Es would conform to the 1895 order of 700 Martini-Metford Mark I rifles which took the Pattern 1888. The RSAF Enfield supplier complied with this request as the production records at Enfield show. The RSAF Enfield Annual Accounts of the Ordnance Factories for the Year 1897-98 lists "200 M-E Mark I, fitted to take the Pattern 1888 sword bayonet. Rate, 2 shillings 7 1/4 pence each"[15] indicating that the arms were already converted Sealed Pattern M-E Mark Is taken from store and modified for the Pattern 1888 bayonet by having the new Rigby one piece nose cap/bayonet boss fitted. There is also a note in the production manuscript to the effect that 200 M-E Is were "fitted for S.B. Patt. 88" and "sighted for black Powder for West Australia".[16] On 17th December 1898 a despatch to W.A. was received which clarifies the nature of the offer of 27 August 1897. Evidently, some of the exchanged W.A. Martini-Henrys were unfit for future conversion as subsequent correspondence from the Colonial Secretary in England to the Governor of W.A. states:

> "With regard to Secret Despatch of 27th August 1897 respecting this exchange of Martini-Henrys for Martini-Enfield rifles, I have the honour to inform you that as the arms returned have in some instances proved to be unfit for conversion the War Office have requested that in the case of future

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[13] Public Records Office, London. (Supplied by Mr B.A. Temple.)

[14] Battye Library. Secret and Confidential Despatches from Sec. of State to Governor of W.A. 1898. Acc. 391.

[15] RSAF Archives - Annual Accounts for the Ordnance Factories 1897-98 pp 220-221.

[16] RSAF Archives. Unsigned, undated manuscript of production.

Table 1 Expenditure on Small Arms and their Maintenance

Year ending 30th June	Budget Estimate	Actual Expenditure	Under Expenditure	Excess Expenditure	Reason for under or excess expenditure
1893-94	2984	39.17.0	2944.3.0		New rifles ordered 17.1.93 not arrived
1894-95	2500	3223.12.4		723.12.4.	(not explained)
1895-96	150	134.2.7		14.5.1	Erroneous debits
1896-97	2000	41.0.0	1959		Stores not arrived from England
1897-98	2359	1113.9.0	1245		-ditto-
1898-99	300	189.5.0	110.15.0		Votes in excess of requirements
1899-1900	800	120.5.6	659.14.6		Agent-General's account received too late for payment
1900-01	2000	5250.8.10		2505.5.10	Payment for 1000 rifles ordered in previous year

Note: All amounts are in pounds.

> consignments none may be sent home which are not considered by the Colonial Military authorities to be in thoroughly good condition except as regards to the barrels".[17]

This document is confirmation that W.A. availed itself of the exchange scheme and that 200 M-E Is modified at RSAF Enfield for W.A. in 1898 undoubtedly originated there. That these two fairly large quantities of arms arrived in 1895 (700 M-M Is) and again in 1898 (200 M-M IIs, 200 M-E Is) is supported by the already mentioned W.A. Government expenditures for Small Arms in those years (see Table 1) and also by the expenditure listed by the W.A. Agent-General in London for its Military Adviser on military stores in the years 1893, 1894 and 1898.[18] The Military Adviser who "passed all Arms, Ammunition, and Military Stores requisitioned for" sent accounts for his services which coincide with the dates of the two lots of arms. The M-Es also appear for the first time in the W.A. Naval and Military Returns for 1898 where 89 are listed as being on issue to the Geraldton Rifle Volunteers at Geraldton[19] (Figures 1, 2). These Geraldton issue arms have been positively identified as Mark I Modified, WA Pattern in Figure 2. These arms conform to the specifications of the Group one arms described in Part I of this paper.

Table 1 shows the large expenditure for the financial years 1894-5, 1897-8 and 1900-1, which coincide with the acquisitions of the arms of this study.

After the receipt of the 200 M-M IIs and 200 M-E Is in 1898, the following year, 1899, saw little movement in Small Arms acquisitions but as the tension in South Africa was obviously leading to war, military preparedness was becoming more important in government and military circles. The need for more arms and military stores became a pressing matter in 1899 and 1900 and with

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[17] Battye Library. Secret and Confidential Despatches from Sec. of State to Governor of WA 1898 Acc 391. No subsequent correspondence was found which clarified the number of WA Martini-Henrys exchanged or the number of arms unfit for conversion. It is also not known whether W.A. made up this number of unfit arms by sending any additional Martini-Henrys.

[18] Battye Library. Annual Reports of the Agent General 1893-1904.

[19] Battye Library. W.A. Returns for Naval and Military Expenditure. Quoted in W.A. Statistical Register 1898.

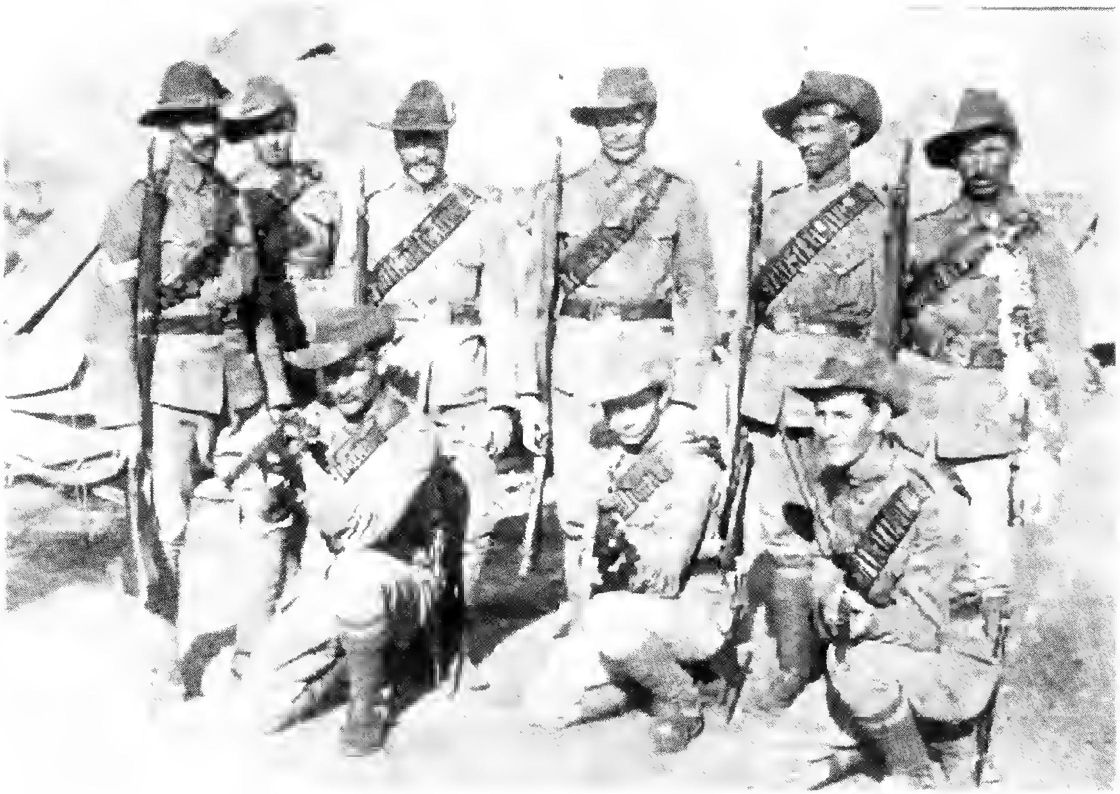

Figure 1 W.A. Mounted Infantry of the Boer War. There are two distinct groups of soldiers. One group is armed with W.A. Pattern Martini-Metfords Mark I (back row, L-R 1, 4, 6; Front row, centre) the other with W.A. Pattern Martini-Enfields Mark I. (back row, L-R, 3,5,; front row 1,3.) Each group of men wear distinctly different uniforms. It is thought the group armed with Martini-Enfields are members of the Geraldton Rifle Volunteers who are posing with men of a Contingent to the Boer War c.1900. All men are armed with the Pattern 1888 bayonet. (Photo courtesy of Geraldton Historical Society. Battye Library 29789P)

the British Military having priority over colonials in the matter of obtaining ships and transports for war material and troops, W.A. was forced to endure delays in the arrival of military stores from England. The Report of the Commandant of Local Forces for the year ending 30th June 1899 asks the W.A. Government for Defence expenditure votes to be made to expand the number of companies in the W.A. Defence Force, partly due to the British recommendation that W.A. should have arms and equipment to serve at least 1500 men[20] and also partly due to the South African political situation. He also states that "it will be necessary in the near future to provide for a reserve of rifles, there being at present practically none". Reinforcing the intention to convert WA Martini-Henrys to .303 inch (initially voiced in his 1896 Report) the Commandant goes on to say "There are 574 Martini-Henry rifles in store which it is proposed to convert into .303 M-E rifles at an early date".[21] These points were evidently attended to, as by his next report in June 1900, the Commandant reports that he has established 11 new Corps of Infantry, each corps consisting of

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[20] Battye Library. Secret and Confidential Despatches from Colonial Secretary to Governor of WA 1898 Acc 391.

[21] Battye Library. Quoted in Votes and Proceedings of the WA Parliament 1899.

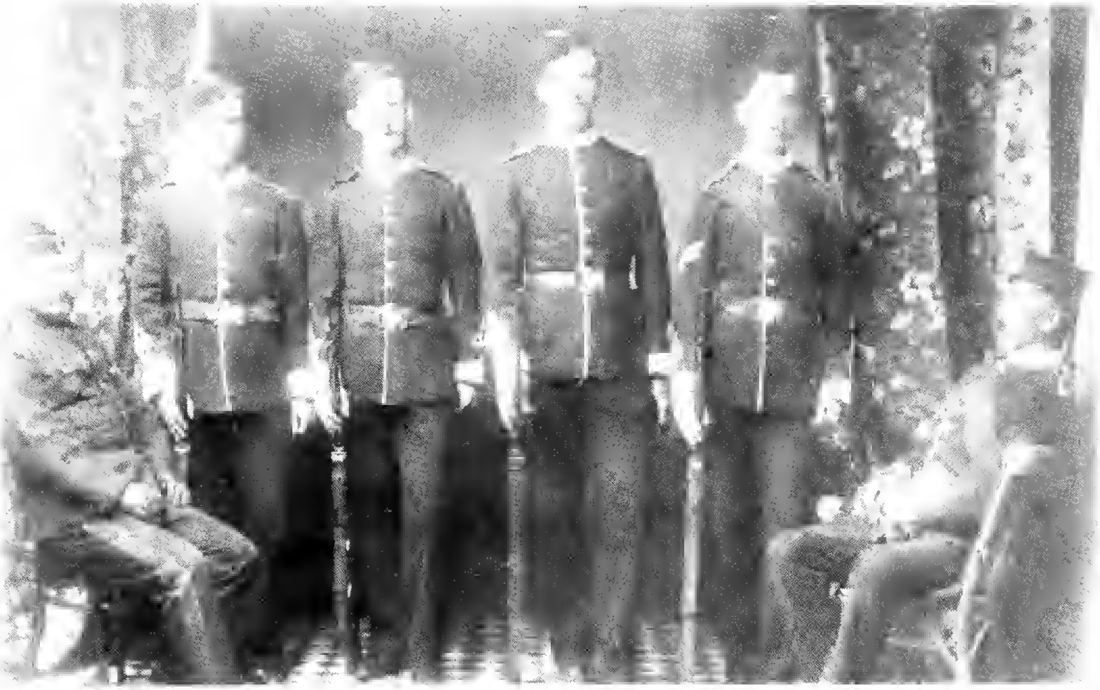

Figure 2 Four members of the Geraldton Rifle Volunteers armed with the Martini-Enfield Rifle Mark I Modified, W.A. Pattern and the Pattern 1888 sword Bayonet. (Courtesy of the Geraldton Historical Society. Battye Library 2302B.)

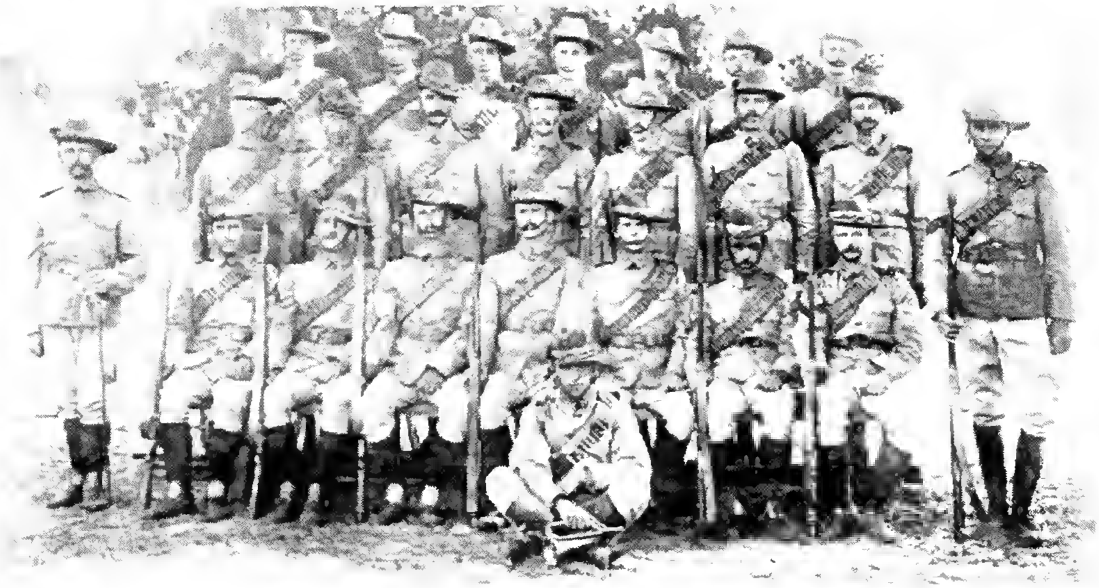

Figure 3 Soldiers of the Second Contingent prior to departure for South Africa. The men are armed with a mixture of W.A. Pattern Martini-Metfords Mark I and Martini-Enfields Mark I. (front row, L-R) troopers 4, 6, 7 and the NCO on the right are armed with the Martini-Enfield. Obvious differences are the shorter barrel and the different sling placement of the Enfields. (Photo D. Elford, W.A.M.)

Figure 4 This photograph shows members of the Fourth Contingent (The Imperial Bushmen) prior to departure for South Africa. The photograph illustrates a mixture of arms which include the Martini-Metford Mk II in the hands of the trooper seated in the front of the group. The troopers in the front row 5,7,8,9,10 (from left), are holding what appear to be Unofficial Conversions, identified by their short barrels and their sling attachment which is from nose cap to trigger guard like the original Martini-Henrys from which they were converted. The lack of any provision for a butt sling swivel indicates that they are not Enfield products like the Martini-Enfield Mk Is and IIs of Figures 1, 2 and 3. (Photo D. Elford, W.A.M.)

60 men. In addition he has raised four new Mounted Infantry Contingents for South Africa as well as raising three corps of Volunteer Mounted Infantry with others proposed for the following year. The Karrakatta range was in constant use training the first two contingents to South Africa who took, in addition to training use, a "very large" amount of ammunition and 219 rifles to South Africa.[22] In the matter of Small Arms and the need to expand his stores the Commandant continued with a reference to rifles. "Since last years report, 200 .303 M-E rifles have been ordered from England, and ought to arrive shortly. There are now 251 Martini-Henry rifles in store, which will be converted to .303 M-E rifles, as the necessary parts arrive from England".[23] The importance of this report cannot be overstated. It clarifies two important points. Firstly, it confirms that W.A. did indeed convert W.A. Defence Force Martini-Henrys into Martini-Enfields locally, using parts supplied from England. These Martini-Henrys were acquired and issued in 1874[24] and 1890[25] and were on issue until replaced by the .303 inch Martini-Metford beginning in 1895. These Martini-Henrys are undoubtedly the source of the Unofficial Conversions located by the survey. According to the Local Commandant's June 1900 Report these local conversions number at least 251 (Figure 4). These W.A. converted arms conform to the description of the Group Three arms described in Part I.

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[22] Battye Library. Report of the Commandant of Local Forces for the year ended 30th June 1900. Quoted in the Votes and Proceedings of the W.A. Parliament 1900.

[23] Battye Library. Quoted in Votes and Proceedings of WA Parliament 1900.

[24] Weick, G. The Volunteer Movement in Western Australia 1861-1903. Paterson Brokensha, Perth. n.d. Pp38, 70.

[25] Battye Library. WA Returns for Naval and Military Expenditure. Quoted in the W.A. Yearbook 1890 (583 Martini-Henry rifles of .450 calibre).

Table 2 Martini-Enfield Mk I and II production totals for the years 1896-1903.

	M-H III conv: M-E I	M-H II conv: M-E II
1896	20,069	1
1897	26,205	1
1898	1,759	520
1899	-	-
1900	-	13,042
1901	-	17,149
1902	461	1,871
1903	116	439

In confirming the origin and number of the 1900 group of 251 Unofficial Conversions the question of the discrepancy between the numbers of Martini-Henrys mentioned in the Commandant's June 1899 Report (574) and the June 1900 Report (251) must be addressed. These figures indicate that 323 Martini-Henrys have left the store between these dates. It is not known whether these arms were sent elsewhere in W.A.[26] or sent to England in exchange for the 200 M-Es ordered from there "since last years report" (i.e. between June 1899 and June 1900), and to also make up for the unspecified number of "unfit" arms sent to England by W.A. in 1897-98. In view of the Commandants clear intentions (commencing in 1896) to convert these arms to Martini-Enfields it is also quite possible that these arms were indeed converted locally "at an early date", from parts purchased in the earlier budget outlays of 1897-99 (Table 1). Because of the uncertainty of the ultimate fate of these 323 rifles, they are only recorded as Exchange/Unofficial Conversions/ Surplus with a question mark, and listed in Table 3.

The second point of importance is that another lot of 200 M-E rifles in addition to the first lot of 200 M-Es of 1898, have been ordered "since last years report" i.e. between 1st July 1899 and 30th June 1900. Although the Mark of M-E is not stated, and there is no record to link the 1900 dated M-E Mark IIs located by the survey with this 1900 order for 200 M-Es, the M-E *Mark I* Modified, WA Pattern is referred to in the 1900 RSAF Enfield records. It is believed that this reference may explain the Group two M-Es of 1900 described in Part I. The Annual Accounts of the Ordnance Factories for 1899-1900 show "100 Martini-Enfield Mark 1, fitted to take the pattern 1888 sword bayonet. Rate 4 shillings 10 1/4 pence"[27] indicating again that already converted Sealed Pattern arms were taken from store and modified for the Pattern 1888 bayonet. In this case, unlike the 700 M-M Is of 1895, the 200 M-M IIs and the first lot of 200 M-E Is of 1898, there is no record in the production manuscript to indicate where these 100 arms were sent, however, in view of W.A.s known unique association with this type of arm it presents a strong possibility that W.A. was the destination. These 100 M-E Is coincide with W.A.s known 1900 order for 200 M-Es, also, the modification conforms to the W.A. Pattern. It is relevant here to also refer to the RSAF Enfield production records which show that during the years 1899-1901 *no Mark I M-Es* at all were converted there (see Table 2). Therefore the 100 M-E Mark Is referred to in the Annual Accounts of the Ordnance Factories must have been taken from stock still remaining on hand from the 1896-98 production run. Considering the strong demand from the various colonies it is certain that

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[26] Dominion Returns for Land Forces to 31st December 1904, show that W.A. still had 287 Martini-Henry rifles and 26 carbines, for a total of 313. These may be the remainder of the 323 under discussion here. (These Returns totals were quoted by B.A. Temple and I. Skennerton in private correspondence. 18.7.91, 18.3.92.)

[27] RSAF Archives. Annual Accounts for the Ordnance Factories 1899-1900. pp. 240-241

stocks of M-E Is were virtually exhausted by 1900 and not enough Martini-Henry Mark IIIs or parts remained on hand to convert more, therefore RSAF Enfield reactivated its conversion facility and commenced production of M-E IIs (from Martini-Henry IIs) in order to satisfy continuing demand for .303 inch Martini-Enfields from around the world. If RSAF Enfield had large stocks of M-E Is still in store from the 1896-98 production or Martini-Henry Mark IIIs or parts from which to make more, this time and cost conscious organization would have utilized these instead of changing to M-E Mark II production, especially at this busy (Boer War) time. It is highly probable that Mark II production commenced in earnest in 1900 because no more Mark Is could be produced. It is likely therefore that if the 100 M-E Is described in the RSAF records for 1899-1900 were indeed sent to W.A. then it is also likely that RSAF Enfield filled the remainder of W.A.s 1900 order for 200 M-Es by augmenting the 100 M-E Is with 100 M-E IIs from current 1900 production, which was the only source of M-Es available at that date. This augmentation would certainly explain the existence of the Group two RSAF converted, 1900 dated, W.A. marked M-E Mark II, Modified, WA Patterns located by the survey and described in Part I. As the documentary record at RSAF contains omissions and gaps due to loss it may never be possible to verify this matter archivally.

The hypothesis presented which illustrates the possibility that a mixed lot of M-E Is and IIs were sent to W.A. would be established by the location of documentary evidence or a pre 1899 dated, RSAF Enfield converted M-E Mark I rifle with the characteristics of the 1900 dated Mark IIs described in Part I. That is, a Mark I M-E, modified to the same specifications as the survey Mark IIs. It should have cordite sighting and a non bored-through nose cap, (as the clearing rod was abolished in May 1899). The cordite sighting was necessary as by 1900 no more black powder ammunition was manufactured and W.A., having exhausted its stock of black powder ammunition by 1900,[28] was by then acquiring cordite sighted arms, as evidenced by the 1900 dated M-E IIs. A modified Mark I such as that which has just been described would be readily identifiable as being different from the Group One M-E Is and indeed, would constitute a new sub-variation in it's own right.

From the archival record it can be calculated that the 1900 order for 200 M-Es and conversion parts for the additional 251 Unofficial Conversions was made in early 1900.[29] They arrived, accompanied by 1000 .303 inch Lee-Speed Magazine repeating rifles between July and December 1900. The 200 M-Es are listed as being sent in May 1900[30], and 821 Lee-Speeds were listed as on issue in the Naval and Military Returns for that year.[31] This large order for "small arms and their maintenance" is referred to in the Public Accounts document (Table 1) where an unbudgeted excess of 2505 pounds was expended for "1000 rifles ordered in the previous (financial) year", i.e. between July 1899 and June 1900. Between 1895-1900, the Martini-Metfords of 1895, the M-E Is of 1898 (Geraldton) and the Lee-Speeds of 1900 are recorded in official Returns together with the Volunteer units to which they were issued. The 1900 M-Es and Unofficial Conversions appear to have been issued exclusively to the various Boer War contingents and unlike the Volunteers arms are therefore not recorded on the W.A. Returns of 1899 and 1900. The submission of Annual Returns by W.A. ceased after 1900.

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[28] Battye Library. Colonial Secretary Telegram to the Agent general in London Jan. 8, 1901 confirming the taking of 52,400 rounds of .303 ammunition to south Africa by the First and Second Contingents. C.S.O. 18/227.

[29] Battye Library Newspaper Archives. West Australian 23 February 1900. It is noted that the Premier, in response to concern that all the arms in the colony had now been issued to the contingents, ordered more.

[30] Public Records Office, London. "Issues of .303" Arms made to the Colonies since Introduction." (supplied by B.A. Temple).

[31] Battye Library. W.A. Naval and Military Expenditure. Quoted in W.A. Statistical Register 1900.

Table 3 Procurement of .303 inch Martini Arms by W.A. 1893-1900.

Arm	Number	Order	Received	Sights	Bayonets
Martini-Metford Mk I	700	17.1.1893	1895	Black Powder	Pat. '88
Martini-Metford Mk II	200	30.4.1897	1898	Black Powder	Pat. '87
Martini-Enfield Mk I	200	27.8.1897	1898	Black Powder	Pat. '88
Exchange/Unofficial Conversion/Surplus?	323	1899/1900			
Martini-Enfield (Mk I & II)	200	Feb. 1900	1900	Cordite	Pat. '88
Unofficial Conversion Martini-Enfield Mk I	251	Feb. 1900	1900	Unknown, probably cordite	
Magazine Lee-Speed	1000	Jan. Feb. 1900	1900	Unknown, probably cordite	Pat. '88

These arms described in the archival record and listed in Table 3 are the last procured by W.A. at the end of the colonial period. On January 1st 1901 W.A. became a State in the new Commonwealth and all subsequent arms purchases were controlled by the Commonwealth.

No other type of Martini-Enfield arm is known to have been procured and issued in W.A. prior to 1901. There is a recommendation in a Military Report of the Commandant of Local Forces (dated 19.9.1898) by Lt. Col. A. Wilson, that "Senior Cadets be issued with M-E carbines"[32] and Skennerton states that M-E Carbines Mark I were issued in W.A. in "small numbers".[33] The author found no archival or photographic evidence to support this. It is possible that M-E carbines were issued in W.A. after Federation[34] but none have been noted here with W.A. markings. This type of arm also fixes the Pattern 1888 bayonet.

CONCLUSION

It can be seen from the archival records previously discussed, that the procurement of .303 inch Martini-Enfields by W.A. between 1898-1900 is essentially reduced to three major acquisitions or groups. Group one are the 200 M-E Mark Is of 1898, group two are the 200 M-E Marks (possibly mixed Is and IIs) of 1900 and group three are the Unofficial Conversions converted from W.A. Defence Force Martini-Henrys between 1899-1900. These local conversions number at least 251 and may be higher. It has been demonstrated that the three groups of arms as described in "The Martini-Enfield Rifle In Western Australia" Part I, fit precisely into the order periods and order descriptions recorded in the archival documents. The M-E Is of 1898 and the Unofficial Conversions of 1899-1900 described in Part I are unquestionably the arms ordered by W.A. as recorded in Part II of this paper. The establishment of the survey M-E IIs of 1900 as part of this ordering process is quite compelling but must await the location of corroborating archival evidence

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[32] Battye Library. Colonial Office Microfilm. Military Report C.O. 80/225.

[33] Skennerton, I.D. "Australian Service Longarms" Privately Published. Qld 1975 p. 120.

[34] Battye Library "Commonwealth Parliamentary Act, Cadet Forces Australia 1904". "Adoption by Secondary School Senior Cadets of .303 M-E (single loader)" p. 3.
There is no mention of M-E carbines in the "Issue of .303: Arms made to the Colonies since Introduction" referred to earlier in this discussion. This list however does contain omissions of known shipments so is not completely comprehensive.

and/or the location of further specimens as discussed in the text. A reasonable hypothesis has been presented which illustrates the possibility of a mixed lot of M-E Is and IIs arriving in 1900. Only further research will establish, modify or reject this hypothesis.

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THE MARTINI-ENFIELD RIFLE IN WESTERN AUSTRALIA

PART III

The Pattern 1888 Sword Bayonet in Colonial W.A.

George B. Trotter*

ABSTRACT

The examination of the three groups of unique Martini-Enfield Modified, W.A. Pattern rifles, discussed in Parts I and II, is extended to include discussion of the Pattern 1888 sword bayonet which accompanied them to W.A. The use of this bayonet on W.A. Martini-Enfield arms is an extension of a purchasing policy for this combination which began in 1893-95 and continued in W.A. through to the early Federation period. The exclusive use of the Pattern 1888 bayonet on its .303 inch Martini-Enfield rifles between 1898-1900 sets W.A. apart from all other users of the Martini-Enfield throughout Australia and possibly the world. Evidence is examined which indicates that W.A. never issued the Sealed Pattern Martini-Enfield or the accompanying Pattern 1895 socket bayonet as has hitherto been supposed.

INTRODUCTION

The physical characteristics of the three groups of WA Pattern Martini-Enfield rifles and their procurement by the colony of Western Australia has been described in Parts I & II of this series. Similarly, their predecessor arms, the Martini-Metfords and their successors, the Lee-Speeds have also been discussed in order to maintain the continuity of the procurement programme adopted by the Colonial Government. The common link between these various types and models of arms has been their ability to accept the Pattern 1888 sword bayonet. It is the nose-cap which was fitted to these rifles to facilitate this bayonet which makes the WA Pattern Martini-Enfields unique in Australia. All the evidence uncovered in this study points to Western Australia issuing the WA Pattern arms only; ignoring the other types of Martini-Enfields.

Abbreviations which may be found in the text are as follows:

M-E = Martini-Enfield; M-H = Martini-Henry; M-M = Martini-Metford; Mk = Mark; ML-E = Magazine Lee-Enfield; Pat. '95 = Pattern 1895; Pat. '88 = Pattern 1888; RSAF = Royal Small Arms Factories; SMLE = Short, Magazine Lee-Enfield.

W.A. ISSUE RIFLES AND BAYONETS 1895-1900

In studies of Australian colonial military arms, references have been made to the effect that the Sealed Pattern Martini-Enfield Mark I and II and its accompanying Pattern 1895 socket bayonet were used in all the Australian Colonies. The most notable work to make this statement is Ian Skennerton's excellent reference book "Australian Service Longarms". In describing the Sealed

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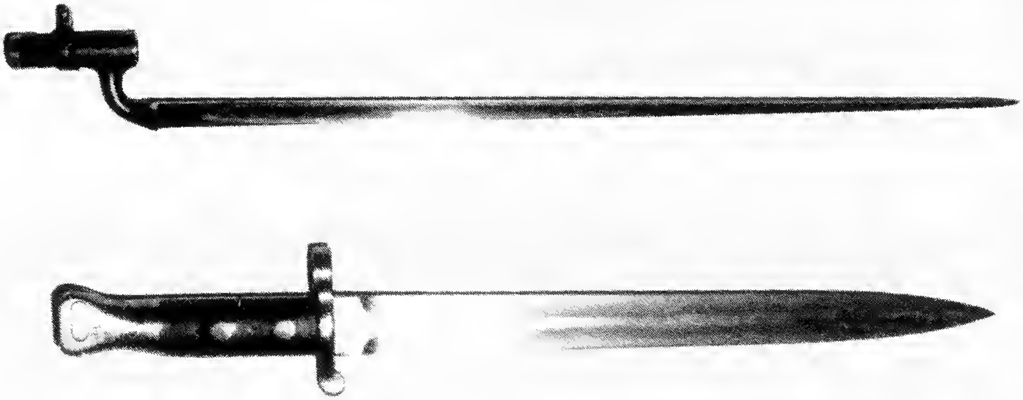

Figure 1 The bayonets which accompany the Martini-Enfield Rifles. (Top) The Pattern 1895 which was issued with the Sealed Pattern Martini-Enfield, and (bottom) the Pattern 1888, which was used on the Martini-Enfields Marks I and II Modified W.A. Pattern. (Photo R. Stein)

Pattern Mark I (page 115), the Mark II (page 117) and their Pattern 1895 bayonet he states that these arms were used "by all the Colonial Governments".[1] When this work was written (1976) nothing was known about the Martini-Enfield Mark I and II Modified W.A. Pattern rifles or the Unofficial Conversion Martini-Enfield Mark I WA Pattern located and described in Part I of this paper. In the intervening 18 years only the M-E Mark I Modified WA Pattern has been described, (1989) and then only from archival sources[2] as no actual specimen had ever been located until this present work was compiled. In contrast, much is known about the Sealed Pattern M-E Marks I and II and their various Australian colonial issue histories. Thus, as little was known about W.A. issue arms other than W.A. was known to have had "Martini-Enfields", and the fact that colonial arms research done in the Eastern States seldom ever includes W.A. led to the not unreasonable conclusion that W.A. used Sealed Pattern arms and Pattern 1895 socket bayonets like the other Australian colonies.

As mentioned most authorities on Australian arms state that the Sealed Pattern Martini-Enfield Mk I & II with the Pattern 1895 bayonet was issued and used in all the Australian colonies, a reasonable assumption in view of the lack of evidence to the contrary. Evidence gathered by the author tends to refute this assumption. In fact it is felt that no Sealed Pattern Martini-Enfields or Pattern 1895 bayonets were ever issued in W.A. to Defence Force members during the Colonial period ending on 31st December 1900. The evidence to support this conclusion is not derived from archival or physical evidence which proves that they were not used, but rather from a *lack* of evidence which might indicate that they *were* used, indeed the evidence uncovered shows only the WA Pattern - Pattern 1888 combination in use here.

As discussed in Part I and II the contemporary documentary, photographic and physical evidence uncovered shows that only the W.A. Pattern Martini-Metfords, Martini-Enfields and

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[1] Skennerton I. D., Australian Service Longarms. Privately Published. Qld. 1975

[2] Temple B.A., and Skennerton I.D., Treatise on the British Military Martini. Vol. 1 (1983) Vol. 2 (1989). Privately Published. Qld. Vol 2 Pp 417-419

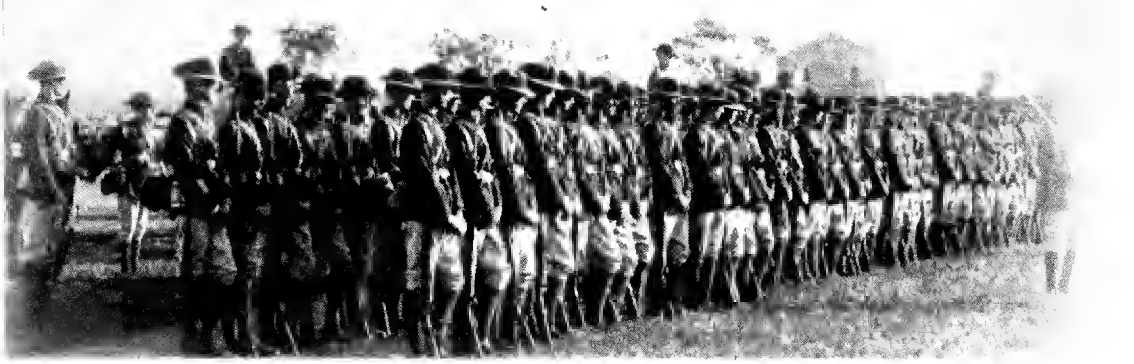

Figure 2 The First W.A. Contingent to the Boer War on Parade prior to departure. All men bear W.A. Pattern Martini-Metford and Martini-Enfield rifles. Back row (L-R) soldier number 1 and front row soldiers 10 and 11, are armed with Martini-Enfield rifles identifiable by their shorter barrels and different sling placement. All these rifles bear fixed Pattern 1888 bayonets. (Photo courtesy of Geraldton Historical Society Battye Library 66270P)

Lee-Speed rifles and their Pattern 1888 bayonet were ever issued here during the late Colonial era. Not one contemporary photograph was found which shows either the Sealed Pattern Rifle or the Pattern 1895 bayonet in the hands of W.A. Defence Force members. Additionally the 1904 Returns list the total of .303 rifles of all types and in addition all types of bayonets used in W.A. The total of .303 rifles comes to 5106 of all types,[3] including the M-M, M-E and Lee-Speeds described in Parts I and II. The total for bayonets is "about" 5000 Pattern 1888 bayonets. *No* Pattern 1895 bayonets are listed.[4] It can be seen that the number of rifles to the number of Pattern 1888 bayonets, closely tallies. Thus the Returns totals which pairs a Pattern 1888 bayonet to each rifle, combined with the absolute lack of W.A. marked Sealed Pattern arms or Pattern 1895 bayonets physically located or even appearing in photographs or Returns tends to the conclusion that the Sealed Pattern rifle and the Pattern 1895 bayonet were not W.A. issue, as has been supposed. Any Sealed Pattern M-Es and Pattern 1895 bayonets now found in W.A. probably emanated from the Eastern States as Reserve arms after 1903,[5] as all those examined bore Eastern states Colonial and/or Commonwealth markings. It is doubtful whether any Pattern 1895 bayonets accompanied these arms on issue to the rifle club reservists as they do not appear in the 1904 Returns.

There is one exception to this general use of the Pattern 1888 bayonet. The 200 Martini-Metford Mark IIs purchased in 1898, being Sealed Pattern rifles, took the Pat. 1887 bayonet, but as the bayonets do not appear in contemporary photographs or in the 1904 Returns, it is concluded that the bayonets apparently did not accompany the rifles to W.A., instead, there is evidence to suggest that the rifles were possibly modified to accept Pattern 1876 M-H socket bayonets. Two interesting photographs were found, one in the W.A. Museum Photograph Collection (W.A.M. 7600 396)

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[3] Dominion Returns for Land Forces to 31 December 1904, quoted by Temple and Skennerton in private correspondence. 18-7-91, 18-3-92. The other types of .303 arm used by W.A. Troops and making up the remainder of this total were the various Lee Magazine rifles issued in South Africa and also acquired in the early Federation period 1901-03.

[4] Skennerton I.D., and Richardson R. "British and Commonwealth Bayonets" Privately Published. Qld. 1986 p. 274.

[5] Army Museum of WA. archives. General Order 263, 26th November 1903. This order describes the allocation of 600 M-E .303 rifles to W.A. for loan to rifle club members. Bayonets are not mentioned.

Table 1 W.A. Pattern Arms and their issue bayonets.

ARM	NUMBER	DATE	BAYONET
Martini-Metford Mark I (WA Pattern)	700	1895	Pat. 1888
Martini-Metford Mark II	200	1898	Pat. 1887*
Martini-Enfield Mark I WA Pattern	200	1898	Pat. 1888
Exchange/Unofficial Conversion/Surplus	323 (if converted)	1899/1900	Pat. 1888
Martini-Enfield Mark I & II WA Pattern	200	1900	Pat. 1888
Unofficial Conversion M-E Mark I WA Pattern	251	1900	Pat. 1888

* Sealed Pattern rifle taking the Pattern 1887 sword bayonet.

and one in Battye Library (2272 B/17) which supports the possibility of this modification having occurred. The photographs show the men of the Third Contingent riding through respectively, North Fremantle and Fremantle in March 1900. The men are armed with Martini-Metfords Mk II, and as the photographs were taken from behind the troopers some of their bayonets are visible. Those visible are unmistakably Pattern 1876 Martini-Henry socket bayonets. Although the diameter of the barrel was correct for the Pattern 1876, this bayonet would not fit the M-M II as the foresight has a short 'ramp' behind it preventing the bayonet locking into place. The square 'post' sight of the original M-H from which the M-M II was converted and for which the bayonet was made easily facilitates this operation. Very little metal has to be filed away however to remove this 'ramp', indeed an unskilled man with an ordinary file could modify the sight in a matter of minutes. It would also be necessary to modify the socket bayonet sight bridge and locking ring to accommodate the higher M-M II foresight. As the M-M II alone, out of the various M-M and M-E conversions in W.A. service, has the same large diameter barrel as the original M-H, it is the only arm which would have been capable of readily accepting the Pattern 1876 after this simple modification. It is also the only arm which would require a bayonet different from the Pattern 1888 used on the other conversions, as the Pattern 1888 muzzle ring is smaller in diameter being designed to fit the slimmer profile of the .303 barrels of the M-M I and the M-Es. Such a modification would have allowed the W.A. Government to save the purchase price of 200 Pattern 1887 sword bayonets by using some obsolete bayonets they already had in store. These photographs certainly point to the possibility that the Third Contingent was issued with a number of M-M IIs modified to take the modified Pattern 1876 socket bayonet.[6] The use of the Pattern 1876 would help explain the lack of Pattern 1887 bayonets appearing in any contemporary photographs or documents. Even though the photographs depicting the M-M II and the Pattern 1876 bayonet are clear enough to identify the "post" shape of the foresight, they are not clear enough to see details of the bayonet socket. The contention of the modification of the sight will have to await the

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[6] A number of Pattern 1876 bayonets with this modification are known in local collections but as this type has been imported from overseas in recent years it may not be possible to identify a W.A. specimen and so confirm this hypothesis.

discovery of further supporting photographs or an original M-M II with modified sight to confirm it, but the indications are that this modification was done. The same reservations apply to the modified Pattern 1876 bayonet. The possibility that the men are actually holding .450 inch Martini-Henrys is discounted by the .303 ammunition bandoliers and the thin .303 inch clearing rods visible in the photographs (see Figure 4 in Part II). It is also known that the .450 inch Martini-Henry was obsolcte by 1895 and many were in the process of being converted locally to .303 inch, by 1899-1900, and thus would be unlikely to have been issued in their obsolete form. Apart from this one tentative departure, all other .303 inch Martinis in W.A. service were fitted to take the Pattern 1888 sword bayonet.

CONCLUSION

The rifles taking the Pattern 1888 bayonet have been identified in Part I of this paper and their procurement has been chronicled in Part II. All these arms take the Pattern 1888 Sword Bayonet (see Table 1) with the exception of the 200 Martini-Metford Mark IIs of 1898. The possibility of these rifles being adapted to utilize the Pattern 1876 Martini-Henry socket bayonet has been discussed and the evidence to support this proposition has been described. Although inconclusive without confirmation in the form of documentary or physical evidence, the possibility is presented in the hope that it will stimulate interest and further research to confirm or dismiss the proposal. All WA Pattern Martini-Enfields described in Part I and II are designed to fix the Pattern 1888 bayonet but will, without modification also fix the Pattern 1895 socket bayonet. However, the fact that it has been shown that W.A. specifically requested the means to fix the 1888 bayonet (the nose cap), and as no 1895 bayonets are pictured, documented or listed in the 1904 Returns, the conclusion that the Pattern 1888 bayonet alone was used by W.A. on .303 Martini-Enfield rifles is supported.

The author would welcome information regarding additional specimens of W.A. Pattern rifles and bayonets.

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    (b) Photographic Collcction.
    (c) W.A. Colonial Secretary's Office correspondence 1876-1902.
    (d) Colonial Office correspondence 1893-1900.
    (e) Agent General's Reports 1896-1900.
    (f) Agent General's Reports 1893-1904.
    (g) W.A. Statistical Registers 1895-1900.
    (h) W.A. Year Books 1886-1904.

- (i) Parliamentary Debates 1900.
- (j) Newspaper archives.
- (k) Votes and Proceedings of W.A. Parliament 1893-1901

6. Phil Hodgson, Family Photograph Collection.
7. Treasury Department Archives. Auditor General's Reports 1895-1901.
8. W.A. Army Museum
    - (a) General Orders 1903-1909
    - (b) Arms Collection
9. W.A. Museum
    - (a) Arms and Armour Collection
    - (b) W.A.M. Photograph Collection
10. Royal Small Arms Factory Archives
    - (a) Annual Accounts 1897-1900
    - (b) Manuscript of Production.

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RANGE EXTENSIONS, RANGE DEFINITIONS AND CALL STRUCTURES FOR FROGS FROM WESTERN AUSTRALIA

J.D. Roberts and C.M. Majors*

ABSTRACT

Ranges are defined or extended for ten frog species from Western Australia: *Crinia subinsignifera, Litoria adelaidensis, Myobatrachus gouldii, Neobatrachus centralis, N. fulvus, N. kunapalari, N. pelobatoides, N. sutor, Notaden nichollsi* and *Pseudophryne guentheri.* Call structures are also defined for *Neobatrachus fulvus.*

INTRODUCTION

Tyler, Smith and Johnstone (1984) give the most recent data on the ranges and biology of frogs from Western Australia. However, since the publication of this book we have observed several species well outside the ranges reported by Tyler *et al.* (1984). Furthermore the ranges of some new species were poorly defined at the time of initial description (e.g. *Neobatrachus* species in Mahony and Roberts 1986). Here we report range extensions, define ranges or comment on range limits for *Crinia subinsignifera* Littlejohn, *Litoria adelaidensis* (Gray), *Myobatrachus gouldii* (Gray), *Neobatrachus pelobatoides* (Werner), *N. fulvus* Mahony and Roberts, *N. sutor* Main, *N. kunapalari* Mahony and Roberts, *N. centralis* (Parker), *Notaden nichollsi* Parker and *Pseudophryne guentheri* Boulenger.

Mahony and Roberts (1986) described *Neobatrachus kunapalari* and questioned the status of records of *N. centralis* from inland Western Australia. *N. kunapalari* and *N. centralis* both have tetraploid karyotypes but can be distinguished by the position of the nucleolar organiser region (Mahony and Robinson 1980; Mahony and Roberts 1986). Here we report the first certain occurrence of *N. centralis* in Western Australia and define the range of *N. kunapalari.*

Mahony and Roberts (1986) described *Neobatrachus fulvus* but had calls from only one specimen available. Because the data from a single specimen may be unrepresentative, here we report call data from an additional 24 specimens.

Specimen numbers (e.g. R 93203) refer to voucher specimens held in the Western Australian Museum. References to tape recordings are to cassettes or reel to reel tapes held in the collection of J. D. Roberts, Department of Zoology, University of Western Australia.

RESULTS AND DISCUSSION

Crinia subinsignifera

Main (1965) reported this species from near Manjimup to Cheyne's Beach just east of Albany. Tyler *et al.* (1984) reported only four records in the same general range. In late May 1990 we conducted field work between Albany and Cape Arid National Park, east of Esperance. The calls of *C. subinsignifera* were heard at many sites along the Hassell Highway north-east from Many

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Peaks as far east as the Pallinup River. A. Chapman (pers. comm. as a tape recording) has also recorded this species from the Fitzgerald River National Park. C. M. Majors and A. Savage heard and tape recorded this species on May 24, 1990 on Poison Creek Road in the Cape Arid National Park (Tape JDR#198, cuts 2 & 5; Tape JDR#199, cuts 1 - 3 & 5). *Crinia subinsignifera* may occur throughout the area from Cheyne's Beach to Cape Arid: the intervening area was not surveyed in detail. The Cape Arid record extends the range of this species east-north-east by almost 500 km.

Litoria adelaidensis

Tyler *et al.* (1984) figured the range of this species as extending north only to the Moore River. J.D. Richards recently collected two specimens of this species 15.7 km south-east of Port Gregory, north of Geraldton (WAM R113516-17). This record extends the range of this species north-north-west by more than 350 km.

Myobatrachus gouldii

This species has a wide distribution on the coastal plain north of Perth and in the central and south-eastern wheat-belt. The call of this species is distinct (Roberts 1981). On June 17, 1987, J.D. Roberts heard calls of this species at Mount Walker, 43 km north-north-east of Hyden, at Gibb Rock, 39.5 km north-north-east of Hyden, 6 km west of Gibb Rock and 73.5 km south of Southern Cross. G. Smith (CSIRO Division of Wildlife and Ecology, Helena Valley, W.A.) caught one specimen of this species in a pit trap on the Duracoppin Nature Reserve (north of Kellerberin) on December 4, 1990. These records extend the range of this species marginally to the east and north of that reported by Tyler *et al.* (1984) and the range defined by Roberts (1981). The record of calling by this species in June is also interesting. Roberts (1981) reported peak calling levels in a population near Perth in November but did not hear calling in mid-winter. None of the specimens at Mount Walker were seen: all were calling below a thick carpet of *Casuarina* needles. This is comparable with *Myobatrachus* from near Perth where calling early in the season is always from underground (Roberts 1981).

Neobatrachus centralis

We collected six specimens of this species from 21 km west-south-west of Mount Magnet (WAM R 103596-601) the calls of three of which were recorded (Cassette JDR#25, cuts 4 - 6, R 103596-8). We recorded another 7 specimens, 17 km south of Mount Magnet on January 6, 1989 and 28 February, 1989 (Cassette JDR#25, cuts 8 - 11 and Cassette JDR#28, cuts 2 - 4). These specimens have been identified by karyotype (M. Mahony, University of Newcastle, pers. comm.) and call. They are readily distinguished from *N. kunapalari* by body size (smaller in *N. centralis*) and the shape of the metatarsal tubercle (shape in *N. centralis* is comparable with that of *N. fulvus* - see Mahony and Roberts 1986 for illustration and comparison with metatarsal tubercle of *N. kunapalari*). However, although *N. centralis* is readily distinguished from *N. sutor* by karyotype (*N. sutor* is diploid, *N. centralis* is tetraploid), morphologically these two frogs are difficult to distinguish. Until morphological characters are defined to distinguish these two species, or, the ploidy level of preserved specimens is determined (Mahony and Robinson 1980 show this is possible with silver staining techniques), the distributions of *N. centralis* and *N. sutor* in W.A. will remain uncertain except where records are based on call or karyotype data (see below for *N. sutor*).

We have also heard calls like those of *N. centralis* near Cue, Menzies and Laverton. At

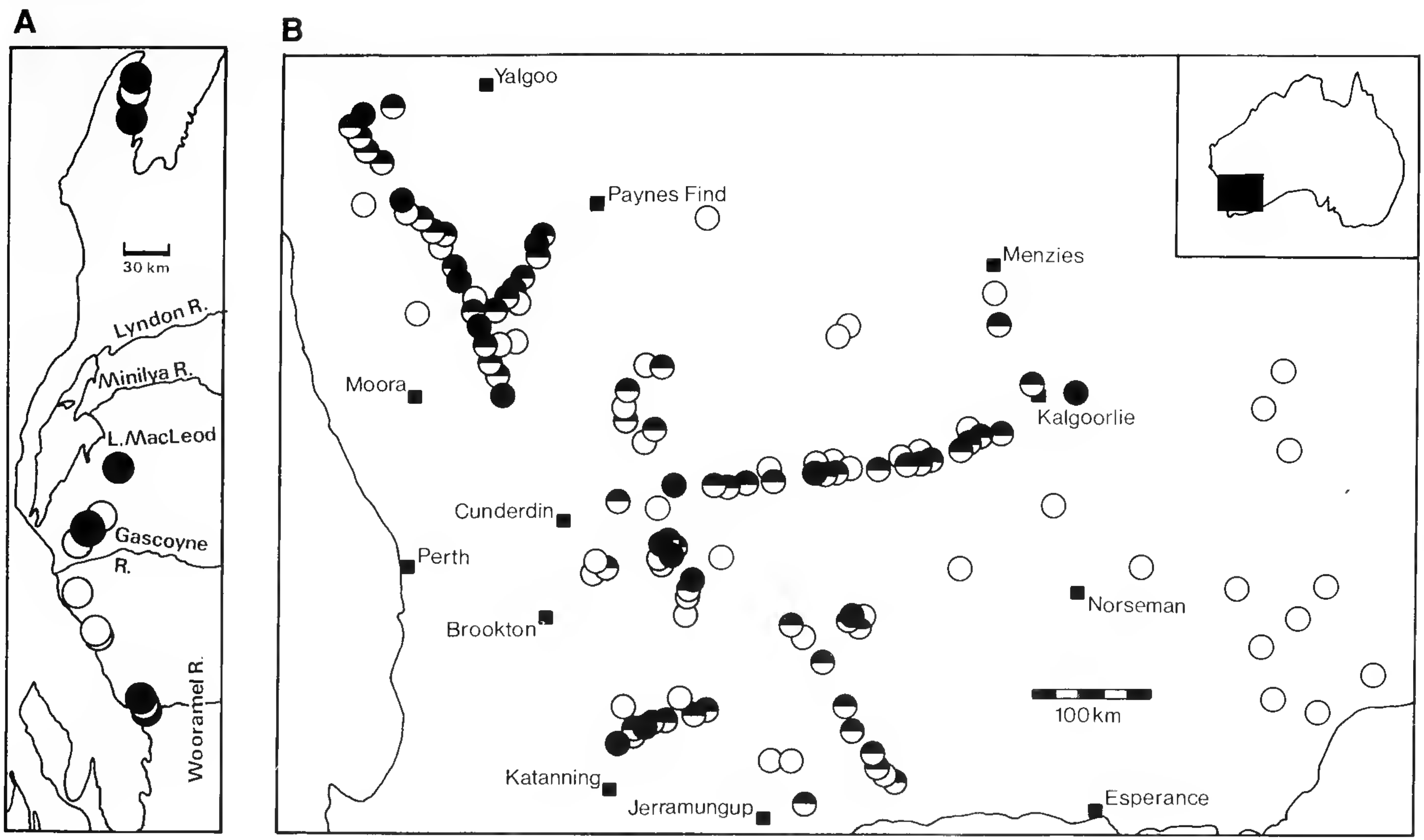

Figure 1 A, Distribution of *Neobatrachus fulvus*. Solid circles, sites where specimens have been recorded. Open circles sites where this species was heard calling. Where multiple data are available for a single site, call recordings take precedence over calls heard. **B**, Distribution of *Neobatrachus kunapalari*. Solid circles, sites with call recordings; half solid circles, sites where calls have been heard; open circles represent specimen records. Where multiple data are available for a single site, call recordings take precedence over calls heard, and calls heard are plotted in preference to specimen records.

Table 1 Call data for *Neobatrachus fulvus* - temperature independent variables. Values given are mean, standard error and range. The data for the single male reported by Mahony and Roberts (1986) are given in the bottom line.

n		Pulses per Call	Pulse Duration (ms)	Dominant Frequency (kHz)	Rise Time as % Duration	Temperature (°C)
Mean	23	16.81	15.0	1.530	49.04	25.1
S.E.		0.48	0.39	0.02	1.02	0.3
Range		12-21	9.7- 18.3	1.33-1.71	39.5-57.0	22.9-27.2
1986	1	13.7	16.6	1.503	50.0	23.2

Menzies calls like those of *N. kunapalari* were also heard. These two species may occur sympatrically. The nature of any interactions that may occur between them, such as whether they hybridize have not yet been defined. Records from sites where *N. kunapalari* and *N. centralis* may be sympatric are not plotted on Figure 1B.

Neobatrachus fulvus (Figure 1A)

This species was reported from Exmouth, Learmonth and Gnaraloo by Mahony and Roberts (1986). Following cyclonic rains in the Exmouth area in January, 1990 we recorded this species at several sites in the Exmouth - Learmonth area and at sites from the Wooramel River north to 80 km north-east of Carnavon. Sites where we heard or recorded calls of *N. fulvus* are given on Figure 1A. Specimen records reported by Mahony and Roberts (1986) are not included on Figure 1A.

This species was abundant at all sites visited. In the area between Exmouth and Learmonth *N. fulvus* was sympatric with *N. sutor*. *N. sutor* was not reported from the Exmouth region by Storr and Hanlon (1980). South of Minilya, *N. fulvus* was sympatric with both *N. sutor* and *N. wilsmorei*. The region between Learmonth and Minilya was not accessible due to flooding and was not surveyed. We have no data on the eastern or north-eastern extent of the range of *N. fulvus* but neither this species, nor any other *Neobatrachus* species, was observed between Devil Creek (49 km west-south-west of Karratha) and Toolunga Creek, approximately 66 km north of the Nanutarra Roadhouse (on the Ashburton River) after heavy rain associated with Cyclone Ian in early March 1992. *Cyclorana maini* and *Litoria rubella* were actively breeding following this rain: *C. maini* was heard at 32 sites and *L. rubella* at 6 sites.

Call analysis techniques for *N. fulvus* follow Mahony and Roberts (1986) except that pulse repetition rates were averaged over the whole call rather than over pulses 7 - 10. The call data reported here are from a total of 23 new frogs recorded at the following sites: 2.3 km south of Exmouth (n = 3); 0.5 km north of the Shothole Canyon turnoff (15 km S of Exmouth, n = 7); Learmonth Air Base (n = 4); Yalobia Outstation, approximately 80 km north-east of Carnavon (n = 4); Yoondoo Well (Yandoo Creek crossing on North-West Coastal Highway, approximately 32.5 km north-east of Carnavon, n = 3); 15 km north of the Wooramel River (n = 1) and 1 km south of the Wooramel Roadhouse (n = 1). All call variables were regressed on temperature. Only one call variable, pulse repetition rate, was significantly affected by temperature. For all variables we compared the mean values for the sample formed by the Learmonth - Exmouth area with those data from further south where there is an additional, sympatric *Neobatrachus* species. For temperature independent variables, comparisons were made by ANOVA run on Statview SE

+ Graphics on a Macintosh SE computer. In all cases there were no significant differences. Data from all sites were combined and are presented in Table 1. For pulse repetition rate, slopes and elevations of regression lines for the two zones were compared. There were no significant differences in either slope or elevation. For comparison with a slope of zero the overall regression was significant, $F_{1,22} = 22.57, p < 0.001$. The regression equation is: Pulses/second = 0.87 water temperature - 3.52. Standard error of the slope estimate is 0.18.

These extensive call data are directly comparable with the data from a single frog reported by Mahony and Roberts (1986). For pulses/second Mahony and Roberts reported a value of 14.2. The predicted value at 23.2°C is 16.66. Our earlier value is lower than expected but the proportion of variance explained by the regression is low ($r^2 = 0.51$) and equally divergent values occur within the data set.

Neobatrachus kunapalari (Figure 1B)

Mahony and Roberts (1986) broadly described the range of this species and speculated that many inland records of *N. centralis* in W.A. actually represented records of this species. Both the call and karyotype of *N. kunapalari* are distinct from those of *N. centralis* (Mahony and Roberts 1986; Mahony and Robinson 1980; Roberts, unpublished data for call). The morphology of these two species is also distinct (Parker 1940 *c.f.* Mahony and Roberts 1986). In Figure 1B we have plotted the distribution of *N. kunapalari*, based on data from sites where we have recorded *N. kunapalari* or heard it calling and on specimen records from the W.A. Museum collection (list of specimens examined in Appendix 1). This species is common in the eastern wheatbelt and adjacent goldfields and extends into the northeastern wheatbelt in a relatively narrow tongue. Contrary to suggestions by Mahony and Roberts (1986) this species does not occur in the inland desert regions of W.A.

Neobatrachus pelobatoides

The range of this species is reported as basically within the area of reliable winter rainfall (Main 1965) but with records extending east to Norseman and north-east to Morawa and Mount Jackson (Tyler *et al.* 1984). The call of this species can be distinguished from conspecifics by its low frequency, high pulse repetition rate and high pulse number (Mahony and Roberts 1986). C. M. Majors made tape-recordings from two specimens of this species on April 24, 1990, in a floodway 2.5 km north of Payne's Find on the Great Northern Highway (Cassette JDR #43, cut 1). Calls of this species were also heard in roadside ponds and floodways at sites on the Great Northern Highway 12.5 km south-west and 8.5 km north-north-east of Ninghan Station. Although these records extend the range of this species about 150 km east and north-east of previous records on the edge of the north-eastern wheatbelt the area has an annual rainfall and rainfall distribution comparable with sites near Norseman where *N. pelobatoides* has previously been recorded.

Neobatrachus sutor

Main (1965) and Tyler *et al.* (1984) report this species from sites in the goldfields, the north-eastern and central wheatbelt and two remote sites in the central desert (Jigalong and Warburton Range). The call of *N. sutor* is a distinctive, short click (Littlejohn and Main 1959). Using this character and based on field records of JDR from the last 14 years, we have plotted the distribution of *N. sutor*. We have heard this species at sites near Morawa, from Ninghan Station through to Meekatharra on the Great Northern Highway, from Exmouth to the Wooramel River on the North-West Coastal Highway and from Menzies and Laverton. This is not a complete record of the distribution of this species as sites reported by Main (1965) and Tyler *et al*. (1984) are not included. We have never heard *N. sutor* on the western margin of the wheatbelt, immediately east of Perth as reported in Figure 1 of Main (1965). We have also never heard this species in the eastern wheatbelt after either summer or winter rains. Field work in the eastern wheatbelt after summer rains has covered the area from Northam to Merredin, Narembeen and Kondinin. Field work after autumn and early winter rains has covered similar areas but north to Bencubbin, east to Coolgardie, south to Hyden, Hopetoun and Jerramungup and north to Leonora and Laverton. This species is abundant at sites in the arid zone and may be widespread through western and into central Australia, with recent reports from Ayers Rock (Tyler and Davies 1986) and north-western South Australia (Tyler 1983). We have no evidence to suggest that *N. sutor* now occurs in the wheatbelt except in the north-east at the type locality, Gnoolowa Hill, and near Mingenew, Morawa and Mullewa. We suspect the records of *N. sutor* between Northam and Southern Cross and south-east of Southern Cross reported by Chapman and Dell (1985) may be mis-identified but this cannot be checked because Chapman and Dell (*op cit*.) did not give register numbers to support their data. In our experience immature *N. kunapalari* may easily be confused with *N. sutor*. Diploid and tetraploid species of *Neobatrachus* can be distinguished by red cell diameter (Mahony and Robinson 1980) and this character can be determined from dried blood smears. The preparation of such smears from future specimens could avoid mis-identification of *N. sutor*.

Notaden nichollsi

This species is widely distributed in northern and inland W.A. We collected 9 specimens (WAM R103572-80) near Yalobia Outstation, approximately 80 km north-east of Carnavon, on January 28, 1990. This represents a southwest range extension of approximately 500 km from the nearest coastal records at Dampier and Karratha and about the same distance from the southernmost inland records from near the Canning Stock Route. Frogs were collected from a large breeding chorus in a natural swamp. They were sympatric with *Neobatrachus fulvus, N. wilsmorei, N. sutor, Cyclorana platycephalus* and *C. maini*. We did not hear this species south of this locality (a further 8 sites were visited to just south of the Wooramel River on the same night), nor were they heard in the Exmouth-Learmonth area the previous night.

Pseudophryne guentheri

This species has been reported from sites throughout the wheatbelt and the forested areas of south-western Australia (Main 1965; Tyler *et al*. 1984). We collected a single specimen of this species 21 km south-east of Mount Magnet on the Yalgoo road on January 6, 1988 (WAM R101128). This species is distinguished from *P. occidentalis*, the only other congeneric species known from this area, by back pattern, ventral pattern (see detailed descriptions in Main 1965) and the number of phalanges in the inner toe (two in *P. occidentalis* and one in *P. guentheri*; Parker 1940). The single female specimen had characteristics of *P. guentheri* for all three distinguishing characters. This record apparently extends the range of this species approximately 250 km north-east of the nearest records of this species in the north-eastern wheatbelt reported by Tyler *et al*. (1984). However, Chapman and Dell (1985) reported a more extensive range for this species with one record close to the site noted above. We examined all available specimens of *Pseudophryne* held by the W.A. Museum from the area defined by latitudes 26 and 29° South and longitudes 115 and 119° East (Appendix 2). R84131-33 from 12 km south of Wuraga were *P. guentheri* judged by toe phalangeal formula. These are the closest records to the site reported above for R101218. Three specimens could not be found: R56133 and R34282 -83. The former specimen is from 40 km south of Yalgoo. The latter were collected by W.H. Butler on November 7, 1965 from a site 20 miles west of Mount Magnet and are registered as *P. guentheri*. R101218 confirms Butler's record of *P. guentheri* from close to Mount Magnet and indicates that the distribution reported by Tyler *et al.* (1984) is incomplete.

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Appendix 1

Specimens of *Neobatrachus* from the W.A. Museum collection examined and identified as *N. kunapalari*. Data presented are: register number, latitude, longitude (latitude and longitude records (from W.A. Museum register data) as degrees and minutes south and east respectively in italics) and locality.

Specimens examined: 4336, *30°17', 116°45'*, Dalwallinu, east of; 9371-3, 9375-6, 9378-9, 9612, 10020, *29°13', 116°01'*, Morawa; 12902, *31°18,' 119°43'*, Karalee, No 7 Pump, 13 km east; 17392, *32°22', 123°41'*, Noondoonia Home Stead, 5 miles south-west; 19634, *32°07', 123°11'*, Newman Rock; 19697, *32°55', 123°30'*, Coragina Rock; 9732, *31°30', 121°35'*, Widgiemooltha; 26386 and 26388, *29°56', 121°07'*, Comet Vale; 30646, *31°18',119 08*, Moorine Rock; 30647, *30°26', 123°34'*, Queen Victoria Spring; 30648, *31°02', 123°34'*, Zanthus; 30649, *31°18', 119°08'*, Moorine Rock; 30650-1, *29°10', 115°40'*, 18 Mile Creek, Morawa-Mingenew Road; 30652, *31°02', 123°34'*, Zanthus; 30653, *30°26', 123°34'*, Queen Victoria Spring; 30654, *31°01', 120°52'*, Bullabulling; 30655, *29°10', 115°40'*, 18 Mile Creek, Morawa-Mingenew Road; 30656, *31°18', 119°08'*, Moorine Rock; 30660, *31°01'*, *120°52'*, Bullabulling; 30662, *31°18', 119°08'*, Moorine Rock; 30663, *29°10', 115°40'*, 18 Mile Creek, Morawa-Mingenew Road; 30665, site cannot be located, Narrogin, Yarding turn-off; 30667, *31°18', 119°08'*, Moorine Rock; 30668, *31°02', 123°34'*, Zanthus; 30669, *31°18', 119°39'*, Yellowdine; 30670, *31°01', 120°52'*, Bullabulling; 30671, *29°13', 116°01'*, Morawa; 30672, *31°02', 123°34'*, Zanthus; 30673, site cannot be located, Narrogin, Yarding turn-off; 30674, *31°18', 119°39'*, Yellowdine; 30676, *30°26', 123°34'*, Queen Victoria Spring; 30677, *31°01', 120°52'*, Bullabulling; 32352, locality unknown, registered as *Hyla caerulea;* 32441, *31°18', 119°08'*, Moorine Rock; 32810-1, 32813-5, 32817, 32819-47, 32850, *29°13', 116°01'*, Morawa; 32851, *31°19', 119°04'*, Moorine Rock; 32852, *31°02', 123°34'*, Zanthus; 32853, site cannot be located, Narrogin, Yarding turn-off; 33040, *31°13', 119°28'*, Southern Cross, 7-10 miles east; 33041, *31°01', 120°52'*, Bullabulling; 33042, *29°10', 115°40'*, 18 Mile Creek, Morawa-Mingenew Road; 33045, *31°01', 120°52'*, Bullabulling; 36293-7, *31°17', 119°45'*, Southern Cross, 26 miles east; 36388-97, 36399-10, 36412-19, *30°55', 119°38'*, Lake Seabrook; 39171, *30°29', 118°07'*, Wialki; 39870, *33°29', 118°54'*, Greenfields Soak, 1 mile north-east; 39901, *33°30', 119°02'*, Greenfields Soak, 12 miles east; 40066-8, *32°59', 118°14'*, North Tarin Rock Reserve; 43664-5, 43667, *29°59', 116°36'*, Buntine Nature Reserve; 45333-4, 45336, *33°30', 119°08'*, Lake Magenta Reserve; 46385, 46387-8, *31°05', 118°01'*, Billyacatting Nature Reserve; 48668-74, 48696, *30°28', 123°34'*, Queen Victoria Spring, 3 km south; 49573, 49792, *33°02', 117°43'*, Dongolocking Nature Reserve; 50150-1, 50158-9, *30°14', 116°56'*, Dalwallinu, 20 km east; 51126-7, *30°13', 116°49'*, Dalwallinu, 12 km north-east; 52413-5, 52417-9, *31°52', 117°33'*, Quairading, 21 km north-east; 52419, *20°50', 116°58'*, Jibberding; 52479-81, *31°59', 117°30'*, Quairading, 11 km east, Badjaling Nature Reserve; 52499, 52548, *32°01', 117°31'*, Quairading, 13 km east; 52623, *32°22', 118°21'*, Bendering, 8 km north-east; 57581, 57773, *30°03', 116°05'*, Marchagee, 15 km north; 59535, 59549, *31°53', 118°40'*, Bruce Rock, 57 km east; 59932-3, *32°28', 123°25'*, Charlina Rock, 12 km north; 65064, *31°57', 122°18'*, Pioneer Siding, 62 km bearing 97 degrees; 65143, *32°23', 119°45'*, Lake Cronin, 0.6 km west; 65202, *32°23', 119°45'*, Lake Cronin, 0.7 km west-south-west; 65208, *32°23', 119°45'*, Lake Cronin, 0.6 km west; 65327, *32°03', 120°42'*, McDermid Rock, 6.3 km south-west; 65659, *30°41', 123°22'*, Cundeelee Mission, 8 km north-west; 66170, *32°02', 120°42'*, McDermid Rock, 3.7 km south-south-west; 68258, *30°00', 116°36'*, Buntine Reserve; 70789, *30°32', 122°16'*, Yowie Rockhole, 10 km bearing 220 degrees; 72136-7, *30°18', 119°42'*, Bungalbin Hill, 12 km north-north-east; 72152-6, *30°12', 119°49'*, Bungalbin, 25 km north-east; 72215, 72229-30, 72275, 72281, 72294, *31°13', 120°19'*, Boorabbin, near; 74322-5, 74327-38, 74340-3, *32°00', 120°45'*, McDermid Rock, 3 km east; 74409, *31°13', 120°19'*, Boorabbin, near; 81638-40, *20°50', 116°58'*, Jibberding; 87392, *29°17', 118°37'*, Lake Barlee and Vermin Fence, between; 91626, *32°55', 124°27'*, Toolinna Rockhole, 53 km west-north-west; 93175, *32°04', 123°57'*, Kilidwerinia Granite Rock, 5 km east-south-east; 93203, *32°04', 124°01'*, Balladonia Hotel-Motel, 50 km north-east; 93206, *33°00', 123°56'*, Balladonia, Six Mile; 93486-8, *31°36', 118°12'*, Hines Hill, 14 km south-east; 93489-90, *31°33', 118°12'*, Merredin, 8 km south-west; 93491, *31°36', 118°12'*, Hines Hill, 14 km south-east; 93492, *31°53', 118°51'*, Bruce Rock; 93493, *32°10', 118°20'*, South Kumminin, 2 km north; 93561-2, *31°33', 118°12'*, Merredin, 8 km south-west; 94665, *33°35', 120°03'*, Ravensthorpe; 97259-61, *31°18', 119°43'*, Karalee, No 7 Pump, 13 km east; 101187, *33°32', 120°00'*, Ravensthorpe, 7 km north-north-west; 101188, *32°30', 119°24'*, Holt Rock, 20 km north; 101189, *29°47', 116°27'*, Latham, 3 km south-south-east; 101190-1, *30°27', 116°08'*, Perenjori, 20 km north-north-west; 101192-8, *29°11', 116°01'*, Morawa, 4 km north; 101199, *30°27', 116°08'*, Perenjori, 20 km north-north-west; 101200, *28°31', 115°42'*, Pindar, 10 km west-south-west; 101201, *33°25', 119°56'*, Ravensthorpe, 20 km north-north-west; 101202-8, *31°58', 117°51'*, Yoting; 101209, *30°59', 117°51'*, Bencubbin; 101210-1, *30°50', 117°51'*, Bencubbin, 2 km south; 101212, *32°10', 118°20'*, Narembeen, 13 km south-south-west; 101213, *29°35', 117°09'*, Ninghan Station, 21 km south-south-west; 101214-6, *30°24', 119°38'*, Bungalbin; 101207, *31°58', 117°51'*, Yoting; 106124, *21°34', 117°10'*, Ninghan Station, 21 km south-south-west.

Appendix 2

Pseudophryne specimens from near Mount Magnet: WAM Register Numbers. Specimens identified by phalangeal formula for inner toe.

Specimens: 34282 - 83, not located; 35294, *P. occidentalis;* 51663, *P. occidentalis;* 54210 - 13, *P. occidentalis;* 56133, not located; 84131 - 33, *P. guentheri;* 87778, *P. occidentalis;* 101218, *P. guentheri.*

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DESCRIPTION OF A NEW CAVE-DWELLING PHOLCID SPIDER FROM NORTH-WESTERN AUSTRALIA, WITH AN IDENTIFICATION KEY TO THE GENERA OF AUSTRALIAN PHOLCIDAE (ARANEAE)

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ABSTRACT

A new species of cave-dwelling pholcid spider is described. *Trichocyclus septentrionalis* sp.nov. was collected in various caves in North West Cape, northern Western Australia; it does not show troglobitic features in its morphology and was also found outside caves. The genus *Trichocyclus* is diagnosed and differences with related genera are indicated. The type species, *T. nigropunctatus* Simon, 1908, is redescribed. An identification key to all pholcid genera of Australia is presented.

INTRODUCTION

Scientific exploration of the Australian cave fauna has been relatively recent. Such explorations have revealed a rich spider fauna associated with caves in many parts of southern Australia (Gray 1973a,b; Main 1976) and more recently in Chillagoe caves and Undara lava tubes. A specialised cave spider fauna was recorded and partly described by Main (1969), Gray (1973a) and Main and Gray (1985). Caves in limestones of different geological ages in Western Australia harbour spiders (Watson, *et al.* 1990). In recent years the Western Australian Museum has conducted extensive surveys of caves in the Cape Range, North West Cape, Western Australia (Humphreys 1991). Nevertheless much of the cave spider fauna of Australia remains undescribed. The pholcid spiders collected in North West Cape belong to one species only. They do not exhibit any morphological cave-adaptations such as reduction of eye size or pigmentation; the environment may however have effected a lengthening of the legs.

The following abbreviations are used: AME, PME: anterior, posterior median eyes; ALE, PLE: anterior, posterior lateral eyes; MNHN: Museum national d'Histoire naturelle, Paris; RMNH: Rijksmuseum van Natuurlijke Historie, Leiden; ZMH: Zoologisches Museum, Hamburg.

KEY TO AUSTRALIAN PHOLCID GENERA

1. Abdomen globular, higher than long or a little longer than high 2
   Abdomen cylindrical 8
2. 6 eyes; male palp with conductor .... "*Spermophora*" Hentz
   8 eyes; male palp without conductor 3
3. Thorax separated from head by Y-shaped groove, continuous with foveal groove, which extends to posterior margin, male paracymbium not converging and pointed; spinnerets most often close to epigastric fold 4

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Separation head-thorax discontinuous with foveal groove, the latter in the shape of a round or oval depression behind the eye region 6

4. AME almost the size of ALE; male chelicerae with prominent lateral ridge, paracymbium not converging, with blunt or rounded tip .... *Trichocyclus* Simon

Diameter AME less than half that of ALE 5

5. Male chelicerae with spurs or apophyses or without; palpal femur relatively slender, paracymbium slender; female chelicerae without stridulating ridges, palp normal ... . *Psilochorus* Simon

Male chelicerae partly covered with a two-horned projection of the clypeus; palpal femur bulky, almost as wide as long, paracymbium more voluminous; female chelicerae with stridulating ridges, palpal tarsi swollen .... *Holocneminus* Berland

6. Male palpal paracymbium converging, tip pointed 7

Male palpal paracymbium spade-like, tip truncate; relatively large spiders .... *Artema* Walckenaer

7. AME situated between ALE; epigyne with one or a pair of hooked prominences in front; palpal femur massive, larger and more bulky than tibia; abdomen higher than long, rounded posteriorly .... *Physocyclus* Simon

AME in front of ALE; epigyne without hooked prominences; palpal femur smaller than tibia; femora of leg I-IV with dark blotches; abdomen longer than high, produced posteriorly .... *Crossopriza* Simon

8. Spiders pale green, carapace flat, abdomen vermiform; eye triads widely separated .... *Micromerys* Bradley

Spider not green nor with flat carapace 9

9. Carapace with large round or oval depression behind the eye region; paracymbium converging, tip pointed, no separate conductor 10

Carapace with Y-shaped groove separating head and thorax, separate conductor present 11

10. Male with femur I having a row of ventral spines; female palpal tarsi inflated .... *Holocnemus* Simon

Male without a row of spines on femur I, female palps with tarsus normal .... *Smeringopus* Simon

11. Male palp elongate, paracymbium with one or several transverse chitinous ridges ventrally, conductor one straight sclerite; epigyne a wrinkled scape; six eyes .... *Panjange* Deeleman-Reinhold and Deeleman

Male palp compact, paracymbium with "elbow", without ventral transverse ridges, embolus resting between two branches of conductor; epigyne different; usually eight eyes .... *Pholcus* Walckenaer

SYSTEMATICS

Trichocyclus Simon, 1908

Trichocyclus Simon, 1908: 407.

Type species

Trichocyclus nigropunctatus Simon, 1908, by monotypy.

Diagnosis

Carapace separated from thorax by deep Y-shaped groove; AME the size of ALE or almost. Abdomen higher than long, spinnerets close to the epigastric fold. Legs moderately long (femur I 4-7 x the length of carapace). Male chelicerae with voluminous lateral ridge or protrusion. Palpal femur massive, paracymbium truncate, embolus in prolongation of bulb, conductor absent. Epigyne bulgy, covered with a pre-genital and a post-genital transverse chitinized plate. Distinct from *Holocneminus* by the large AME and the longer legs (in *Holocneminus* femur I 1-3 x the length of carapace). Distinct from *Physocyclus* by the foveal groove reaching the posterior border of carapace, the large AME and the truncate paracymbium and in the epigyne absence of anterior prominence.

Remarks

The new species is placed in the genus *Trichocyclus* Simon. *Trichocyclus* has sometimes been regarded as a synonym of *Physocyclus* (Main 1964, 1976); Davies (1985) regarded the genus *Trichocyclus* as valid. In fact, it is more closely related to members of *Psilochorus* and *Holocneminus*. The type species of *Trichocyclus*, *T. nigropunctatus* Simon was described from Yalgoo, about 500 km south of Cape Range. It has been collected again, but has never again been recorded in the literature. An adult female labelled "*Trichocyclus nigromaculatus*" (sic), preserved in the Museum in Paris, probably served Simon for the original description. The genus is distinct from related genera by the relatively large anterior median eyes and the male and female sexual organs. I am convinced that the new species described here is congeneric with the type species of *Trichocyclus* in spite of a difference in position of the posterior eyes; this difference in position could very well be correlated with the height of the ocular elevation.

Trichocyclus nigropunctatus Simon, 1908

Figure 1A-F

Trichocyclus nigropunctatus Simon 1908: 407 (description female Yalgoo, Western Australia)

Lectotype

Female, by present designation, labelled "*Trichocyclus nigromaculatus*", (lapsus Simon), Western Australia leg. Michaelsen, MNHN (Collection Simon 23021).

Other material examined

1 nonadult male (ZMH), in poor condition, labelled *Trichocyclus nigropunctatus*, in handwriting Simon, Hamburg S.W.Australien Exp. 1905, Yalgoo 77, E.Simon publ. 1908, Dr.W.Michaelsen dedit 11.VII.1908, later incorrectly added: "holotype" (Rack 1961:57).

Redescription

Measurements in mm (nonadult male, Yalgoo): total length 2 mm, carapace 0.95 long, 0.95

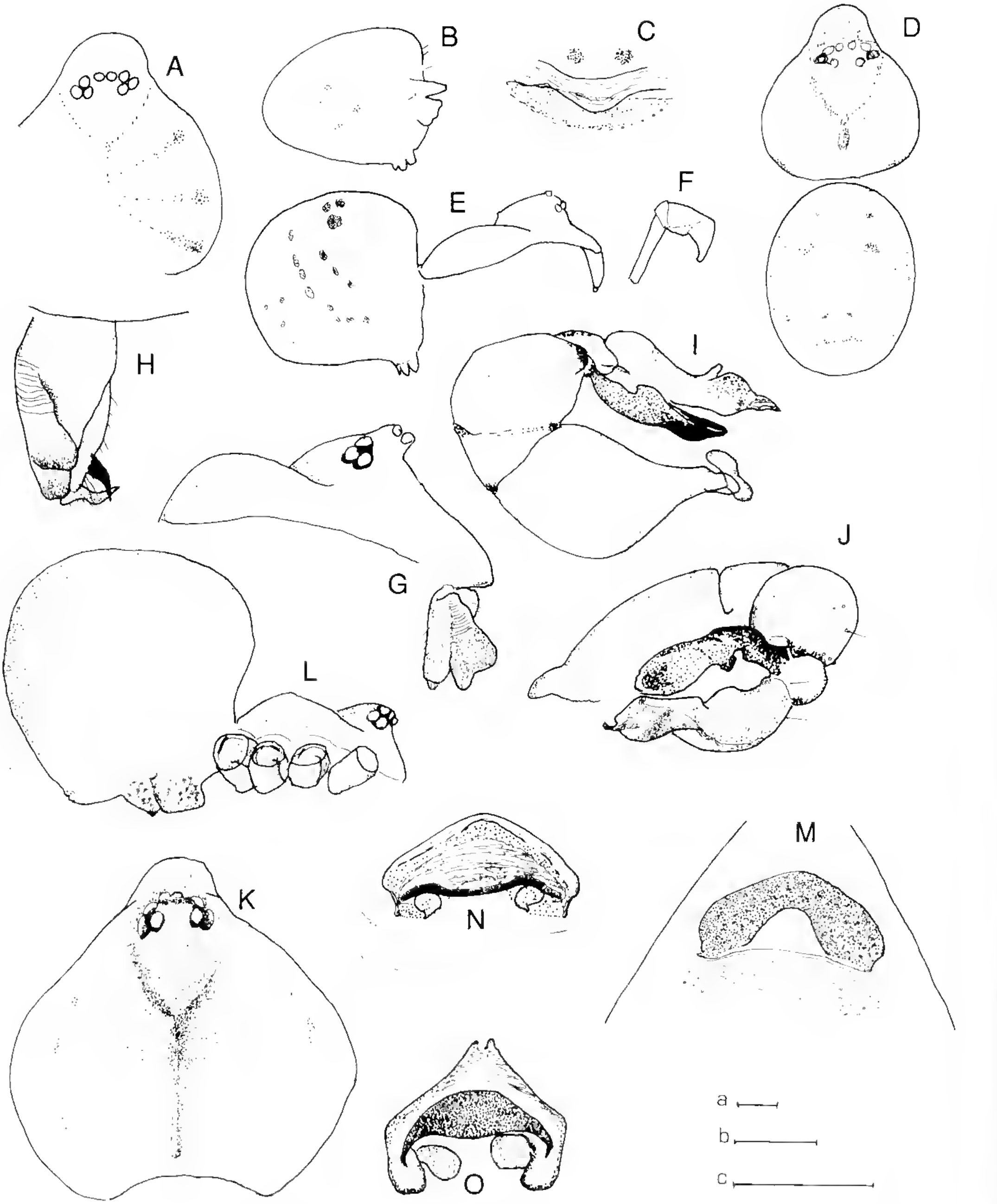

Figure 1 A-F. *Trichocyclus nigropunctatus*. A-C. Female (Lectotype MNHN 23021). **A**, eye position; **B**, abdomen, lateral; **C**, epigyne; **D-F**. Subadult male (ZMH 77, Yalgoo). **D**, carapace and abdomen, dorsal (b); **E**, id., lateral (b); **F**, palp (b). **G-N**. *Trichocyclus septentrionalis*. **G-J**. Male. **G**, carapace and chelicer, lateral (b); **H**, chelicer, front (c); **I**, right palp, lateral; **J**, id., anterior (b). **K-N**. Female. **K**, carapace (b); **L**, carapace and abdomen, lateral (a); **M**, epigyne (b); **N**, vulva, dorsal (b). **O**, *Physocyclus globosus*, vulva, dorsal (b). Scales in brackets: 0.5 mm.

wide, width eye region 0.45, abdomen 1.20 long. Legs:

	femur	patella	tibia	metatarsus	tarsus	total
I	3.70	0.35	3.45	4.10	1.20	12.80
II	3.10	0.35	2.40	3.20	0.95	10.00
III	2.15	0.35	1.70	2.40	0.80	6.60
IV	3.15	0.35	2.40	3.40	0.80	10.10
palp	0.40	patella + tibia 0.30			tarsus 0.25	

Carapace (Figure 1A,D) with darkened clypeus and foveal area, from the latter radiating dark bands, almost reaching the margin; sternum probably darkened in the middle. Abdomen (Figure 1B,D,E) with irregular groups of black spots. Eye region relatively wide, eyes approximately of equal diameter, AME slightly smaller than ALE or equal, AME ½ diameter apart, touching ALE, posterior eyerow procurved, PME 2 diameters apart, touching PLE. Chelicerae probably without stridulatory ridges. Epigyne Figure 1B,C.

Trichocyclus septentrionalis sp. nov.

Figure 1G-N

Holotype

Male, cave C.227, Cape Range, Western Australia, 22°02'49"S, 114°00'30"E, 24 May 1990, outside cave, J.M.Waldock (WAM 92/629).

Paratypes

Western Australia: Cape Range: 1 male, cave C.162, 22°09'00"S, 113°59'51"E, 22 September 1988, J.M. Waldock (WAM 91/549); 1 male, same data (WAM 91/551); 1 male, cave C.68, 22°05'48"S, 113°58'45"E, 17 May 1990, antechamber, J.M. Waldock (WAM 92/131); 1 male, cave C.106, 22°04'21"S, 114°00'39"E, 21 June 1989, M.S. Harvey (RMNH); 1 male, cave C.177, 22°06'S, 113°58'E, 7 July 1989, M. East (RMNH); 1 female, Bunbury Cave, 21°51'S, 114°043E, 27 September 1988, J.M. Waldock (WAM 91/553); 1 female, cave C.60, 22°06'05"S, 113°59'09"E, 9 July 1989, M. East (WAM 92/634); 1 female, cave C.68, 17 May 1990, antechamber, J.M. Waldock (WAM 92/633); 1 female, cave C.96, 22°15'05"S,113°57'24"E, 19 September 1988, J.M. Waldock (WAM 91/248); 1 female, cave C.111, 22°55'08"S, 114°00'17"E, 5 July 1989, (R. Wood (WAM 92/636); 1 female, id., (WAM 92/635); 1 female, cave C.147, 22°07'34"S,113°59'31"E, 23 June 1989, R. Wood (WAM 92/637); 1 female, cave C.162, 22°09'00"S, 113°59'51"E, 22 September 1988, J.M. Waldock (WAM); 1 female, id., (WAM 91/552) ; 1 female, cave C.162, 20 June 1989, M.S. Harvey (RMNH); 1 female, cave C.177, 22°06'19"S, 113°57'48"E, 7 July 1989, R. Wood (WAM 92/638); 1 female, cave C.177, 7 July 1989, M. East (WAM 92/639); 2 females, cave C.215, 22°01'40"S, 113°55'55"E, 15 July 1989, R. Young (WAM 92/640-1); 1 female, cave C.215, 15 July 1989, M. East (WAM 92/642); 1 female, cave C.224, 21°56'26"S, 114°05'40"E, 30 June 1989, M. East (WAM 92/643); 1 female, cave C.227, 22°02'49"S, 114°00'30"E, 24 May 1990, outside cave, J.M. Waldock (WAM 92/629); 1 female with egg sac, cave C.295, 22°04'11"S, 114°00'53"E, 17 August 1989, M. East (WAM 92/644); 2 females, 1 juv. male, cave C.291, 22°16'01"S, 113°57'53"E, 26 May 1990, antechamber, J.M. Waldock (WAM 92/630-632).

Diagnosis

Distinct from *T. nigropunctatus* by narrower eye region, posterior eye row recurved, different markings of the carapace, larger body dimensions, longer legs and clear differences in the epigyne.

Description

Male

Measurements in mm: male holotype: total length 4.30, carapace 1.90 long, 1.90 wide, width eye region 0.53, abdomen 2.65 long. Legs:

	femur	patella	tibia	metatarsus	tarsus	total
I	13.90	0.85	14.40	21.10	3.35	53.60
II	11.50	0.85	11.30	16.30	1.90	41.85
III	8.60	0.85	7.70	10.75	1.70	29.60
IV	11.70	0.85	10.10	14.70	1.90	39.25
palp	1.45	0.45	0.95		1.20	

Carapace and legs pale ochre, tip of femora and base and tip of tibiae lighter, head and an area on either side of the fovea dark, three pairs of lateral spots on carapace; sternum darkened in the middle. Abdomen almost white with irregular groups of black spots. Eye region (Figure 1K) relatively narrow, posterior row recurved, AME slightly smaller than ALE, on a small projection, PLE 2 diameters apart. Chelicerae (Figure 1G,H) with a proximolateral protrusion which is as large as basal segment of chelicera, proximal half with transverse grooves on the lateral surface, tip of protrusions bifid: a dorsal rounded and a ventral more or less conical tip, both darkened. Legs, particularly tibiae, metatarsi and tarsi, densely covered with stiff straight hair, 2-8 times the leg diameter. Palp as in Figure 1I,J, bulb slender, embolus in prolongation of it, paracymbium widening distally.

Female

Measurements in mm: female paratype (WAM 92/636): total length 5.30, carapace 2.15 long, 2.15 wide, width eye region 0.55, abdomen 4.10 long. Legs:

	femur	patella	tibia	metatarsus	tarsus	total
I	13.45	0.95	14.40	18.70	2.90	50.40
II	9.60	0.95	9.60	13.90	2.15	36.20
III	7.20	0.95	6.70	9.40	1.45	25.70
IV	10.10	0.95	9.10	12.75	1.90	34.80
palp	0.60	0.20	0.25		0.50	

Measurements of a small female (WAM 92/643): total length 2.90, carapace 1.20 long, 1.10 wide, width eye region 0.35, femur I 6.00. Measurements of the other specimens not much disparate to the measured specimens. Markings (Figure 1K) as in the male, AME a little smaller than laterals and almost touching them, PME only one diameter apart. Chelicerae without stridulatory ridges. Epigyne (Figure 1L,M) a chitinized pre-genital transverse arch, excavated in the middle and a post-genital tranverse strip; atrium membranous, with ventrally an arched transverse valve with a double rounded elevation in the middle, and internally (postero-dorsally) a transverse bar, hinged on lateral extremities of the epigynal plate and provided with a pair of reniform flexible appendages (Figure 1N).

Remarks

Another, closely related but smaller species was collected from a cave on Barrow Island. The material comprises one adult specimen only (female) which in this case I consider insufficient to describe.

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FIRST RECORD OF A SPATANGOID ECHINOID FROM THE PALEOCENE OF THE PERTH BASIN, WESTERN AUSTRALIA

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ABSTRACT

A new species of a spatangoid echinoid, *Hemifaorina? rex*, is described from the upper part of the Late Paleocene Kings Park Formation. The outer layer of the test of the material upon which the species is based is not preserved. Consequently, the lack of preservation of fascioles makes the generic assignment tentative. This represents the first echinoid species described from the Tertiary of the Perth Basin. *Hemifaorina* had previously only been described from the Miocene of Java.

INTRODUCTION

During the construction of the Narrows Bridge across the Swan River in Perth, Western Australia in the early 1970's a number of caissons were driven deep into the Kings Park Formation. Two of these caissons, N6 L2 and N6 L3, situated north-west of the elevated road that leads off the southern end of William Street onto the northern approach road to the Narrows Bridge (Narrows Interchange Project locality of Quilty, 1974a), yielded a quantity of fossil material, including, in addition to a hitherto undescribed species of echinoid, molluscs and corals. Collections made by Mr P.R.I. Saunders of the Main Roads Department and Mr G.W. Kendrick of the Western Australian Museum in November 1971 contain, in addition to the echinoid, the nuculanid bivalve *Sarepta* sp., the propeamussiid bivalve *Parvamussium* sp., the carditid bivalve cf. *Glans* sp., the laternulid bivalve cf. *Laternula* sp. and a generically indeterminate pectinid bivalve; the scaphopod *Laevidentalium* sp.; the turbinellid gastropod *Columbarium* sp.; an indeterminate naticid gastropod; and indeterminate corals, cephalopods and possible annelids (G.W. Kendrick, pers. comm.).

This paper describes the echinoid material from this collection and, questioningly, places it in the schizasterid echinoid genus *Hemifaorina*. This genus has previously only been described from the Miocene of Java (Jeannet and Martin 1937).

AGE AND STRATIGRAPHY

Seven echinoids, all assignable to the same species, were collected from Caisson N6 L3 at a level 5 m below the top of the Kings Park Formation. At this location the top of the Kings Park Formation is 32 m below State mean sea level (SMSL). The bottom of the Kings Park Formation in this caisson was in excess of 300 m below SMSL (Quilty 1974a). In the Perth region the formation is known to reach over 500 m in thickness (Playford *et al.* 1975), but nowhere does it outcrop at the surface.

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The Kings Park Formation consists of dark, glauconitic shales, siltstones and sandstones. The lithology of the top of the section from where the echinoids were collected consists of a dark-grey, glauconitic, fine-grained, lithic sandstone, rich in small shell fragments. McGowran (1964) regarded the entire Kings Park Formation as being of Late Paleocene age. However, Quilty (1974a,b) considered that the formation ranges in age from Late Paleocene to Early Eocene (planktonic foraminiferal zones P4 - 6). According to Quilty (1974b) the Kings Park Formation onshore is entirely Late Paleocene (P4) in age. His analysis of material from the Narrows Interchange revealed that the formation was entirely of Late Paleocene age. Consequently, the newly described species of *Hemifaorina?* is assigned a Late Paleocene age.

The Kings Park Formation is considered (Quilty 1974a) to have been deposited in a shallow marine environment, on the basis of the faunal elements. The thick sequence close to the course of the present Swan River represents infilling of a deep valley incised into underlying sediments by an ancestral Swan River. This valley may have connected with the Perth Canyon which cuts the continental slope west of Rottnest Island (Cockbain 1990).

MATERIALS AND METHODS

All specimens of the new species are housed in the invertebrate palaeontology collections of the Western Australian Museum (WAM). A specimen referred to with the prefix RGM is from the collections of the Nationaal Natuurhistorisch Museum, Leiden. All of the specimens from the Kings Park Formation have been dorso-ventrally flattened; thus it was not possible to measure test height. Measurements were made with an electronic calliper to an accuracy of 0.1 mm. A number of parameters are expressed as percentages of test length (%TL).

SYSTEMATIC PALAEONTOLOGY

Order Spatangoida Claus, 1876

Family Schizasteridae Lambert, 1905

Genus *Hemifaorina?* Jeannet and Martin, 1937

Type species

Hemiaster tuber Herklots 1854; by original designation of Jeannet and Martin 1937, p.289.

Remarks

Members of the Schizasteridae are usually (although not always) distinguished from members of the Hemiasteridae by the presence of a complete lateroanal fasciole. Notable exceptions include the schizasterids *Proraster*, in which the lateroanal fasciole may be incomplete or absent; *Abatus*, in which a lateroanal fasciole is present in the juvenile, but lacking in the adult stage; and *Amphineustes*, which lacks both fascioles. Furthermore, in *Brisaster*, the lateroanal fasciole may be absent or reduced in the adult (Mortensen 1951); in *Tripylus*, *Parabrissus* and *Hemifaorina* the lateroanal fasciole is incomplete; and in *Kina* it is absent (Henderson 1975). While the nature of the apical system can also assist in the familial emplacement of genera, as with the fascioles, there are exceptions to the general rule of the Schizasteridae possessing an ethmolyic apical system and the Hemiasteridae having an ethmophract apical system.

In the case of the Kings Park Formation spatangoid although the fascioles are absent, due to the nature of the preservation, the presence of an ethmolytic apical system with four gonopores would seem to indicate that it is a schizasterid. Furthermore, the presence on the aboral surface of petals that show a distinct inequality of length, with the anterior being much longer than the posterior, is a feature of a number of schizasterids. The presence of only a faint anterior notch, and the form of the petals, is a combination only found in one poorly known schizasterid, *Hemifaorina* from the Miocene of Java (Jeannet and Martin 1937). Although the hemiasterid *Hemiaster (Trachyaster)* has an ethmolytic apical system with four genital pores, most species assigned to the subgenus *Trachyaster* possess deeper petals and a more pronounced anterior notch than the Kings Park Formation spatangoid. Furthermore *Trachyaster* species have more widely divergent anterior petals and less disparate petal lengths. Thus the Kings Park Formation spatangoid is morphologically closest to *Hemifaorina.*

Although Mortensen (1951) characterised *Hemifaorina* as possessing both peripetalous and lateroanal fascioles, he omitted to point out that the lateroanal fasciole was incomplete. Inspection of type material of *Hemifaorina tuber* has revealed that the lateroanal fasciole is only present as a thin thread beneath the periproct, as in some specimens of *Proraster* (McNamara and Philip 1980). *Hemifaorina* is characterised by its ovoid test outline; poorly defined anterior notch, apical system set just posterior of centre; moderately depressed ambulacrum III aborally; and broad petals, the anterior of which are not highly divergent and which are much longer than the very short posterior petals, being about three times their length. All of these features are shared by the Kings Park Formation schizasterid, and indeed it is hard to distinguish between the two forms on the basis of aboral coronal characteristics alone.

Hemifaorina? rex sp. nov.

Figures 1, 2A

Holotype

WAM 71.1518 (Figures 1A,B;2A) from Perth, Western Australia; at a depth of 35 m below SMSL in Caisson N6 L3 of Narrows Interchange system, which is beneath slipway leading from William Street onto the Narrows Bridge, close to junction of William Street with The Esplanade; Kings Park Formation (Late Paleocene, planktonic foraminferal zone P4), 5 m below the top of the formation.

Paratypes

WAM 71.1502-71.1507 from same horizon and locality as the holotype.

Etymology

From the Latin *rex*, meaning 'king', alluding to the occurrence of the species in the Kings Park Formation.

Diagnosis

Ambulacrum III with about 20 near transverse pore pairs aborally; peristome small; labrum almost transverse anteriorly, not projecting anteriorly across labrum; posteriorly initially strongly constricted, before widening to about peristome width where abuts plastron.

Description

Test outline subcircular, reaching up to 46 mm TL; anterior notch weakly developed; although all specimens have been crushed to varying degrees, it is apparent that the test is highest posteriorly in interambulacrum 5, midway between apical system and posterior ambitus, forming a distinct keel; original height unknown due to effects of compaction; test slightly wider than long ranging between 97-98%TL. Apical system posteriorly eccentric, 54-56%TL from anterior ambitus; ethmolytic, with four genital pores.

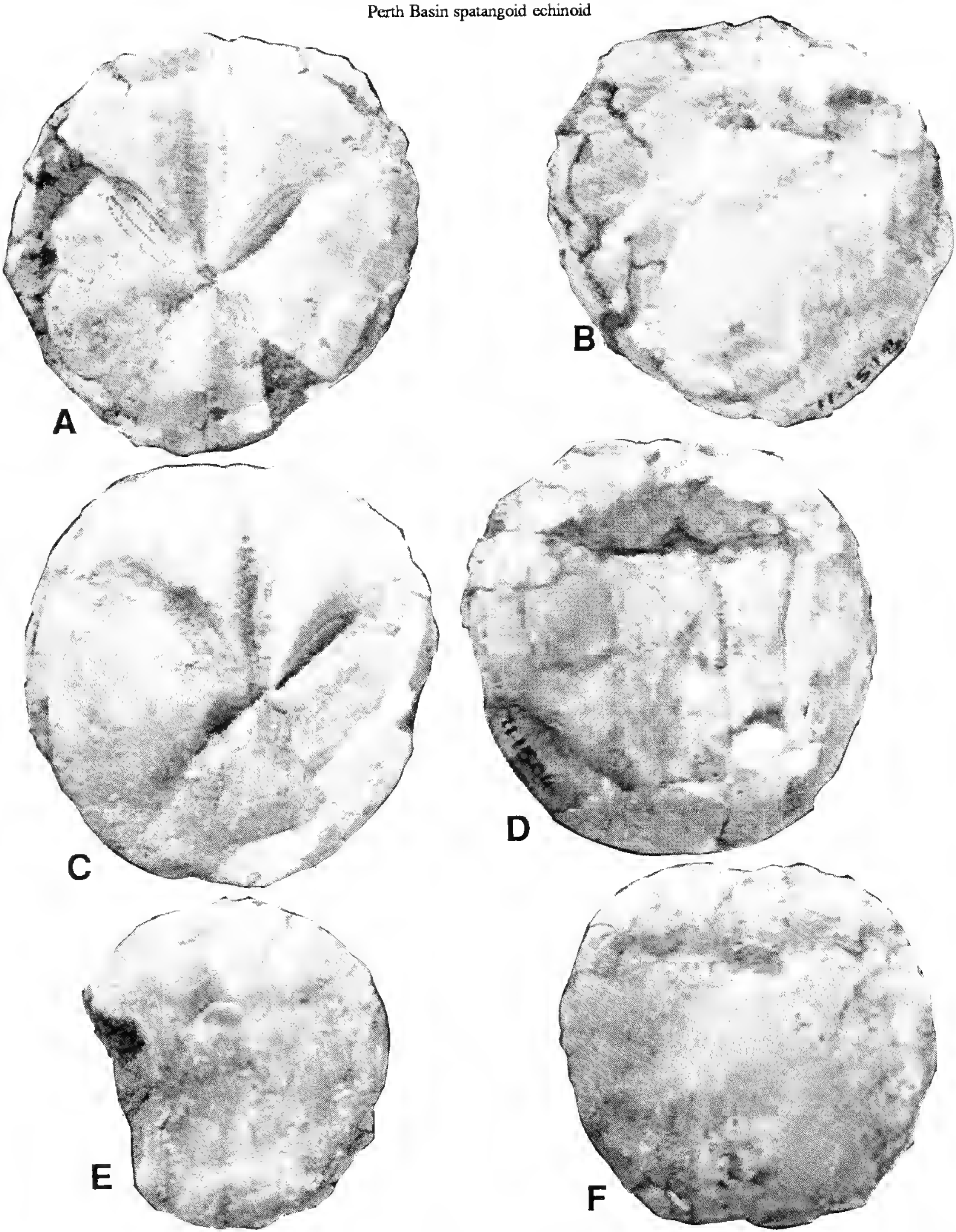

Figure 1 *Hemifaorina? rex* sp. nov, Kings Park Formation (Late Paleocene) from Caisson N6 L3 of Narrows Interchange system, Perth, Western Australia. **A**, **B**, WAM 71.1518, holotype, aboral and adoral views respectively; **C**,**D**, WAM 71.1504, paratype, aboral and adoral views respectively; **E**, WAM 71.1503, paratype, adoral view; **F**, WAM 71.1502, paratype, adoral view; all x1.4.

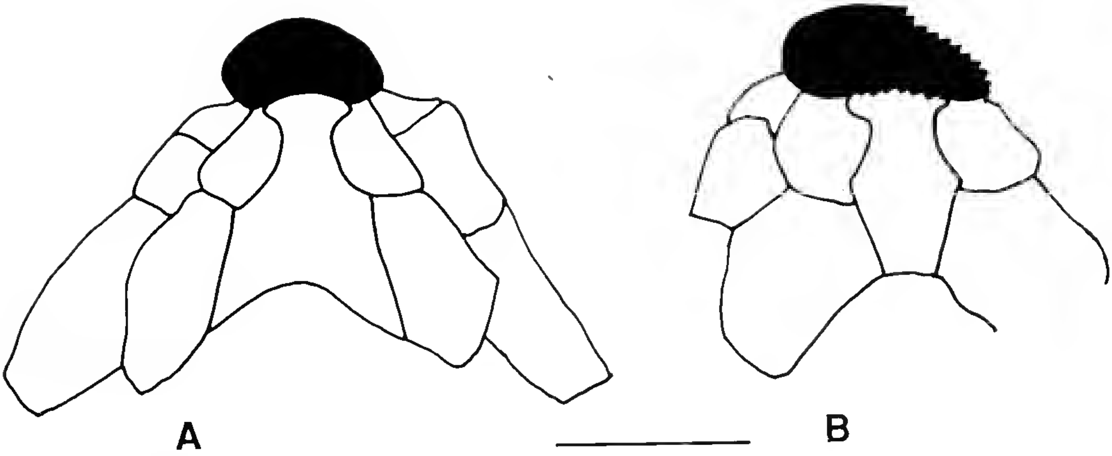

Figure 2 A, labrum of *Hemifaorina? rex* sp. nov, WAM 71.1518; **B**, labrum of *Hemifaorina tuber* (Herklots), RGM 4280. Bar represents 5 mm.

Ambulacrum III relatively broad, rows of pore pairs about 10%TL apart; moderately incised close to apical system, but shallows a little abapically; bears about 20 pore pairs, within a pair each pore separated by raised interporal partition; pores almost transversely aligned in a pair (Figure 1A); slightly oblique adapically. Anterior petals deep; broad, width 10-13%TL; diverge anteriorly at about 90°; slightly flexed antero-laterally; relatively long, 30-31%TL in two specimens (WAM 71.1518 and 71.1504), but 35%TL in WAM 71.1502; bear about 38 pore pairs; pores within each pair widely spaced, elongate, not conjugate. Posterior petals also deep; much shorter than anterior, 10-12%TL, that is about one-third the length of anterior petals; bear about 16 pore pairs in each row.

Peristome narrow, width 10-13%TL; slightly sunken; form of phyllode unknown; peristome situated 20-22%TL from anterior ambitus. Labrum long, up to 12%TL; decreases slightly in width posteriorly initially, then progressively widens posteriorly to become wider than peristome and over twice width at constriction (Figure 2A); anteriorly labrum does not project forward. Plastron length 43%TL; width 36%TL; almost flat; like some other adoral interambulacral plates on specimen WAM 71.1502 (Figure 1F) has five prominent growth lines on the plastron arranged around a central growth line-free area. Periproct unknown.

Discussion

The aboral surface of the test of *Hemifaorina? rex* is almost identical to that of the Javanese Miocene species *Hemifaorina tuber* (Herklots 1854), both species sharing the characteristic features of the genus, notably a very shallow anterior notch and very short posterior petals that are about one-third the length of the anterior pair (Jeannet and Martin 1937, Fig.60). The only way that the two species can be distinguished is in the shape and size of the peristome and labrum. In *H? rex* the peristome is 10-13%TL in width, whereas in *H. tuber* it is 15-16%TL wide. The labrum of *H? rex* differs from that of *H. tuber* in being very wide posteriorly. In *H. tuber* the labrum is similar to that of *H? rex* anteriorly, but instead of continuing to widen posteriorly from the median constriction, it narrows close to the plastron (Figure 2B). This occurs because of lateral growth of the adjoining ambulacral plates.

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A NEW SPECIES OF THE SURF-INHABITING ATHERINIFORM *ISO* (PISCES: ISONIDAE)

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ABSTRACT

Specimens of an atheriniform fish collected in the American Samoa and Pitcairn Island are described as a new species of *Iso*. On external morphology, it is distinct from all other members of the genus except for *Iso hawaiiensis*, with which it shares gill raker, midlateral and vertebral counts. Using a novel procedure to study small bones with a scanning electron microscope, *Iso nesiotes* is shown to be unique in having a short coracoid, long dorsal processes of the urohyal, and the third orbital possessing a lateral shelf. From its closest relative, *Iso hawaiiensis*, the new species can be distinguished by absence of the intercalar, structure of the pectoral girdle and the shapes of the opercle and haemal spines. Externally, the new species is recognised by the absence of an oval spot on the caudal peduncle. The two populations of *Iso nesiotes* show minor differences in the position of anus and in fin ray, gill raker and scale counts. A key to the species of *Iso* is also given.

INTRODUCTION

Members of the family Isonidae are difficult to catch because of their preferred habitat, the surf. They are therefore not well known and have no common name. Ogilby (1895) referred to them as surf fishes whilst Jordan and Starks (1901) used translations of Japanese: "shore sardines" or alternatively, "flowers of the wave". Since isonids are not sardines, "flowers of the wave" seems to be a more apt description of silvery fish buffeted by the surf.

In the various studies of the group, nomenclatorial and some systematic problems were more or less resolved over the years: *Iso* Jordan and Starks, 1901 replaced the preoccupied name *Tropidostethus* Ogilby, 1895 (Waite 1904). Schultz, in 1948, placed "flowers of the wave" into a subfamily of their own but created confusion by erecting Tropidostethinae, (see Schultz 1948, 1950; Ivantsoff 1984, 1986). Rosen (1964) finally erected Isonidae but based his description on the second genus of the family, *Notocheirus hubbsi* Clark, 1937. On the basis of Said's (1987) more recent studies, it is now clear that the family Isonidae is monogeneric. *Notocheirus hubbsi* which was variously placed together with *Iso* in Notocheirinae, Notocheiridae or Isonidae, warrants a family of its own, Notocheiridae, which is monotypic. Notocheiridae and Isonidae are regarded as sister groups but are distinct from one another on the basis of absence of first dorsal fin, presence of appendages on body scales, pelvic bones with ventral process in Notocheiridae, versus presence of first dorsal fin, lack of appendages on body scales and with no ventral process on pelvics in Isonidae. In addition, other autapomorphic characters distinguish the families (Said 1987).

Isonids have been reviewed on a number of occasions (Herre 1944; Gosline 1952) but the last major study by Said (1983) is still awaiting publication. Said recognised only five nominal species including the one described herein. He considered *Iso flosindicus* Herre (1944) to be indistinct from *I. natalensis* Regan (1919) which has priority.

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MATERIALS AND METHODS

Morphometrics and meristics

Methods of measuring and counting used by previous workers (Herre 1944; Gosline 1952) on the genus *Iso* are used in this study. Standard length (SL) is taken from most anterior tip of mouth to midbase of caudal fin (end of hypural plates). Head length is measured from tip of snout to posterior edge of opercle. Body depth is vertical measurement at origin of pectoral fin. Width of midlateral silvery band is measured along vertical line through origin of anal fin. Length of caudal peduncle is taken from rear of origin of last anal fin ray to end of hypural plates. Caudal peduncle depth is least depth of caudal peduncle near end of lateral band. Eye measurement is the horizontal diameter of orbit. Distance between dorsals is the measurement between origin of two dorsal fins. Snout length is taken from anterior tip of mouth to anterior border of orbit. Anal-anus is the measurement between posterior end of anus and origin of anal fin. Midlateral scales are counted from dorsal origin of pectoral fin to hypural joint. Gill raker count includes all rudiments in the first lower gill arch and rakers in the angle of the arch.

Osteology

Osteological descriptions are those used by Patterson (1964) and Rosen (1964). Specimens were cleared and stained following Taylor (1967). The specimens were then stored in 100% glycerol. The bones were either drawn with the aid of a camera lucida attachment to a dissecting microscope or subjected to further preparation for scanning electron microscopy as described below. Although a similar technique has been used for eggs and larvae (Boehlert 1983) as well as scale preparation and analysis (Hughes 1980) the technique for preparation of small fish bones for minute examination has not, to our knowledge, been described in literature. The technique used is therefore presented below.

The neurocranium and other delicate bones of fresh, stained or preserved specimens can be best observed and studied under the scanning electron microscope (SEM) (Figure 3A-C).

1. If the specimen has been previously cleared and stained, the glycerol is removed by washing in 50% ethanol.
2. The specimen is placed in 1-2% cold solution of sodium hypochlorite (bleaching agent) and examined under a dissecting microscope. Epithelial tissues will dissolve rapidly whilst the ligaments and muscles will persist. A small soft haired paint brush should be used to move away the remaining tissues which can then be picked up by fine forceps. Breaking the skin of the specimen before immersion will reduce the maceration and bleaching time which is important to prevent disarticulation.
3. The specimen is returned to 50% ethanol to arrest the action of the bleaching agent.
4. The specimen is dehydrated by immersion in ever increasing concentration of ethanol (10% increase at each step for 30 minutes) to 100% solution.
5. To avoid damage due to surface tension, the specimen is then dried using the critical point drying method in a Sorvall Critical Point Drying System where the dehydrated specimen is treated with liquid CO_2, taken to a temperature of 31°C and pressure of about 7580kp.
6. The specimen is mounted and attached to an aluminium stub with silver tape treated with an adhesive on both sides. This provides a smooth conductive background and allows the specimen to adhere to the stub.
7. The specimens are coated with thin layer of gold (about 8nm in 8 seconds) in a polatron spatter coater.

The specimen is then ready for examination under a Robinson back-scatter detector in a Scanning Electron Microscope. Mounted specimens should be stored in a cool, dry place for subsequent use.

The material examined has been deposited in the following institutions: The Australian Museum, Sydney (AMS); British Museum (Natural History), London (BMNH); Bernice P. Bishop Museum, Honolulu (BPBM); California Academy of Sciences, San Francisco (CAS); United States National Museum, Washington (USNM).

KEY TO THE SPECIES OF THE GENUS *ISO*

Said's (1983) revision of the genus includes a description of new species and synonymy of another. A new key to the species of *Iso* is therefore presented in this study. The species are best identified on the basis of their osteology but for field identification, external characters are easier to use. A detailed osteological key will be published in a complete revision of both families, Isonidae and Notocheiridae.

1. Midlateral band discontinuous at caudal peduncle with silvery oval spot present near caudal fin base 2

   Midlateral band continuous; no silvery oval spot present near caudal fin base (Figure 1) 3

2. Teeth on external surface of premaxilla clearly visible; palatine teeth usually present. Midlateral scale count 41-66 .... *I. natalensis*

   No teeth on external surface of premaxilla. Palatine teeth also absent. Midlateral scales 34-55 4

3. Midlateral band extending halfway along caudal peduncle; midlateral scales 35-41 .... *I. nesiotes*

   Midlateral band extending to hypural joint; midlateral scales 50-63 .... *I. flosmaris*

4. Midlateral scales 34-39. Teeth extending more than half way along free edge of premaxilla .... *I. hawaiiensis*

   Midlateral scales 42-55. Teeth restricted to first quarter along free edge of premaxilla in Taiwanese and Japanese populations (c.f. Figure 2A); as for *I. hawaiiensis* in Australian populations .... *I. rhothophilus*

SYSTEMATICS

Family Isonidae Rosen, 1964

Genus *Iso* Jordan and Starks, 1901

Iso nesiotes sp. nov.

Figures 1-3

Iso sp. Wass 1984: 9.

Holotype

AMS I.24183-001, 25.5 mm SL, Fagasa, Tutuila Island, American Samoa, 14°10'S 169°38'E, collected by R.C. Wass, June 6, 1980.

Paratypes

33 specimens, AMS I.24182-001, (15), 19.2-26.6 mm SL, (including 5 stained specimens); BMNH 1983.10.20.1-2, (2), 23.7-25.1 mm SL; BPBM 29308, (1), 24.6 mm SL; CAS 52304, (3), 25.6-26.1 mm SL; USNM 263125, (3), 23.1-25.3 mm SL. Data as for the holotype. BPBM 16718, (9), West Harbour, Pitcairn Island, 25°04'S 130°06'W, 17.8-25.6 mm SL.

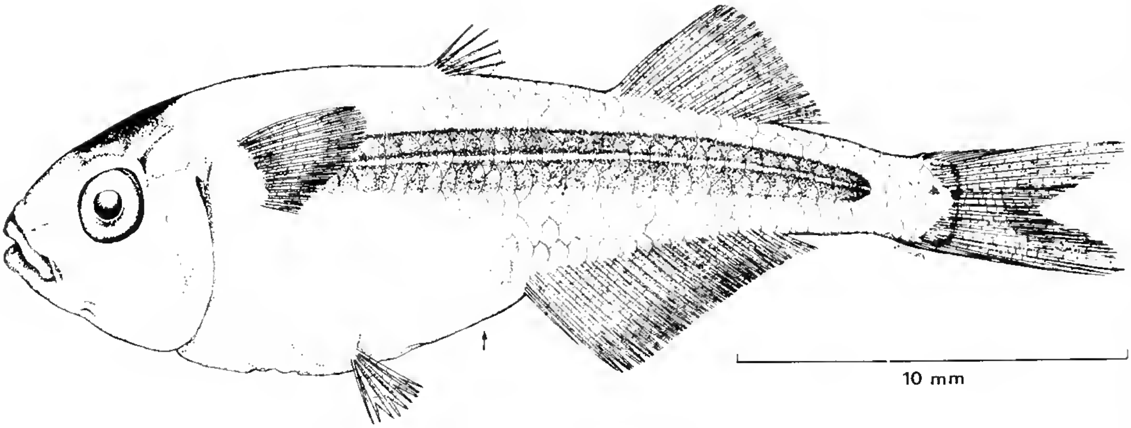


Figure 1 *Iso nesiotes*, paratype AMS I.24182-001, 24.4 mm SL.Arrow indicates position of anus. Second dorsal, ventral, pectoral and anal fin rays are preceded by a weak spine.

One of the nine Pitcairn specimens was specially processed for the osteological study in addition to the paratype AMS I.24182-001. All comparative work was done on the material used by Said (1983).

Diagnosis

Iso nesiotes can be distinguished from all other species of the genus by the following: no oval spot near caudal-fin base (Figure 1); third infraorbital with lateral shelf (Figure 2B). posterior dorsal processes of urohyal very long and extending vertically (Figure 2C a); coracoid very short (Figure 2D a). Intercalar absent in *I. nesiotes* (Figure 3A) but present in *I. hawaiiensis* Gosline, 1952 (Figure 3B). In other species, intercalar absent but with pterotic extending laterally in that region to lie over exoccipital (Figure 3C).

Description

All measurements and counts taken from the holotype, paratypes and specimens by locality are presented in Table 1. Measurements descriptive of the species throughout its known range are presented below.

Morphometrics (expressed as means and ranges)

Head 4.5 (4.1-5.0); greatest body depth 3.4 (2.7-4.1); width of lateral silvery band 15.3 (13.8-17.8); caudal peduncle length 5.6 (4.7-7.3); least depth of caudal peduncle 14.1 (12.5-16.2), all in SL; eye in head 2.6 (2.4-3.0); snout in eye 1.3 (1.0-1.6).

Meristics

Midlateral scales 38.2 (35-41); first dorsal fin 5.0(4-6), second dorsal fin rays 13.9 (12-16); anal fin rays 21.4 (19-24); pectoral fin rays 12.2 (11-13). Rays in last 3 fins preceded by one spine and one unbranched ray. Gill rakers in first lower gill arch 9.7 (9-12). Vertebrae 37.4 (36-39).

External morphology

Body highly compressed, head small, snout rounded. Mouth very oblique to horizontal, upper jaw not protractile; lower jaw deeply elevated posteriorly. Teeth on jaws small, curving backwards into mouth. Gill rakers well developed and moderately long, equal to one diameter of pupil. Gill

Table 1 Measurements and counts for the holotype and paratypes of *Iso nesiotes*. Also a comparison of populations from American Samoa and Pitcairn Island expressed as means, ranges and standard deviation. Abbreviations: N, number of specimens; D1, first dorsal fin; D2, second dorsal fin.

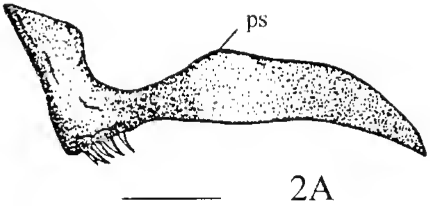
Character	Holotype	Paratypes		Paratypes		Paratypes	
		American Samoa N=25		Pitcairn Island N=9		Total sample N=35	
Morphometric values							
In SL							
Head	4.5	4.5(4.1-5.0)	0.25	4.4(4.3-4.9)	0.20	4.5(4.1-5.0)	0.23
Body depth	3.0	3.3(2.7-3.8)	0.30	3.6(3.0-4.1)	0.37	3.4(2.7-4.1)	0.31
Width silvery band	14.6	14.9(13.8-16.3)	0.67	16.5(15.0-17.8)	0.96	15.3(13.8-17.8)	0.74
Caudal peduncle Length	5.9	5.5(5.0-6.1)	0.35	5.8(4.7-7.3)	0.77	5.6(4.7-7.3)	0.46
Caudal peduncle Depth	13.4	13.9(12.5-14.9)	0.70	14.7(13.9-16.2)	0.72	14.1(12.5-16.2)	0.71
In Head							
Eye	2.5	2.6(2.5-2.8)	0.10	2.7(2.4-3.0)	0.22	2.6(2.4-3.0)	0.13
Interorbital	2.5	2.7(2.4-3.0)	0.18	3.0(2.6-3.3)	0.22	2.8(2.4-3.3)	0.19
D1-D2	1.2	1.3(1.0-1.6)	0.15	1.4(1.2-1.7)	0.14	1.3(1.0-1.7)	0.15
In Eye							
Snout length	1.3	1.3(1.0-1.6)	0.13	1.4(1.3-1.6)	0.10	1.3(1.0-1.6)	0.12
Anal-anus	1.1	1.2(0.8-1.6)	0.21	1.7(0.8-3.1)	0.78	1.3(0.8-3.1)	0.36
Meristic values							
Pectoral fin rays*	13	12.1(11-13)	0.53	12.3(11-13)	0.71	12.2(11-13)	0.57
D1 fin spines	6	5.1(4-6)	0.40	4.8(4-5)	0.44	5.0(4-6)	0.41
D2 fin rays*	14	14.0(12-16)	1.02	13.8(13-14)	0.44	13.9(12-16)	0.87
Anal fin rays*	23	21.4(19-24)	1.15	21.4(20-22)	0.73	21.4(19-24)	1.03
Gill rakers	9	9.3(9-10)	0.48	10.8(10-12)	0.78	9.7(9-12)	0.90
Midlateral scales	41	38.4(35-41)	2.00	37.8(35-39)	1.28	38.2(35-41)	1.81
Vertebrae	38	37.3(36-39)	0.85	37.9(37-39)	0.26	37.4(36-39)	0.87

* Spines of the fins excluded from the count

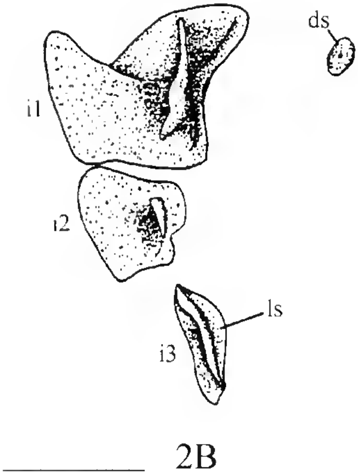
slit behind last gill arch present. Anus close to origin of anal fin. First dorsal fin originating about middle of body, its small weak spines of about equal length. Second dorsal fin originating behind vertical through anal origin; both second dorsal and anal fins high anteriorly but tapering downwards posteriorly. Pectoral short and inserted high on body. Scales cycloid and small. Sides of head and anterior part of abdomen naked. Scaled part of body (Figure 1) originating at dorsal origin of pectoral and extending upwards and backwards to first dorsal origin and rest of body. Midlateral band wide, silvery in live fish, extending from base of pectoral and terminating midway along caudal peduncle.

Osteology

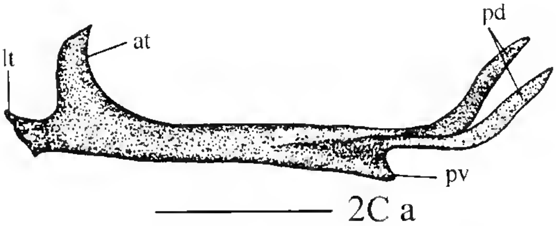
Premaxilla with one postmaxillary process; teeth restricted to first anterior fifth of free edge of premaxilla (Figure 2A). Third infraorbital with lateral shelf; dermosphenoid rounded (Figure 2B). Urohyal with short posterior ventral process and with very long posterior dorsal processes extending vertically (Figure 2C a). Cleithrum reaching scapular foramen; cleithrum process absent (Figure 2D a). Opercular notch on dorsal edge present (Figure 2E a). Intercalar absent (Figure 3A); pterotic projection on exoccipital absent (Figure 3A). Parietals small, not forming part of posttemporal fossa. Pelvic girdle with anterior lateral process longer than posterior ventral process. Pleural ribs 9-11. Middle vertebrae with very long posterior ventral zygapophyses.



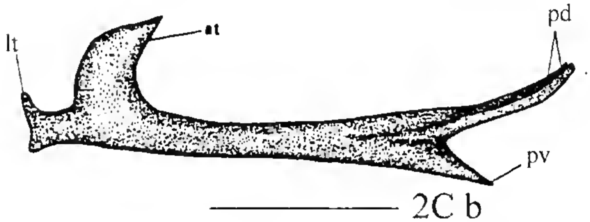
2A



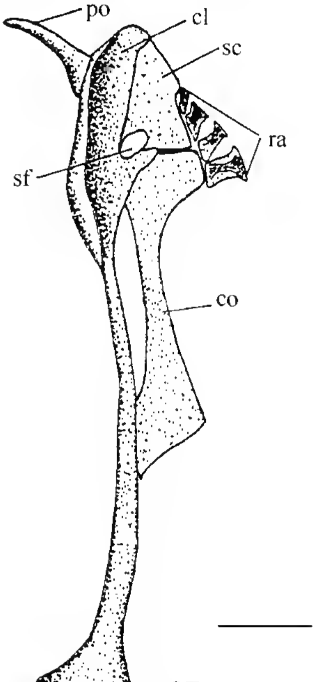
2B



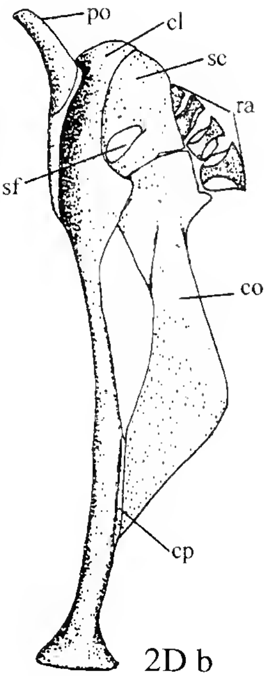
2C a



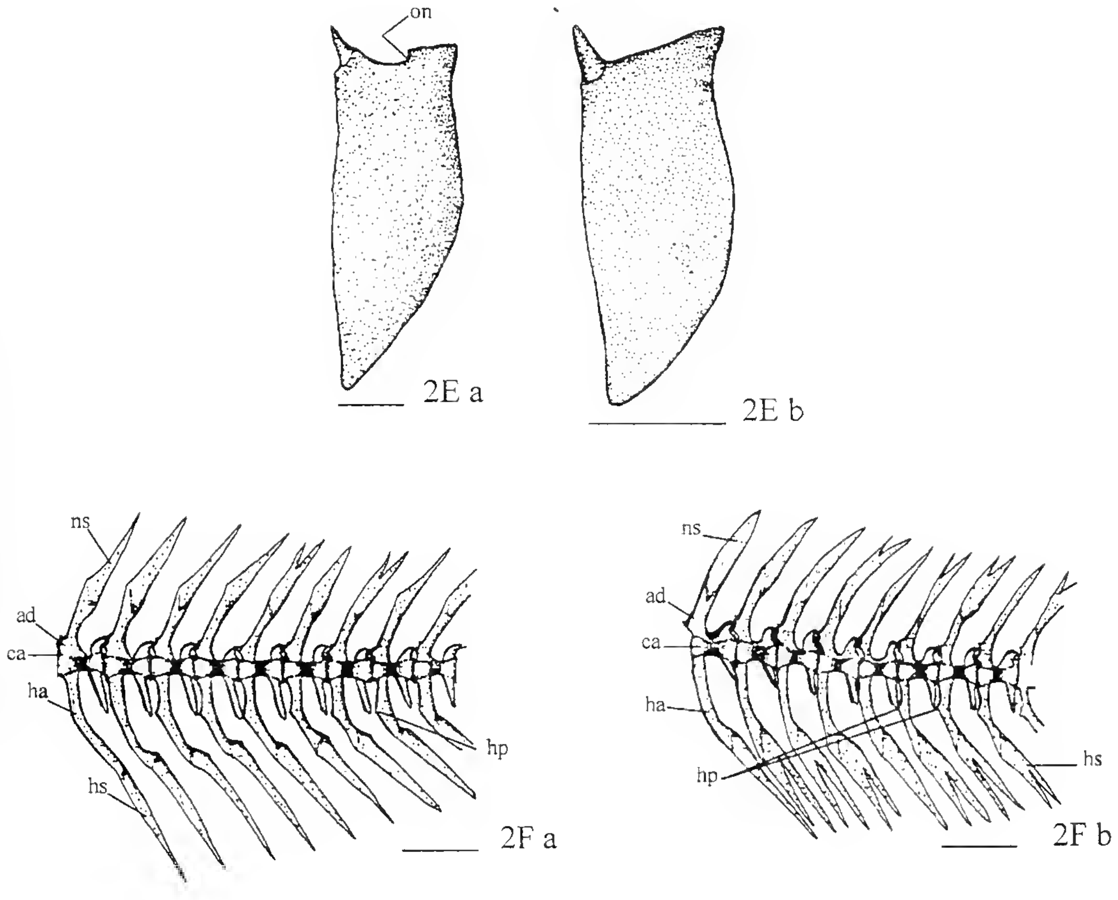
2C b



2D a



2D b



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◀ **Figure 2** *Iso nesiotes*, American Samoa, AMS I.24182-001, 26.6 mm SL, cleared and stained specimen. Scale 1 mm.

A. Premaxilla
B. Left infraorbitals
C. a. Urohyal b. Urohyal of *I. hawaiiensis* for comparison
D. a. Pectoral girdle b. Pectoral girdle of *I. hawaiiensis* for comparison
E. a. Opercle b. Opercle of *I. hawaiiensis* for comparison
F. a. Haemal elements. b. Haemal elements of *I. hawaiiensis* for comparison

Abbreviations

ad	anterior dorsal zygapophysis
at	antero-dorsal process of urohyal
ca	first caudal vertebra
cl	cleithrum
co	coracoid
cp	cleithrum process
ds	dermosphenoid
ha	haemal arch
hp	haemal arch process
hs	haemal spine
il-i3	infraorbitals 1-3
lt	process of ligament to hypohyal
ls	lateral shelf of third infraorbital
ns	neural spine
on	opercular notch
pd	posterior dorsal process of urohyal
po	posttemporal
ps	postmaxillary process of premaxilla
pv	posterior ventral process of urohyal
ra	proximal radials
sc	scapular
sf	scapular foramen

Colour

Preserved specimens from type locality whitish, with silvery midlateral band. Pitcairn specimens uniformly brown with darker brown midlateral band.

Variability

A number of minor variations were observed (Table 1) between the populations from American Samoa and Pitcairn Island. The Samoan population exhibits a wider range in the number of second dorsal rays, anal rays and midlateral scales. The mean for the width of the silvery midlateral band in the Pitcairn Island population is higher. The range of variation for the position of anus in relationship to the origin of anal is greater in the Pitcairn Island specimens. In the Samoan fish, the gill raker count and the ratios of anus to anal fin in eye, and least depth of caudal peduncle

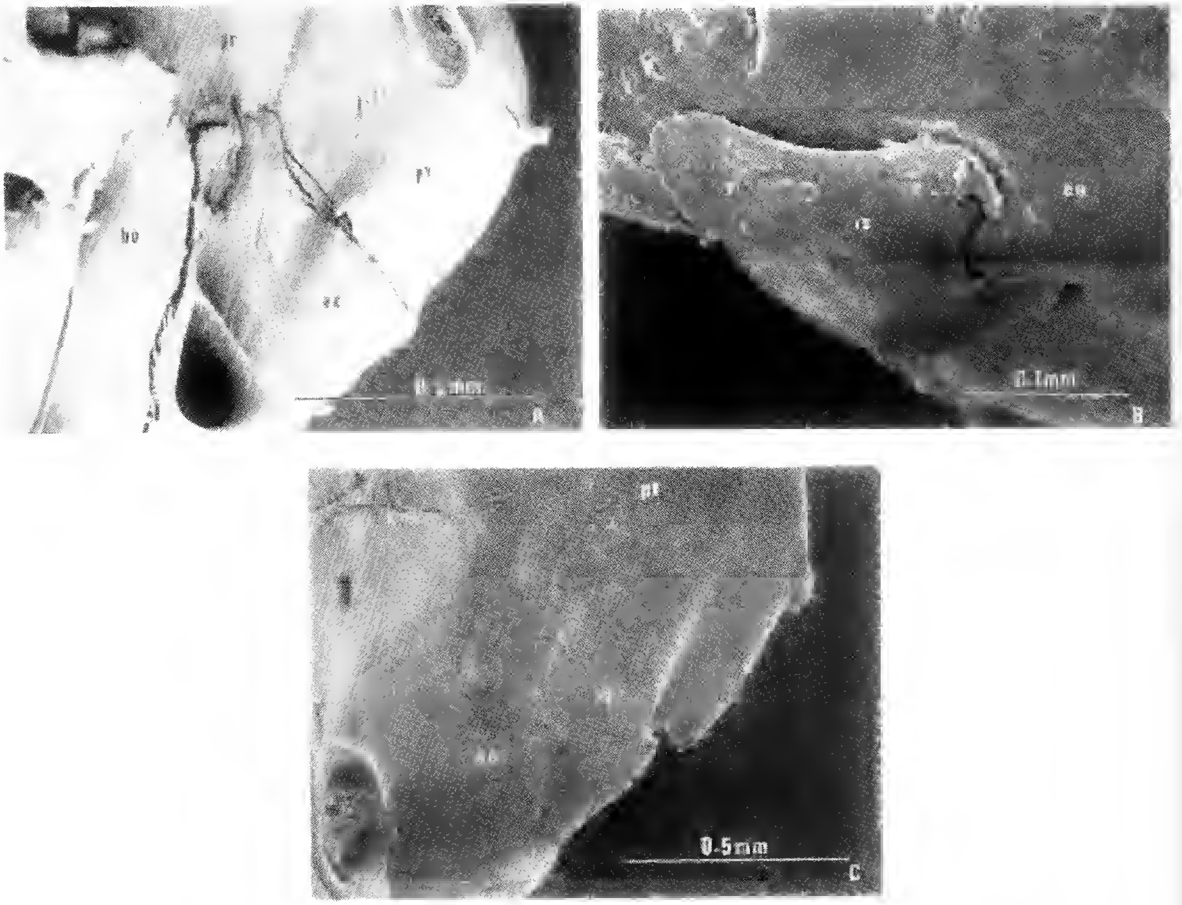

Figure 3 Scanning electron micrographs showing posteroventral views of skulls of A, *Iso nesiotes*, AMS I.24183-001 paratype, 25 mm SL, American Samoa. B, *I. hawaiiensis*, BPBM 10012, 28 mm SL, Hawaiian Islands. C, *I. flosmaris*, SOSC VGS-68-30*, 52 mm SL, Taiwan.

Abbreviations

bo	basioccipital	ic	intercalar	pr	prootic
eo	exoccipital	pj	pterotic projection	pt	pterotic

* Smithsonian Oceanographic Sorting Center, Washington D.C., field registration number.

Table 2 Comparison of measurements and counts of five species of *Iso* (from Said 1983). Data presented as in Table 1.

Character	*I. rhothophilus*[1] N=83	*I. natalensis*[2] N=121	*I. flosmaris*[3] N=53	*I. hawaiiensis*[4] N=15	*I. nesiotes*[5] N=35
Body depth/SL	3.9(3.1-5.1) 0.43	4.1(3.3-5.1) 0.43	4.5(3.4-5.4) 0.38	3.9(3.3-4.6) 0.45	3.4(2.7-4.1) 0.36
Gill rakers	11.3(9-14) 1.04	11.2(10-14) 0.97	13.6(12-15) 0.87	10.4(9-12) 0.86	9.7(9-12) 0.90
Midlateral scales	48.8(42-55) 2.87	50.9(41-66) 6.15	57.6(50-63) 3.49	37.4(34-39) 1.20	38.2(35-41) 1.88
Vertebrae	41.6(38-45) 1.68	40.3(38-42) 0.87	43.2(41-45) 0.93	38.6(37-40) 0.85	37.4(36-39) 0.87

[1] East and west coasts of Australia, Japan and Taiwan.
[2] South Africa, Seychelles and India.
[3] Japan and Taiwan.
[4] Hawaii, Rapa and Marshall Islands.
[5] American Samoa and Pitcairn Island.

in SL, are lower. These differences are not regarded as sufficient to separate these populations into two species especially since the sample size from Pitcairn Island is too small to be representative.

Distribution

I. nesiotes is presently known only from American Samoa and Pitcairn Island. It is probable this species may have a much wider range than presently indicated. Like all other isonids, it lives in the surf near the shore, frequently close to rocky outcrops. Because of the nature of this habitat, isonids are difficult to collect.

Etymology

The name *nesiotes* is a Greek noun or its derivative, meaning insular. The species presently is only known from two islands in the Pacific.

Relationship to other species

Meristic analysis suggests that *I. nesiotes* (Table 2) is most closely related to *I. hawaiiensis* on the basis of the midlateral scale and vertebral counts. With the exception of *I. flosmaris*, however, the counts almost overlap, suggesting a close relationship amongst all *Iso* species. Osteologically, *Iso* species are distinct but their phylogeny is difficult to establish. Of the 45 osteological characters examined, *I. nesiotes* shares 25 with *I. hawaiiensis* but of these, only one (pterotic projection on exoccipital absent) advanced character is uniquely shared between these species. In *I. hawaiiensis*, the presence of intercalars is unique. *I. nesiotes* is unique in possessing: (1) long posterior dorsal process on the urohyals (Figure 2C a,b) (2) short coracoid (long in all other species, Figure 2D a,b) (3) third infraorbital with a lateral shelf which is absent in all other species (4) continuous lateral stripe which does not reach the caudal peduncle. The presence of the opercular notch (Figure 2E a,b) in *I. nesiotes* distinguishes it from *I. hawaiiensis*, *I. flosmaris* and most populations of *I. natalensis* but not from *I. rhothophilus*. The haemal spines are always double in *I. hawaiiensis* (Figure 2F a,b), double or single in *I. rhothophilus*, *I. flosmaris* and single in *I. nesiotes* and *I. natalensis*. *I. nesiotes* can therefore be clearly distinguished from all other species of *Iso* on the basis of its unique characters and by the combination of other osteological characters examined (Said 1983). A complete revision of the genus by the two senior authors is now in progress. This study will provide details on distribution, variability and an additional analysis of systematic relationships of all *Iso* species.

ACKNOWLEDGEMENTS

We thank Richard C. Wass, a biologist in the American Samoa who brought the specimens of the new species to our attention. We are indebted to Dr. J. Randall (BPBM) for access to the fish collection during our visit to the Bishop Museum and allowing us to work on the Pitcairn Island material. Miss Betty Thorn, Macquarie University artist, is gratefully acknowledged for her line drawing of a paratype. We are indebted to Mr. Ron Oldfield and Ms Sue Doyle for providing invaluable assistance with the photography and scanning electron microscopy.

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NEW SPECIES AND NEW RECORDS OF HERSILIIDAE FROM AUSTRALIA, WITH AN UPDATED KEY TO ALL AUSTRALIAN SPECIES (ARACHNIDA: ARANEAE: HERSILIIDAE)

Fourth supplement to the revision of the Australian Hersiliidae

Barbara Baehr* and Martin Baehr*

ABSTRACT

One new species of the genus *Hersilia* Savigny and Audouin and 9 new species of the genus *Tamopsis* Baehr and Baehr from Western Australia, Northern Territory, and New South Wales are described: *Hersilia mimbi* sp. nov., *Tamopsis riverinae* sp. nov., *T. facialis* sp. nov., *T. piankai* sp. nov., *T. harveyi* sp. nov., *T. gibbosa* sp. nov., *T. mainae* sp. nov., *T. triangularis* sp. nov., *T. gracilis* sp. nov., and *T. longbottomi* sp. nov. New records of several other *Tamopsis* species are presented, and the ranges of some species are considerably extended. An updated key to all Australian species of Hersiliidae is presented to replace the key in the revision of the Australian Hersiliidae (Baehr and Baehr 1987). The insufficient knowledge of the habits especially in the group of low-eyed species of the genus *Tamopsis* prevents a better understanding of the phylogenetic relations and biogeography in this group.

INTRODUCTION

Soon after having finished the third supplement (Baehr and Baehr 1992) to our revision of the Australian Hersiliidae (Baehr and Baehr 1987) we received another sample of Hersiliidae from the Western Australian Museum (by courtesy of Dr. M. S. Harvey) that included a new species of *Hersilia* and a further nine new species of *Tamopsis* mainly from Western Australia, as well as specimens of several other recently described species. Although we had decided not to write a further supplement to our revision, until representative material came to hand, we were once more surprised by the results of the highly successful recent collecting efforts of the staff of the Western Australian Museum, Perth, who provided us with so many new and interesting specimens from Western Australia, Northern Territory, and inland New South Wales. Therefore, we decided to present another paper as a fourth supplement to our revision. It is further evidence of the inadequate taxonomic and distributional knowledge of the Australian Hersiliidae, especially in Western Australia. But at the same time it demonstrates, how much a revision can initiate successful collecting work.

Including the species newly described in the present paper, altogether 17 new species of *Tamopsis* have been described since initiating our revision. Although we had extended our key for each new species in the former supplementary papers (Baehr and Baehr 1988, 1989, 1992), we now feel that the key and the supplements to it, together with the present supplements, would be impractical. Hence we include herein a completely updated key to all known species of Hersiliidae from Australia. Nevertheless, this key will not replace our revision nor the supplements, because exact determination is usually only possible with reference to the figures of male palpus and female epigyne and vulva.

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The sequence of the species follows the systematic order in our revision. Descriptions and measurements were taken as indicated previously (Baehr and Baehr 1987, 1988, 1989, 1992). Eye ratio was taken in the following order: AME:ALE:PME:PLE. Maps are provided for the newly described species and for those species whose range has been significantly extended in the present paper.

The sample contained a few juvenile specimens which we did not identify and only tentatively assigned to certain species. These are therefore not included in the present paper.

METHODS

As the fine structures of the female vulva are highly important for identification of species, the vulva should be dissected and examined under the microscope for correct determination. Appropriate immersion of the vulva that makes visible the delicate chitinous structures is crucial for this purpose. We found that the immersion in "Hoyers Gemisch" (see Kraus 1984) gives the best results, because even delicate, almost translucent chitinous membranes are easily seen. It should be noted that this is not always possible when other solutions are used.

LABELS

All labels of type specimens have been exactly copied including all codes and dates of capture, because we believe that the label is a genuine part of any type specimen. For the sake of reproducibility we chose the same procedure in non-typical specimens, too.

ABBREVIATIONS

ALE	anterior lateral eye
AME	anterior median eye
bS	basal segment of posterior lateral spinneret
LB	total length of body
LL	total length of legs
PLE	posterior lateral eye
PLS	posterior lateral spinneret
PME	posterior lateral eye
tS	terminal segment of posterior lateral spinneret
I	1st leg
II	2nd leg
III	3rd leg
IV	4th leg
>	larger or more than
<	smaller of less than
NSW	New South Wales
NT	Northern Territory
WA	Western Australia
AM	Australian Museum, Sydney
CBM	Collection B. Baehr, München
WAM	Western Australian Museum, Perth

SYSTEMATICS

In our revision (Baehr and Baehr 1987) all known species of the former genera *Chalinura* or *Tama*, respectively, were transferred to a new genus *Tamopsis*. Except for the singular *Hersilia australiensis* Baehr and Baehr, all other Australian species of Hersiliidae so far described are included in the genus *Tamopsis*. For the generic diagnoses of both genera see that revision. Most important characters for species differentiation in both genera are the structure of the male palpus and of the female epigyne and vulva.

Genus *Hersilia* Savigny and Audouin, 1827

Hersilia Savigny and Audouin, 1827: 317; Baehr and Baehr 1987: 354.

For differentiation from the genus *Tamopsis* see key in Baehr and Baehr 1987: 354.

KEY TO AUSTRALIAN SPECIES OF GENUS *HERSILIA* SAVIGNY AND AUDOUIN

1. Median apophysis of male palpus simply spoon-shaped. Flagellum of embolus short, base of flagellum deeply hollowed (Baehr and Baehr 1987 Figure 1). Female epigyne with trapezoidal median scapus (Baehr and Baehr 1987 Figure 2). Western part of Arnhem Land, northernmost Northern Territory .... *australiensis* Baehr and Baehr

   Median apophysis of male palpus complex, at base excised, posterior part at apex deeply hollowed. Flagellum of embolus elongate, base of flagellum barely hollowed (Figures 1,2). Female epigyne with quadrate median scapus (Figures 3,4). Kimberley Division, northwestern Australia .... *mimbi* sp. nov.

Hersilia mimbi sp. nov.
(Figures 1-4, 25)

Holotype

Male, W. A., Mimbi Cave 18.45S, 126.05E, 23 July 1990, A. F. Longbottom S.465 (P27/17-18) (WAM 91/35).

Paratype

1 female, same data (WAM 91/36).

Diagnosis

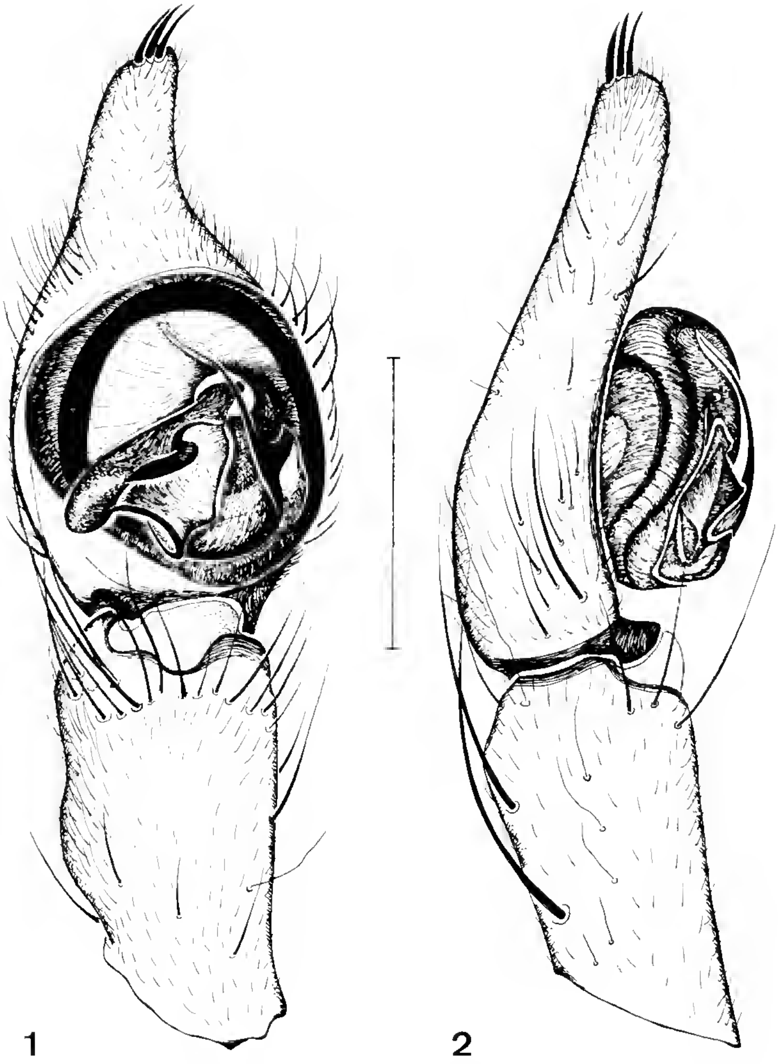
Light coloured, very long-legged species, distinguished from *Hersilia australiensis* Baehr and Baehr by much lighter colour, relatively longer legs, straight, more complex median apophysis of male palpus, longer flagellum of embolus the base of which is not deeply hollowed, and quadrate median scapus of female epigyne.

Description

MALE HOLOTYPE

Measurements

Length: 7.5 mm; cephalothorax length: 3.0 mm; width: 2.9 mm; abdomen length: 4.5 mm;



Figures 1 and 2 *Hersilia mimbi* sp. nov. Male palpus. 1. Ventral view. 2. Lateral view. Scale: 0.5 mm.

width: 3.45 mm. Legs: I: 48.8 mm, II: 44.3 mm, III: 14.5 mm, IV: 39.5 mm; ratio: 1:0.91:0.30:0.81. Ratio LB/LL: 0.15. PLS length: 6.0 mm; bS: 1.1 mm; tS: 4.9 mm. Length ratio PLS/abdomen: 1.33. Eye ratio: 1:0.60:1.10:1.14.

Colour

Whitish to light yellow, area around eyes dark. Dark pattern of abdomen greyish, rather inconspicuous. In anterior half with lancet-shaped median stripe. Lateral borders narrowly dark. Posteriorly with several transverse lines. Legs and PLS light yellow, barely patterned. The very light colour and inconspicuous pattern may be due to fading in alcohol or to the occurrence of the type series in a cave.

Cephalothorax

About circular, narrower than abdomen. Eye area strongly raised, lateral border concave. Clypeus almost as high as eye area. PLE largest, PME larger than AME. Distance AME/AME c. two thirds of diameter of AME, distance AME/ALE slightly <diameter of AME, distance PME/PME c. half of diameter of PME, distance PME/PLE <diameter of PME. Chelicerae c. 2 x as long as wide, anteriorly with 3 large, posteriorly with 4-6 small teeth. Sternum pentagonal, sparsely hirsute.

Abdomen

Much longer than wide, ovalish. Dorsal surface with 4 pairs of circular muscular pits. Ventral muscular pits in a narrow v-shaped arrangement, though very difficult to see. PLS much longer than abdomen, tS very elongate.

Legs

Measurements see above. Very elongate compared with body size. III comparatively short. Metatarsus divided, distal part c. half as long as proximal part.

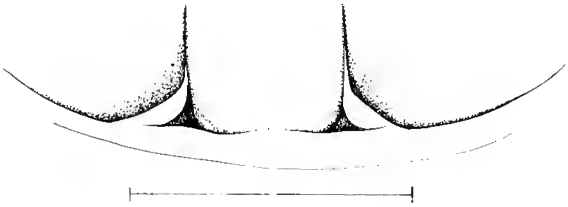
Palpus

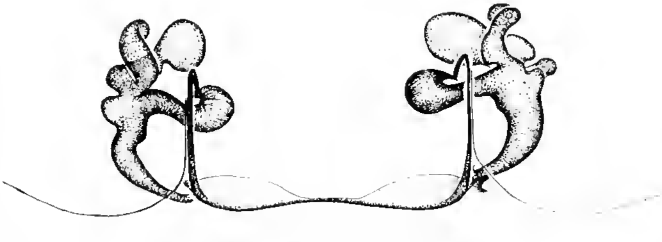
Cymbium with 3 apical spines. Anterior part of median apophysis spoon-shaped, at base excised, posterior part at apex deeply hollowed. Embolus spirally coiled around median apophysis, apex free, very elongate, whip-like, embolus barely excised at base of flagellum.

FEMALE PARATYPE

Measurements

Length: 7.8 mm; cephalothorax length: 3.0 mm; width: 2.9 mm; abdomen length: 4.9 mm; width: 4.15 mm. Legs: I: 32.5 mm, II: 31.4 mm, III: 11.8 mm, IV: 28.8 mm; ratio: 1:0.97:0.36:0.87.





Figures 3 and 4 *Hersilia mimbi* sp. nov. Female. 3. Epigyne. 4. Vulva. Scales: 0.5 mm.

Ratio LB/LL: 0.24. PLS length: 6.3 mm; bS: 1.2 mm; tS: 5.1 mm. Length ratio PLS/abdomen: 1.29. Eye ratio: 1:0.75:1.2:1.28.

Colour

Same colour as in male, but dark parts even more indistinct.

Cephalothorax

About circular, narrower than abdomen. Eye area and clypeus as in male. Size of eyes and distances between them like in male, though AME relatively smaller. Chelicerae as in male.

Abdomen

Slighty longer than wide, considerably wider than cephalothorax. Arrangement of dorsal and ventral muscular pits as in male. PLS slightly shorter in relation to abdomen than in male.

Legs

Measurements see above. Considerably shorter than in male. III relatively longer.

Epigyne

Very simple, with a quadrate scapus.

Vulva

With small, lobate ventral receptaculum seminis, a small, about circular dorsal receptaculum seminis, and a short intraductory duct.

Variation

Apart from some sexual variation in shape of abdomen and length of legs, little variation noted.

Additional material examined

1 juvenile, collected with the types. It is tentatively alluded to this species, but not designated paratype.

Etymology

Alludes to the type locality, *Mimbi* cave.

Distribution

Southern Kimberley Division, northwestern Australia. Known only from type locality.

Habits

Collected in a cave, but collecting circumstances and distance of locality from entrance of the cave unknown.

Relationships

This species is certainly closely related to the other Australian species of genus *Hersilia*, *H. australiensis* Baehr and Baehr, though it is slightly more apomorphic by virtue of the light colour, the even longer legs, and the markedly more complex structure of median apophysis of male palpus. At present, however, it is not known, whether this is an obligate cavernicolous species.

Genus *Tamopsis* Baehr and Baehr, 1987

Tamopsis Baehr and Baehr, 1987: 355; 1988: 13; 1989: 310; 1992: 62.

For diagnosis and differentiation from the genus *Hersilia* Savigny and Audouin see Baehr and Baehr (1987: 354).

KEY TO AUSTRALIAN SPECIES OF THE GENUS *TAMOPSIS* BAEHR AND BAEHR

This key updates all species described since the revision (Baehr and Baehr 1988, 1989, 1992) and the species described in present paper, and it replaces the key in our revision.

1. Males 2

   Females 30

2. Dorsal muscular pits falciform, very elongate. Abdomen elongate, almost parallel. Median apophysis apically with large, hook-shaped process (Baehr and Baehr 1987 Figures 3, 4; Baehr and Baehr 1992 Figures 1-3) 3

   Dorsal muscular pits circular or elliptoid. Abdomen usually shorter and wider. Median apophysis different, hook-shaped process, when present, much shorter 5

3. Cephalothorax wider than abdomen. Process at apex of median apophysis longer, much surpassing lateral border of palpus. Basal part of lateral apophysis very wide (Baehr and Baehr 1987 Figure 3). Southwestern Australia .... *amplithorax* Baehr and Baehr

   Cephalothorax not wider than abdomen. Process at apex of median apophysis shorter. Basal part of lateral apophysis much narrower (Baehr and Baehr 1987 Figure 4; Baehr and Baehr 1992 Figures 1-3) 4

4. Apex of lateral apophysis cap-shaped, tapering but slightly convex (Baehr and Baehr 1987 Figure 4). Eastern central Queensland .... *platycephala* Baehr and Baehr

   Apex of lateral apophysis hollowed, apically widened (Baehr and Baehr 1992 Figures 1-3). Central western part of Western Australia, northern part of central Northern Territory .... *depressa* Baehr and Baehr

5. Eye area just slightly raised, clypeus low, at most c. 2/3 x as high as eye area. Median apophysis apically not ring-shaped 6

   Eye area strongly raised, clypeus as high as eye area. Median apophysis apically ring-shaped 16

6. Median apophysis apically with large, acute, horizontal, hook-shaped process (Baehr and Baehr 1987 Figures 10, 12). Rather large species, length >4 mm 7

   Median apophysis apically without large, acute, hook-shaped process. Medium sized to small species, length <4 mm 8

7. Median apophysis without preapical scopula-like organ, apex of lateral apophysis not excised, nor strongly hooked (Baehr and Baehr 1987 Figure 10). Southeastern Australia .... *eucalypti* (Rainbow)

Median apophysis with preapical scopula-like organ, apex of lateral apophysis excised and with strong hook (Baehr and Baehr 1987 Figure 12). Eastern Queensland and New South Wales .... *brisbanensis* Baehr and Baehr

8. Very small species, length <3 mm. PLS very short, c. 1/2 x as long as abdomen. Palpus dorsally with densely setose area (Baehr and Baehr 1987 Figure 6). Eastern Queensland and New South Wales .... *brachycauda* Baehr and Baehr

Larger species, length >3 mm. PLS longer, at least 3/4 of length of abdomen. Palpus dorsally without densely setose area, sometimes with spinose area ....9.

9. Palpus dorsally with spinose area. Median apophysis contorted, apex spoon-shaped. Legs and PLS very elongate, PLS longer than abdomen (Baehr and Baehr 1987 Figure 8). Eastern Queensland, northeastern New South Wales .... *tweedensis* Baehr and Baehr

Palpus dorsally without spinose area. Median apophysis contorted, apex strongly excised, with a membraneous area within. PLS less elongate, at most as long as abdomen...10

10. AME not much smaller than PME, mostly larger. Lateral apophysis not deeply excised at apex 11

AME considerably smaller than PME. Lateral apophysis deeply excised at apex (Baehr and Baehr 1987 Figure 23). Southeastern Australia ....*raveni* Baehr and Baehr

11. Lateral apophysis apically not much contorted. Median apophysis less deeply excised at apex, bent horizontally (Baehr and Baehr 1987 Figure 14). Northeastern Queensland ....*daviesi* Baehr and Baehr

Lateral apophysis strongly contorted. Median apophysis deeply excised at apex, bent obliquely (Baehr and Baehr 1987 Figures 16, 17, 21; Baehr and Baehr 1992 Figures 4-6; Figures 7, 8) 12

12. Median apophysis very deeply excised. Lateral apophysis deeply channelled at apex (Baehr and Baehr 1987 Figure 21; Baehr and Baehr 1992 Figures 4-6) 13

Median apophysis less deeply excised. Lateral apophysis not conspicuously channelled at apex (Baehr and Baehr 1987 Figures 16, 17; Figures 7, 8) 14

13. Median apophysis with wide excision. Lateral apophysis sinuate (Baehr and Baehr 1987 Figure 21). Southeastern Queensland, eastern New South Wales .... *queenslandica* Baehr and Baehr

Median apophysis with narrow excision. Lateral apophysis barely sinuate (Baehr and Baehr 1992 Figures 4-6). Southwestern Australia ....*distinguenda* Baehr and Baehr

14. Latero-apical part of median apophysis not swollen, without sharp edge. Lateral apophysis not much longer than median apophysis, apex sharply bent, contorted (Baehr and Baehr 1987 Figure 16). Southwestern Australia .... *kochi* Baehr and Baehr

Lateral part of median apophysis swollen, with sharp edge. Lateral apophysis much longer than median apophysis, apex not sharply bent, not much contorted (Baehr and Baehr 1987 Figure 17; Figures 7, 8)... 15

15. Face without conspicuous light spots near eyes. Lateral apophysis at apex not excised (Baehr and Baehr 1987 Figure 17). Central Queensland .... *centralis* Baehr and Baehr

    Face with conspicuous light spots near eyes. Lateral apophysis at apex excised (Figures 7, 8). Western part of Western Australia north to Pilbara region .... *facialis* sp. nov.

16. Median apophysis without a scopula-like organ within apical membranous area. Apex of embolus freely projecting beyond lateral apophysis (Baehr and Baehr 1987 Figures 27, 29), or hidden in lateral apophysis (Baehr and Baehr 1989 Figures 1, 2) .... 17.

    Median apophysis with a scopula-like organ within apical membranous area. Apex of embolus hidden in lateral apophysis (Baehr and Baehr 1987 Figures 31, 33, 37, 39, 41, 43; Baehr and Baehr 1989 Figures 3, 4, 7, 8; Figures 19-22) .... 20.

17. Apex of embolus hidden in lateral apophysis. Apex of median apophysis with a peculiar, excised, projecting process within, without a hooked process on lateral rim (Baehr and Baehr 1989 Figures 1, 2; Baehr and Baehr 1992 Figures 9-11) .... 18.

    Apex of embolus freely projecting beyond median apophysis. Apex of median apophysis without a projecting process within, but with a hooked process on lateral rim (Baehr and Baehr 1987 Figures 27, 29) .... 19.

18. Apical process of median apophysis shorter. Lateral part of apex of lateral apophysis not widened nor excised (Baehr and Baehr 1989 Figures 1, 2). Northwestern Australia south of Great Sandy Desert .... *nanutarrae* Baehr and Baehr

    Apical process of median apophysis longer. Lateral part of apex of lateral apophysis distinctly widened and excised (Baehr and Baehr 1992 Figures 9-11). Southwestern Australia, northwestern Victoria .... *transiens* Baehr and Baehr

19. Eye area moderately raised, oblique near top. Median apophysis with rather small apical hook-shaped process. Lateral apophysis very simple, without special features, embolus straight, apex free (Baehr and Baehr 1987 Figure 27). Northernmost Northern Territory, northern tip of Queensland .... *arnhemensis* Baehr and Baehr

    Eye area strongly raised, sides concave. Median apophysis with a strong, hook-shaped process. Apex of lateral apophysis trumpet-shaped, spirally coiled, embolus running along apical rim of lateral apophysis (Baehr and Baehr 1987 Figure 29). Southwestern Australia, western Victoria .... *circumvidens* Baehr and Baehr

20. Median apophysis not much contorted, base medially barely excavate. Apex without sharp, elevated lateral rim, median membranous area not deeply sunken in (Baehr and Baehr 1987 Figures 31, 33; Baehr and Baehr 1988 Figure 1) .... 21.

    Median apophysis more strongly contorted, medially excavate. Apex with more or less elevated, sharp lateral rim, median membranous area deeply sunken in (Baehr and Baehr 1987 Figures 37, 39, 41, 43; Baehr and Baehr 1989 Figures 3, 4, 7, 8; Figures 19-22) .... 23.

21. III relatively short. Apical process of median apophysis short, apex of lateral apophysis barely

excised (Baehr and Baehr 1987 Figure 31). North Queensland .... *tropica* Baehr and Baehr

III more elongate. Apical process of median apophysis elongate, apex of lateral apophysis very deeply excised, with 3 elongate spines lateral to excision (Baehr and Baehr 1987 Figure 33; Baehr and Baehr 1988 Figure 1) 22

22\. Lateral border of median apophysis not modified to a spoon-like process, inner finger of lateral apophysis curved inwards (Baehr and Baehr 1987 Figure 33). Southern central Queensland ....*trionyx* Baehr and Baehr

Lateral border of median apophysis modified to a spoon-like process, napped outside, inner finger of lateral apophysis curved outwards (Baehr and Baehr 1988 Figure 1). Northwestern Queensland ....*forresti* Baehr and Baehr

23\. PLS considerably shorter than abdomen. Sharp lateral rim of median apophysis not crenulate, apical process entire (Baehr and Baehr 1987 Figures 37, 39, 41; Baehr and Baehr 1989 Figures 3, 4, 7, 8; Figures 19-22) 24

PLS as long as or longer than abdomen. Sharp lateral rim of median apophysis crenulate, apical process divided (Baehr and Baehr 1987 Figure 43). Northwestern Australia north of Great Sandy Desert.......................................*fitzroyensis* Baehr and Baehr

24\. Lateral rim of median apophysis deeply incised and doubly excavate. Lateral apophysis (lateral view) not enlarged at apex (Baehr and Baehr 1987 Figure 41; Baehr and Baehr 1989 Figures 3, 4, 7, 8; Figures 21, 22). Western Australia south of Great Sandy Desert, northeastern part of central Northern Territory 25

Lateral rim of median apophysis simple, not doubly excavate. Lateral apophysis (lateral view) enlarged at apex (Baehr and Baehr 1987 Figures 37, 39; Figures 19, 20) 28

25\. Excavate median process of median apophysis triangular and very depressed, lateral process very large. Lateral apophysis strongly contorted and sinuate, apically wide, gently bisinuate at apex (Figures 21, 22). Northern half of Northern Territory .... *longbottomi* sp. nov.

Excavate median process of median apophysis less triangular and not depressed, lateral process much smaller. Lateral apophysis barely contorted and sinuate, apically narrower, at apex excised or spined, though not bisinuate (Baehr and Baehr 1987 Figure 41; Baehr and Baehr 1989 Figures 3, 4, 7, 8). Western Australia south of Great Sandy Desert 26

26\. Lateral apophysis without any excisions, but with a conspicuous spine at apex (Baehr and Baehr 1989 Figures 7, 8). Southwestern Australia .... *mallee* Baehr and Baehr

Lateral apophysis with excisions at apex, without such a spine (Baehr and Baehr 1987 Figure 41; Baehr and Baehr 1989 Figures 3, 4) 27

27\. Lateral apophysis with a deep median and a narrow lateral excision. Lateral rim of median apophysis rather low (Baehr and Baehr 1987 Figure 41). Mid western Australia south of Great Sandy Desert .... *occidentalis* Baehr and Baehr

Lateral apophysis with less deep median and a conspicuously circular lateral excision. Lateral rim of median apophysis high, lamelliform (Baehr and Baehr 1989 Figures 3, 4). Southwestern Australia, southwestern New South Wales ..... *marri* Baehr and Baehr

28. Lateral rim of median apophysis with short cleft near dorsal process. Lateral apophysis barely sinuate in middle, apex slightly enlarged. Legs shorter (Baehr and Baehr 1987 Figure 39). Southwestern Australia .... *perthensis* Baehr and Baehr

Lateral rim of median apophysis without cleft near dorsal process. Lateral apophysis sinuate in middle, apex strongly enlarged. Legs more elongate (Baehr and Baehr 1987 Figure 37; Figures 19, 20) 29

29. Larger species, length >4.5 mm. Excavate process at apex of median apophysis narrower. Lateral apophysis markedly sinuate, voluminous at apex (Baehr and Baehr 1987 Figure 37). Southeastern Australia .... *fickerti* (L. Koch)

Smaller species, length <4 mm. Excavate process at apex of median apophysis much wider. Lateral apophysis less sinuate, narrower at apex (Figures 19, 20). Northwestern Australia south of Great Sandy Desert .... *gracilis* sp. nov.

30. Dorsal muscular pits falciform, very elongate. Abdomen very elongate, laterally with pockets. Vulva with 1 circular receptaculum seminis, this basally swollen and glandular (Baehr and Baehr 1987 Figure 4). Eastern central Queensland .... *platycephala* Baehr and Baehr

Dorsal muscular pits circular or elliptoid. Abdomen much shorter, laterally without conspicuous pockets 31

31. Eye area not much raised, clypeus low, at most 2/3 x as high as eye area 32

Eye area strongly raised, clypeus as high as eye area 52

32. Intraductory ducts of vulva elongate, crossing receptacula seminis, sometimes laterally sharply bent. Ventral receptaculum seminis always distinctly glandular outside or anteriorly (Baehr and Baehr 1987 Figures 18-20, 22, 24; Baehr and Baehr 1992 Figures 7, 8; Figures 9-14) 33

Intraductory ducts of vulva short, not crossing receptacula seminis, not bent. Vulva different, ventral receptaculum seminis not always distinctly glandular (Baehr and Baehr 1987 Figures 7, 9, 11, 13, 25, 26; Figures 5, 6, 15-18) 42

33. Epigyne laterally of vulva with two small, sclerotized pockets on each side (Figures 9, 10). Interior of southwestern Australia .... *piankai* sp. nov.

Epigyne laterally of vulva without such pockets, but sometimes with a pocket near lateral border 34

34. In middle of abdomen dorsally with a distinct hump. Epigyne with a slit-like pocket near lateral border covered by a sclerotized plate. Ventral receptaculum seminis globular

and glandular at anterior border (Figures 13, 14). Southwestern Australia .... *gibbosa* sp. nov.

Abdomen without such hump. Epigyne without pocket. Ventral receptaculum seminis elongate, globular at outer surface (Baehr and Baehr 1987 Figures 18-20, 22, 24; Baehr and Baehr 1992 Figures 7, 8; Figures 11, 12) 35

35\. Apparently only 1 large receptaculum seminis present each side (Baehr and Baehr 1987 Figure 18). South Australia .... *reevesbyana* Baehr and Baehr

2 receptacula seminis present each side (Baehr and Baehr 1987 Figures 19, 20, 22, 24; Baehr and Baehr 1992 Figures 7, 8; Figures 11, 12) 36

36\. Intraductory ducts sharply bent laterally, vulva without conspicuous v-shaped bridge in middle (Baehr and Baehr 1987 Figures 20, 22, 24; Baehr and Baehr 1992 Figures 7, 8; Figures 11, 12) 37

Intraductory ducts not sharply bent laterally, vulva with conspicuous v-shaped bridge in middle (Baehr and Baehr 1987 Figure 19). Eastern New South Wales .... *grayi* Baehr and Baehr

38\. Vulva with intraductory ducts posteriorly sharply bent outwards and produced laterally (Baehr and Baehr 1987 Figure 22; Baehr and Baehr 1992 Figures 7, 8; Figures 11, 12) .... 3.

Vulva with intraductory ducts not bent outwards, nor produced laterally (Baehr and Baehr 1987 Figures 20, 24) 41

39\. AME c. as large as PME, or considerably smaller. Dorsal receptaculum seminis c. as long as ventral receptaculum, or longer (Baehr and Baehr 1987 Figure 22; Figures 11, 12) 40

AME considerably larger than PME. Dorsal receptaculum seminis half as long as ventral receptaculum (Baehr and Baehr 1992 Figures 7, 8). Southwestern Australia .... *distinguenda* Baehr and Baehr

40\. AME considerably smaller than PME. Dorsal receptaculum seminis slightly shorter than ventral receptaculum, apical part of dorsal receptaculum less well divided (Baehr and Baehr 1987 Figure 22). Southeastern Queensland, eastern New South Wales .... *queenslandica* Baehr and Baehr

AME c. as large as PME. Dorsal receptaculum seminis longer than ventral receptaculum, apical part of dorsal receptaculum well divided, globose (Figures 11, 12). Central Northern Territory .... *harveyi* sp. nov.

41\. PLS longer than abdomen. Dorsal receptaculum seminis much smaller than ventral receptaculum (Baehr and Baehr 1987 Figure 20). Southwestern Australia .... *darlingtoniana* Baehr and Baehr

PLS shorter than abdomen. Dorsal receptaculum seminis about as large as ventral receptaculum

(Baehr and Baehr 1987 Figure 24). Southeastern Australia . *raveni* Baehr and Baehr

42. Small species, length <3 mm. PLS extremely short, c. half as long as abdomen. Abdomen dorsally with a conspicuous hump in middle. Vulva with 2 receptacula seminis and a large glandular sac situated ventrally (Baehr and Baehr 1987 Figure 7). Eastern Australia .... *brachycauda* Baehr and Baehr

Usually larger species with longer PLS. Abdomen without such hump. Vulva different ... .43

43. PLS and legs very elongate, PLS longer than abdomen. Vulva widely separated, with 3 not very distinct receptacula seminis, the larger two apically or subapically glandular (Baehr and Baehr 1987 Figure 9). Eastern Queensland, northeastern New South Wales .... *tweedensis* Baehr and Baehr

PLS and legs shorter, PLS not longer than abdomen. Vulva different, at most one receptaculum seminis glandular 44

44. AME considerably larger than PME. Epigyne with tube-like pocket at some distance from lateral border. Vulva with 2 receptacula seminis, dorsal receptaculum elongate and strongly coiled (Baehr and Baehr 1987 Figure 15). Northeastern Queensland .... *daviesi* Baehr and Baehr

AME slightly or considerably smaller than PME. Epigyne with or without pocket. Dorsal receptaculum seminis not as elongate and coiled (Baehr and Baehr 1987 Figures 7, 9, 11, 13, 15, 25, 26; Figures 5, 6, 15-18) 45

45. Vulva with 2 receptacula seminis, dorsal receptaculum clearly visible, ventral receptaculum irregularly shaped, elongate, somewhat sinuose, or globular with an additional ventral sac (Baehr and Baehr 1987 Figures 11, 13, 25; Figures 5, 6) 46

Vulva different, ventral receptaculum seminis rather short (Baehr and Baehr 1987 Figures 7, 9, 15, 26; Figures 15-18) 50

47. PLS and legs elongate, PLS longer than abdomen. Epigyne with tube-like pocket at some distance from lateral border. Ventral receptaculum seminis short, globose, ventrally with a small, circular glandular sac (Baehr and Baehr 1987 Figure 25). Southeastern Queensland .... *cooloolensis* Baehr and Baehr

PLS and legs usually shorter, PLS rarely longer than abdomen. Epigyne without or with pocket. Ventral receptaculum seminis elongate, somewhat sinuate, without additional small, circular sac. Epigyne posteriorly with sclerotized bar (Baehr and Baehr 1987 Figures 11, 13; fig 5, 6) 48

48. PLS considerably shorter than abdomen. Receptacula seminis shorter, approximated (Baehr and Baehr 1987 Figure 11; Figures 5, 6) 49

PLS as long as or longer than abdomen. Epigyne with pocket halfways laterally. Receptacula seminis widely separated (Baehr and Baehr 1987 Figure 13). Eastern Queensland and New South Wales .... *brisbanensis* Baehr and Baehr

49. Epigyne laterally without pocket. Dorsal receptaculum seminis apically less separated, shorter than ventral receptaculum, the latter glandular along whole outer surface (Baehr and Baehr 1987 Figure 11). Southeastern Australia ...... *eucalypti* (Rainbow)

Epigyne laterally with pocket. Dorsal receptaculum seminis apically well separated, globular, slightly longer than ventral receptaculum, the latter glandular only in middle (Figures 5, 6). Riverina country, southern inland New South Wales .... *riverinae* sp. nov.

50. Epigye laterally without a slit-shaped pocket, vulva laterally with a membraneous area (Figures 15, 16). Southwestern Australia .... *mainae* sp. nov.

Epigyne laterally with a slit-like pocket, vulva without such membraneous area (Baehr and Baehr 1987 Figure 26; Figures 17, 18). New South Wales 51

51. Epigyne with large plate bearing conspicuous ridges medially of pocket (Figures 17, 18). Riverina country, southern inland New South Wales .... *triangularis* sp. nov.

Epigyne without such plate (Baehr and Baehr 1987 Figure 26). Eastern New South Wales .... *brevipes* Baehr and Baehr

52. Very small species, length <3 mm. Eye area moderately raised, sides near top oblique. Vulva with 2 elongate receptacula seminis and a mushroom-shaped, glandular basal sac. Epigyne with funnel-shaped pocket medially (Baehr and Baehr 1987 Figure 28). Northernmost Northern Territory, northern tip of Queensland .... *arnhemensis* Baehr and Baehr

Larger species, length >3.5 mm. Eye area strongly raised, sides not oblique near top. Vulva different, without a mushroom-shaped sac. Pocket of epigyne situated more laterally (Baehr and Baehr 1987 Figures 30, 32, 34-36, 38, 40, 42, 44; Baehr and Baehr 1988 Figures 2, 3; Baehr and Baehr 1989 Figures 5, 6; Figures 23, 24) 53

53. Sides of eye area concave. Epigyne with a tubular pocket at some distance from lateral border. Receptacula seminis very elongate, strongly and irregularly coiled (Baehr and Baehr 1987 Figure 30). Southwestern Australia, western Victoria .... *circumvidens* Baehr and Baehr

Sides of eye area straight. Pocket of epigyne variable. Receptacula seminis not very elongate, nor coiled (Baehr and Baehr 1987 Figures 32, 34-36, 38, 40, 42, 44; Baehr and Baehr 1988 Figures 2, 3; Baehr and Baehr 1989 Figures 5, 6) 54

54. Apical section of inner receptaculum seminis conspicuously circular, with narrow duct (Baehr and Baehr 1987 Figures 34-36; Baehr and Baehr 1988 Figures 2, 3; Baehr and Baehr 1989 Figures 5, 6; Figures 23, 24) 55

Apical section of inner receptaculum seminis not conspicuously circular, not separated by a narrow duct (Baehr and Baehr 1987 Figures 32, 38, 40, 42, 44) 60

55. Vulva very wide and with a broad, sclerotized bridge. Lateral receptaculum seminis nearly as long as median receptaculum (Baehr and Baehr 1987 Figure 34; Baehr and Baehr 1988 Figure 3; Baehr and Baehr 1989 Figures 5, 6) 56

Vulva narrower, with a narrow sclerotized bridge. Lateral receptaculum seminis considerably smaller than median receptaculum (Baehr and Baehr 1987 Figures 35, 36; Baehr and Baehr 1988 Figure 2; Figures 23, 24) 58

56. Intraductory duct basally not coiled. Bridge of epigyne located rather posteriorly between receptacula seminis (Baehr and Baehr 1987 Figure 34). Southwestern Australia .... *pseudocircumvidens* Baehr and Baehr

Intraductory duct basally strongly coiled (Baehr and Baehr 1988 Figure 3; Baehr and Baehr 1989 Figures 5, 6). Bridge of epigyne located rather anteriorly or in middle 57

57. Bridge of epigyne located anteriorly at apex of receptacula seminis (Baehr and Baehr 1988 Figure 3). Eastern central South Australia .... *ediacarae* Baehr and Baehr

Bridge of epigyne located more posteriorly between receptacula seminis (Baehr and Baehr 1989 Figures 5, 6). Southwestern Australia, southwestern New South Wales .... *marri* Baehr and Baehr

58. Epigyne with elongate oval scapus (Figure 23). Northern half of Northern Territory .... *longbottomi* sp.nov.

Epigyne without such scapus 59

59. Smaller species with wider body, length <4.5 mm. Legs and PLS rather stout. Lateral receptaculum seminis directed horizontally or posteriorly. Bridge of vulva not a narrow clasp (Baehr and Baehr 1987 Figure 35; Baehr and Baehr 1988 Figure 2) 60

Large, elongate species, length c. 5.5 mm. Legs and PLS elongate. Lateral receptaculum seminis larger, not directed horizontally. Bridge of vulva with approximated clasp-like process (Baehr and Baehr 1987 Figure 36). Southwestern Australia .... *rossi* Baehr and Baehr

60. Lateral receptaculum seminis very small, directed horizontally. Intraductory duct not strongly v-shaped (Baehr and Baehr 1987 Figure 35). Northwestern Queensland, northwestern Australia .... *leichardtiana* Baehr and Baehr

Lateral receptaculum seminis large, elongate, directed posteriorly, apex conspicuously incurved. Intraductory duct strongly v-shaped (Baehr and Baehr 1988 Figure 2). Northwestern Queensland .... *forresti* Baehr and Baehr

61. Medium sized species, length <4 mm (Baehr and Baehr 1987 Figure 32). Northern Queensland, northeastern Northern Territory .... *tropica* Baehr and Baehr

Large species, length >5 mm 62

62. Vulva with entire, sclerotized bridge at posterior border. Ventral receptaculum seminis much more elongate than dorsal receptaculum. Pocket of epigyne consisting of two slits somewhat removed from lateral border (Baehr and Baehr 1987 Figure 44). Northwestern Australia north of Great Sandy Desert .... *fitzroyensis* Baehr and Baehr

Vulva without entire, sclerotized bridge at posterior border. ventral receptaculum seminis just slightly larger than dorsal receptaculum. Pocket of epigyne consisting of 1 slit only (Baehr and Baehr 1987 Figures 38, 40, 42) 63

63\. Intraductory ducts crossing base of receptacula seminis, vulva with conspicuous triangular scapus in middle. Pocket of epigyne situated immediately at lateral border (Baehr and Baehr 1987 Figures 38, 40) 64

Intraductory ducts not crossing base of receptacula seminis, vulva without triangular scapus in middle. Pocket of epigyne far removed from lateral border (Baehr and Baehr 1987 Figure 42). Northwestern Australia south of Great Sandy Desert .... *occidentalis* Baehr and Baehr

64\. Intraductory ducts strongly swollen around base of receptacula seminis, produced dorsomedially. Scapus separated laterally at base from anterior area (Baehr and Baehr 1987 Figure 38). Southeastern Australia .... *fickerti* (L. Koch)

Intraductory ducts not swollen around base of receptacula seminis, not produced dorsomedially. Scapus not separated at base (Baehr and Baehr 1987 Figure 40). Southwestern Australia .... *perthensis* Baehr and Baehr

platycephala-group

Tamopsis amplithorax Baehr and Baehr, 1987

Tamopsis amplithorax Baehr and Baehr, 1987: 360.

New record: WA: 1 male, Grasspatch 33.14S, 121.43E, Fitz. Loc. 41, 18 June 1989, A. F. Longbottom S.286 (WAM 92/125).

This species been described from a single male from the Stirling Range in southwestern Western Australia. The species is distinguished from all other species of the *platycephala*-group by the relatively large cephalothorax and the large and apically wide, rather evenly curved, hook-shaped median apophysis and basally much wider lateral apophysis of male palpus. The male palpus is also considerably larger than in the other species, even in equally sized specimens. The new record enlarges the distribution of *T. amplithorax* somewhat to the east. The specimen was caught "on rusty pipe ladder at house".

Tamopsis depressa Baehr and Baehr, 1992
Figure 25

Tamopsis depressa Baehr and Baehr 1992: 62.

New record: NT: 1 male, Daly Waters, K. F. Adams, 6.VIII.1971 (WAM 92/137).

The male palpus of this species is much more similar to that of eastern *T. platycephala* Baehr and Baehr than to the palpus of western *T. amplithorax*. The species was hitherto known from central western Western Australia only. The new record enlarges the known range considerably to the northern part of central Northern Territory. All records are so far from arid areas in the west and the interior. Hence, this is perhaps a widespread deserticolous species, but its exact range is still unknown.

eucalypti-group

Tamopsis riverinae sp. nov.
Figures 5, 6, 25

Holotype

Female, NSW, Yanco Ck., 11 km SW. of Morundah 35.02S, 146.13E, 29 Dec. 1990, A. F. Longbottom S.654 (P46/4), River gums, "sandside" 50 km SW. of Narrandera (WAM 92/139).

Diagnosis

Species of *eucalypti*-group due to small AME and very similar female epigyne and vulva. Distinguished from *T. eucalypti* (Rainbow) by presence of a lateral pocket in epigyne, longer and more knob-like dorsal receptaculum seminis, and better separated glandular part of ventral receptaculum seminis; from *T. brisbanensis* Baehr and Baehr by shorter PLS, longer and more knob-like receptacula seminis, and much shorter glandular part of ventral receptaculum seminis.

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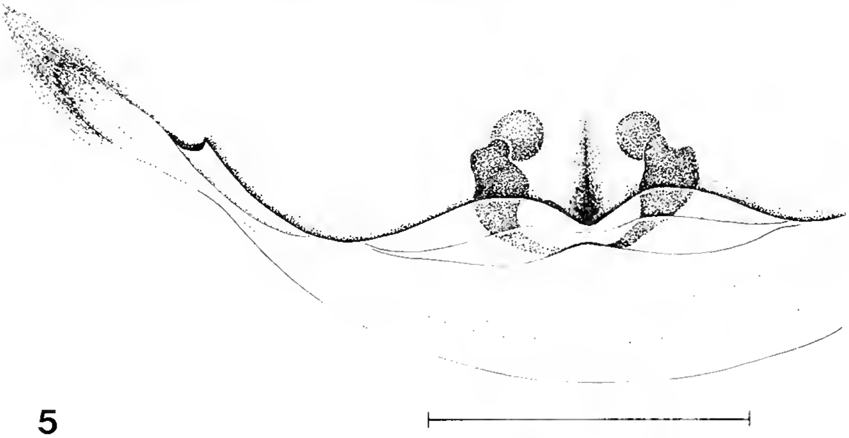

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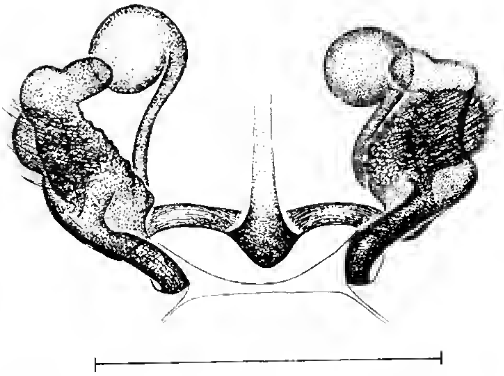


Figures 5 and 6 *Tamopsis riverinae* sp. nov. Female. 5. Epigyne. Scale: 0.5 mm. 6. Vulva. Scale: 0.25 mm.

Description

FEMALE HOLOTYPE

Measurements

Length: 6.5 mm; cephalothorax length: 2.3 mm; width: 2.25 mm; abdomen length: 4.2 mm; width: 3.75 mm. Legs: I: 15.05 mm, II: 14.9 mm, III: 5.45 mm, IV: 14.15 mm; ratio: 1:0.99:0.36:0.94. Ratio LB/LL: 0.43. PLS length: 2.85 mm; bS: 0.65 mm; tS: 2.2 mm. Length ratio PLS/abdomen: 0.68. Eye ratio: 1:0.7:1.32:1.43.

Colour

Cephalothorax yellow, lateral border and some radial stripes narrowly dark. Eye area anteriorly black, posteriorly of eyes with a whitish median stripe. Clypeus whitish. Abdomen whitish, slightly mottled, a lancet-shaped median stripe, the lateral border, and some transverse cross bars in posterior third piceous. Femora and PLS inconspicuously annulate. Ventral surface light.

Cephalothorax

About circular, much narrower than abdomen. Eye area rather depressed, clypeus about half as high as eye area. PLE largest, PME considerably larger than AME, ALE rather large. Distance AME/AME slightly <diameter of AME, distance AME/ALE >diameter of AME, distance PME/PME c. 1/3 of diameter of PME, distance PME/PLE c. as long as diameter of PME. Chelicerae <2 x as long as wide. Sternum pentagonal, sparsely hirsute.

Abdomen

Slightly longer than wide, much wider than cephalothorax, markedly trapezoid, posteriorly widest. Dorsal surface with 5 pairs of circular or slightly elliptoid muscular pits, 3rd pit remarkably large. Ventral muscular pits in a wide, v-shaped arrangement. PLS considerably shorter than abdomen, tS comparatively short.

Legs

Measurements see above. Short compared with body size. III comparatively long.

Epigyne

Rather simple, though with a posteriorly slightly sclerotized pocket halfway along each side.

Vulva

With two receptacula seminis, the dorsal one elongate and with a very distinct knob-like apical part. Glandulose part of ventral receptaculum fairly separated. Posteriorly with a complete transverse bar between either side.

Male

Unknown.

Variation

Unknown.

Etymology

Alludes to the occurrence in the Riverina country of New South Wales.

Distribution

Riverina country, southern New South Wales. Known only from type locality.

Habits

Little known. Holotype caught on "river gum" in December.

Relationships

This species belongs to the *eucalypti*-group of our revision (Baehr and Baehr 1987) and is certainly closely related to *T. eucalypti* (Rainbow). It is perhaps the western vicariant of the strictly eastern and southeastern *T. eucalypti*.

queenslandica-group

Tamopsis distinguenda Baehr and Baehr, 1992

Tamopsis distinguenda Baehr and Baehr, 1992: 66.

New records: WA: 1 male, Ludlow Tuart Forest 33.36S, 115.29E, 16 December 1980, S. J. Curry, Day Trap NO.1 (WAM 92/143, CBM); 1 male, Mt. Cooke 32.25S, 116.18E, 26 Dec. 1990, J. M. Waldock (WAM 91/94).

This species is closely related to the eastern *T. queenslandica* Baehr and Baehr and is perhaps its western vicariant. One of the specimens mentioned above is from the same locality where some specimens of the type series came from, and it has been collected from "open canopy, tuart forest, big clearing, mill paddock 13.I.Ar."

Tamopsis darlingtoniana Baehr and Baehr, 1987

Tamopsis darlingtoniana Baehr and Baehr, 1987: 371.

New record: WA: 1 female, Murdoch 32°04'18"S, 115°49'26"E, D. Mead-Hunter (III), 12 Dec. 1989 (WAM 92/133).

This species was described from a single female found near Perth in southwestern Australia. The new record is very close to the type locality.

Tamopsis facialis sp. nov.

Figures 7, 8, 25

Holotype

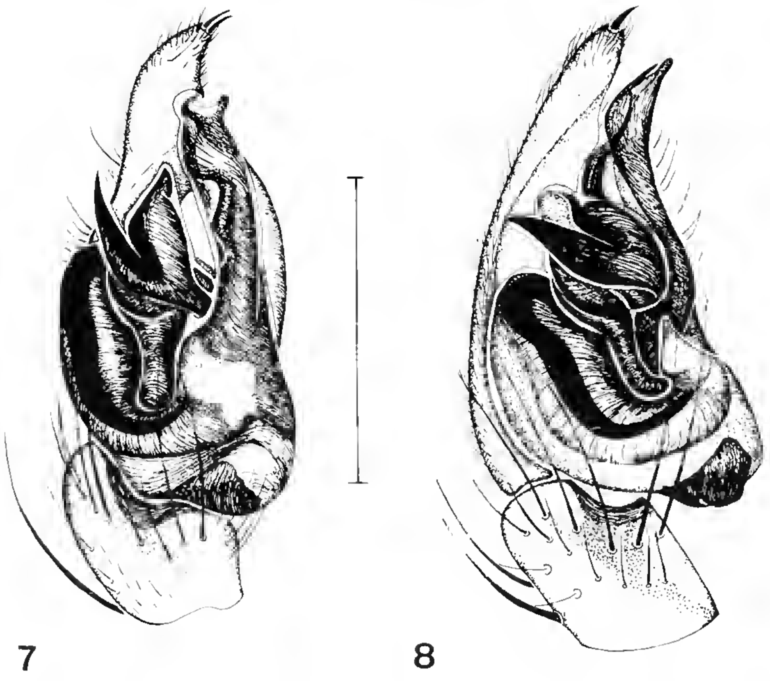
Male, W. A.: Callawa Stn. 20.33S, 120.40E, 4 Aug. 1989, A. E. de Jong (WAM 92/120).

Paratype

1 male, Grasspatch 33.14S, 121.43E, Fitz. Loc. 41, Western Australia, 8 Dec. 1991, A. F. Longbottom (WAM 92/126).

Diagnosis

Species of *queenslandica*-group, closely related to *T. centralis* Baehr and Baehr. Distinguished from that species by conspicuous, face-like pattern of eye area and deeply excised apex of lateral apophysis of male palpus.



Figures 7 and 8 *Tamopsis facialis* sp. nov. Male palpus. 7. Ventral view. 8. Lateral view. Scale: 0.5 mm.

Description

MALE HOLOTYPE

Measurements

Length: 3.3 mm; cephalothorax length: 1.55 mm; width: 1.45 mm; abdomen length: 1.75 mm; width: 1.48 mm. Legs: I: 8.75 mm, II: 9.1 mm, III: 3.7 mm, IV: 8.5 mm; ratio: 1:1.04:0.42:0.97. Ratio LB/LL: 0.36. PLS length: 1.48 mm; bS: 0.4 mm; tS: 1.08 mm. Length ratio PLS/abdomen: 0.85. Eye ratio: 1:0.42:0.85:0.97.

Colour

Cephalothorax dark yellow to light piceous, eye area and lateral borders narrowly black, some radial spots near lateral and posterior borders light yellow. Posterior part of eye area reddish, in middle with a whitish stripe. Anterior border of head apart from middle narrowly black, clypeus in middle with narrow black stripe, laterally below eyes with dark spot, and space between AME and ALE conspicuously yellow, much looking like another "eye". Abdomen whitish, very strongly mottled, a wide, lancet-shaped median stripe, the narrow lateral borders, and some transverse cross bars in posterior third dark piceous, colour of abdomen prevailing dark. Base in middle with a whitish spot on either side. Basal segment of palpi with a conspicuous black stripe on either side. Legs and PLS very inconspicuously annulate. Ventral surface light.

Cephalothorax

Almost circular, almost as wide as abdomen, fairly convex. Eye area rather depressed, clypeus about half as high as eye area. AME largest, PLE larger than PME, ALE moderately large.

Distance AME/AME c. 2/3 of diameter of AME, distance AME/ALE slightly <diameter of AME, distance PME/PME >1/2 of diameter of PME, distance PME/PLE slightly <diameter of PME. Chelicerae <2 x as long as wide. Sternum pentagonal, sparsely hirsute.

Abdomen

Distinctly longer than wide, barely wider than cephalothorax, elliptoid, widest in middle. Dorsal surface with 5 pairs of rather circular to fairly elliptoid muscular pits, 1st and especially 3rd pits very large and deeply sunken in. Ventral muscular pits in a wide, v-shaped arrangement. PLS considerably shorter than abdomen, tS comparatively short.

Legs

Measurements see above. Rather short compared with body size. III comparatively elongate.

Palpus

Median apophysis contorted, deeply excised at apex, inner part of excision slender, outer part convex, laterally with sharp edge. Lateral apophysis also contorted, elongate, apex distinctly excised, base laterally with a lamella.

MALE PARATYPE

Measurements

Length: 3.95 mm; cephalothorax length: 1.7 mm; width: 1.65 mm; abdomen length: 2.25 mm; width: 1.9 mm. Legs: I: 10.5 mm, II: 11.7 mm, III: 4.4 mm, IV: 10.35 mm; ratio: 1:1.11:0.41:0.98. Ratio LB/LL: 0.34. PLS length: 1.82 mm; bS: 0.4 mm; tS: 1.42 mm. Length ratio PLS/abdomen: 0.81. Eye ratio: 1:0.42:0.85:0.95.

Female

Unknown.

Variation

Because the paratype was in the process of moulting, colour and pattern are less distinctive than in holotype. Otherwise, little variation noted.

Etymology

Alludes to the conspicuous face-like pattern of anterior part of head.

Distribution

Southwestern part of Western Australia and southern border of Great Sandy Desert. Actually known only from two localities.

Habits

Largely unknown. Paratype collected "on diesel fuel tank". So far collected in August and December.

Relationships

This species is certainly most closely related to *T. centralis* Baehr and Baehr from central Queensland and shows only minor differences in structure of male palpus and perhaps in colour and pattern of eye area and clypeus.

Tamopsis piankai sp. nov.

Figures 9, 10, 25

Holotype

Female, WA, 39 km E. of Laverton 28.28S, 122.50E, 5-6 Oct. 1990, E. R. Pianka (WAM 92/128).

Diagnosis

Large, short-legged species of *queenslandica*-group due to structure of female vulva. Distinguished from all other species of this group by presence of two small sclerotized pockets on either side of epigyne just laterally of vulva.

Description

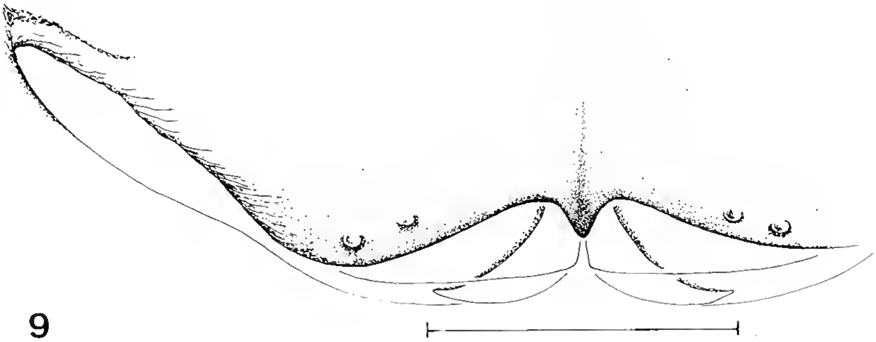
FEMALE HOLOTYPE

Measurements

Length: 5.45 mm; cephalothorax length: 2.10 mm; width: 2.05 mm; abdomen length: 3.35 mm; width: 3.05 mm. Legs: I: 12.05 mm, II: 12.2 mm, III: 4.55 mm, IV: 11.1 mm; ratio: 1:1.01:0.38:0.92. Ratio LB/LL: 0.45. PLS length: 2.7 mm; bS: 0.6 mm; tS: 2.1 mm. Length ratio PLS/abdomen: 0.81. Eye ratio: 1:0.45:0.97:0.96.

Colour

Cephalothorax dark yellow, eye area, lateral border, and a rather ill delimited sublateral band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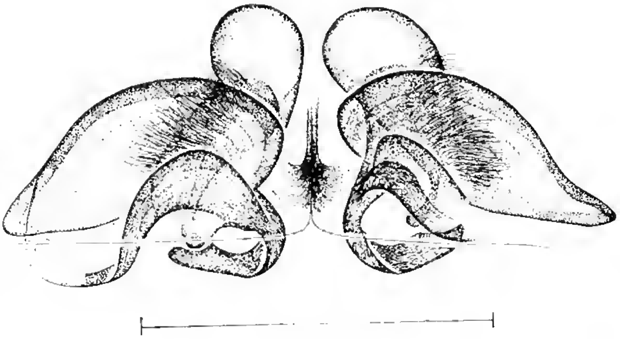
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Figures 9 and 10 *Tamopsis piankai* sp. nov. Female. 9. Epigyne. Scale: 0.5 mm. 10. Vulva. Scale: 0.25 mm.

black, some radial spots near lateral and posterior borders light yellow, area posteriorly of eyes light. Clypeus black, though area ventrolaterally of eyes and lateral part of clypeus with an indistinct light spot each. Chelicerae almost black, palpi with conspicuous black spots on all segments. Abdomen whitish, though very strongly mottled, a wide, lancet-shaped median stripe, the wide lateral borders, and some transverse cross bars in posterior third black, colour of abdomen prevailing dark. Legs barely annulate, though inner and outer surfaces conspicuously striped with black. PLS with two dark rings. Ventral surface light.

Cephalothorax

Almost circular, much narrower than abdomen, fairly convex. Eye area rather depressed, clypeus about half as high as eye area. AME largest, PME as large as PLE, ALE rather large. Distance AME/AME <half of diameter of AME, distance AME/ALE >half of diameter of AME, distance PME/PME c. 1/3 of diameter of PME, distance PME/PLE slightly <diameter of PME. Chelicerae <2 x as long as wide. Sternum pentagonal, sparsely hirsute.

Abdomen

Slightly longer than wide, much wider than cephalothorax, markedly trapezoid, posteriorly widest. Dorsal surface with 5 pairs of rather circular to slightly elliptoid muscular pits, 1st and 3rd pits large and deeply sunken in. Ventral muscular pits in a wide, v-shaped arrangement. PLS considerably shorter than abdomen, tS comparatively short.

Legs

Measurements see above. Very short, III comparatively elongate.

Epigyne

Without lateral pockets, though with two small, sclerotized pockets rather close to vulva.

Vulva

Compact, parts closely adjacent, medially with a narrow, transverse bar. Apparently 1 receptaculum seminis only which has the apical part globular and the basal part extensively glandulose. Intraductory ducts crossing receptaculum seminis, ventro-medially bent inwards, laterally markedly bent and with a short duct directed ventro-laterally.

Male

Unknown.

Variation

Unknown.

Etymology

Named in honour of the collector.

Distribution

Interior of southwestern Australia. Known only from type locality.

Habits

Unknown. Collected in October in "pitfall traps".

Relationships

With regard to structure of female vulva this species is certainly very closely related to *T.*

queenslandica Baehr and Baehr, *T. distinguenda* Baehr and Baehr, and perhaps also *T. reevesbyana* Baehr and Baehr, although it differs from all species by the structure of female epigyne and by the more complexly built intraductory ducts.

Tamopsis harveyi sp. nov.

Figures 11, 12, 26

Holotype

Female, NT: Specimen Hill, Harts Range, Zircon field site 1, 15 May 1991, A. F. Longbottom S.664 (WAM 92/138).

Diagnosis

Large, short-legged species of *queenslandica*-group due to structure of female vulva. Distinguished from other species of this group by absence of a lateral pocket in epigyne, elongate vulva with clearly separated dorsal receptaculum seminis much surpassing ventral receptaculum, intraductory ducts laterally sharply bent, posteriorly bent laterally, and crossing receptaculum.

Description

FEMALE HOLOTYPE

Measurements

Length: 5.75 mm; cephalothorax length: 2.1 mm; width: 2.05 mm; abdomen length: 3.65 mm; width: 3.1 mm. Legs: I: 11.85 mm, II: 11.9 mm, III: 4.75 mm, IV: 11.2 mm; ratio: 1:1:0.4:0.95. Ratio LB/LL: 0.48. PLS length: 2.9 mm; bS: 0.6 mm; tS: 2.3 mm. Length ratio PLS/abdomen: 0.79. Eye ratio: 1:0.41:1:1.04.

Colour

Cephalothorax including eye area piceous, in middle greyish, some radial spots near lateral and posterior borders light yellow, posteriorly of eyes with a light yellow median stripe. Clypeus and chelicerae almost black. Abdomen whitish, rather mottled, a wide, lancet-shaped median stripe, the wide lateral borders, and some transverse cross bars in posterior third black, colour of abdomen prevailing light. Legs, palpi, and PLS conspicuously annulate. Ventral surface light.

Cephalothorax

Almost circular, much narrower than abdomen, fairly convex. Eye area moderately depressed, clypeus slightly >1/2 as high as eye area. PLE largest, though but feebly larger than AME and PME, ALE rather large. Distance AME/AME <half of diameter of AME, distance AME/ALE c. 2/3 of diameter of AME, distance PME/PME c. 1/3 of diameter of PME, distance PME/PLE slightly <diameter of PME. Chelicerae <2 x as long as wide. Sternum pentagonal, sparsely hirsute.

Abdomen

Slightly longer than wide, much wider than cephalothorax, markedly trapezoid, posteriorly widest. Dorsal surface with 5 pairs of rather circular muscular pits, 3rd pit not unusually large, moderately sunken in. Ventral muscular pits in a wide, v-shaped arrangement. PLS considerably shorter than abdomen, tS comparatively short.

Legs

Measurements see above. Very short, III comparatively elongate.

Epigyne

Without lateral pocket or other pecularities.

Vulva

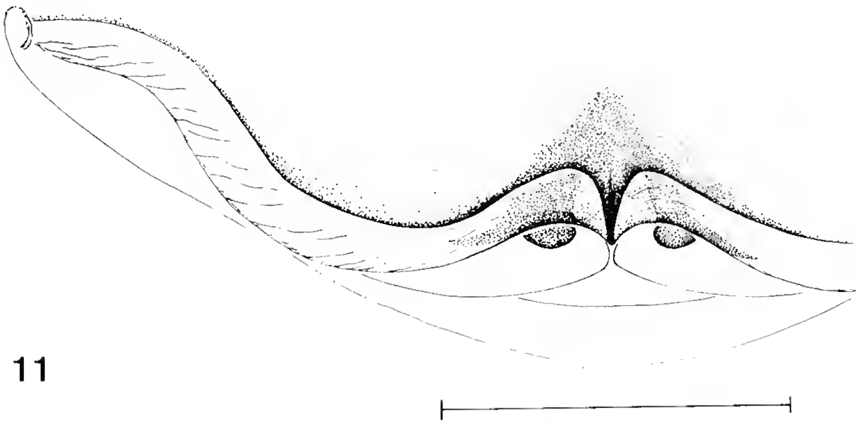
Rather elongate, parts close adjacent, medially with a narrow, transverse bar. With two receptacula seminis, the dorsal receptaculum apically circular and much surpassing the ventral receptaculum which is laterally extensively glandulose. Intraductory ducts crossing receptaculum seminis, laterally markedly bent, with a short duct directed ventro-laterally but rather curved laterally.

Male

Unknown.

Variation

Unknown.



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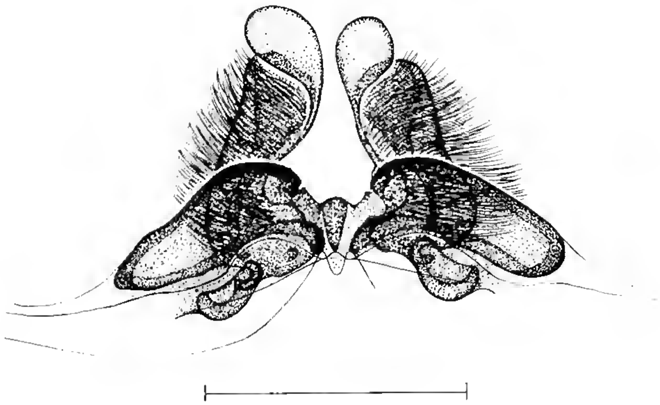

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Figures 11 and 12 *Tamopsis harveyi* sp. nov. Female. 11. Epigyne. Scale: 0.5 mm. 12. Vulva. Scale: 0.25 mm.

Etymology

Named in honour of Mark Harvey who kindly sent this highly interesting sample of specimens.

Distribution

Central Northern Territory. Known only from type locality.

Habits

Holotype collected in May "on dead twig in tree".

Relationships

With regard to structure of female vulva this species is most similar to *T. raveni* Baehr and Baehr of southeastern Queensland. However, as the *queenslandica*-group comprises several closely related species, *T. harveyi* might be also related to some other species.

Tamopsis gibbosa sp. nov.

Figures 13, 14, 26

Holotype

Female, WA, Durokoppin Nature Reserve 31.30S, 117.44.E, 3 Nov. 1988, D. Mitchell et al., DKR beat G (WAM 92/122).

Diagnosis

Species alluded to *queenslandica*-group by virtue of the sclerotized transverse bar and the strongly bent intraductory ducts in female epigyne. Within this group distinguished at first glance by the hump in middle of dorsal surface of abdomen, further by the lateral pocket of epigyne that is concealed by a large sclerotized plate, and by the large, roundish ventral receptaculum seminis which completely conceals the smaller dorsal receptaculum and bears a large, conspicuous, glandulose part in antero-medio-ventral position.

Description

FEMALE HOLOTYPE

Measurements

Length: 4.3 mm; cephalothorax length: 1.6 mm; width: 1.5 mm; abdomen length: 2.7 mm; width: 2.3 mm. Legs: I: 8.8 mm, II: 9.35 mm, III: 3.35 mm, IV: 8.1 mm; ratio: 1:0.95:0.38:0.92. Ratio LB/LL: 0.49. PLS length: 2.1 mm; bS: 0.45 mm; tS: 1.65 mm. Length ratio PLS/abdomen: 0.78. Eye ratio: 1:0.55:1.15:1.25.

Colour

Cephalothorax piceous, eye area inclusive clypeus black, some radial spots near lateral and posterior borders light yellow, posteriorly of eyes with a whitish median stripe. Abdomen whitish, though strongly mottled, a wide, lancet-shaped median stripe, the wide lateral borders, and some transverse cross bars in middle and posterior third dark piceous, colour of abdomen prevailing dark. Legs, palpi, and PLS conspicuously annulate. Ventral surface light.

Cephalothorax

Almost circular, much narrower than abdomen, fairly convex. Eye area rather depressed,

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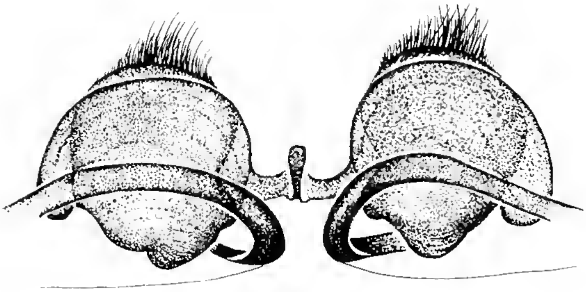

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Figures 13 and 14 *Tamopsis gibbosa* sp. nov. Female. 13. Epigyne. Scale: 0.5 mm. 14. Vulva. Scale: 0.25 mm.

clypeus c. half as high as eye area. PLE largest, PME larger than AME, ALE rather large. Distance AME/AME c. 2/3 of diameter of AME, distance AME/ALE c. diameter of AME, distance PME/PME c. 1/2 of diameter of PME, distance PME/PLE c. as long as diameter of PME. Chelicerae <2 x as long as wide. Sternum pentagonal, sparsely hirsute.

Abdomen

Slightly longer than wide, much wider than cephalothorax, markedly trapezoid, posteriorly widest. In middle of dorsal surface with a fairly acute hump. Dorsal surface with 5 pairs of rather circular muscular pits, 1st and 3rd pits large and deeply sunken in. Ventral muscular pits in a wide, v-shaped arrangement. PLS considerably shorter than abdomen, tS comparatively short.

Legs

Measurements see above. Very short compared with body size. III comparatively elongate.

Epigyne

With a slit-like pocket near lateral border covered by a large, sclerotized plate.

Vulva

Small, compact, parts closely adjacent, medially with a narrow, transverse bar, with 2 receptaculi seminis, the ventral receptaculum conspicuously globular and glandulose in antero-ventral position and covering completely the dorsal receptaculum. Intraductory ducts crossing receptaculum seminis and medially bent sharply inwards.

Male

Unknown.

Variation

Unknown.

Etymology

Alludes to the medially humped dorsal surface of abdomen.

Distribution

Southwestern Australia. Known only from type locality.

Habits

Unknown. Holotype caught in November, according to label perhaps collected by beating.

Relationships

The relationships of this species are somewhat obscure, because the male is still unknown. Hence even the association with the *queenslandica*-group is slightly doubtful. Due to the extremely short legs, the large plate covering the lateral pocket in the female epigyne, and some characters of the female vulva, however, this species could be related to the eastern *T. brevipes* Baehr and Baehr and to the two following species.

Tamopsis mainae sp. nov.

Figures 15, 16, 26

Holotype

Female, Moorine Rock, WA, 21.I.1978, R. P. McMillan (WAM 92/130).

Diagnosis

Species of the *queenslandica*-group, rather remotely related to *T. brevipes* Baehr and Baehr and *T. piankai* sp. nov. (see below) due to the somewhat similar female vulva. Distinguished from both species, however, by absence of a conspicuous lateral pocket in the female epigyne.

Description

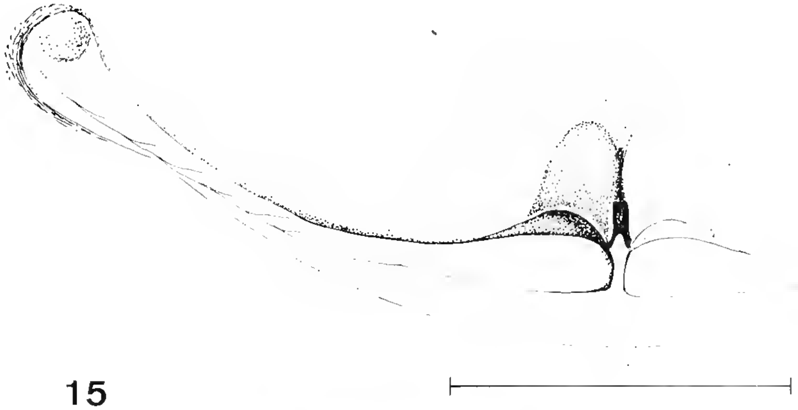
FEMALE HOLOTYPE

Measurements

Length: 5.35 mm; cephalothorax length: 1.95 mm; width: 1.9 mm; abdomen length: 3.4 mm; width: 3.1 mm. Legs: I: 11.1 mm, II: 10.95 mm, III: 4.5 mm, IV: 9.8 mm; ratio: 1:0.99:0.41:0.89. Ratio LB/LL: 0.48. PLS length: c. 2.5 mm, tip broken; bS: 0.55 mm; tS: c. 1.95 mm. Length ratio PLS/abdomen: c. 0.74. Eye ratio: 1:0.43:1.18:1.33.

Colour

Cephalothorax dark yellow to light piceous, eye area and lateral border black, some radial spots



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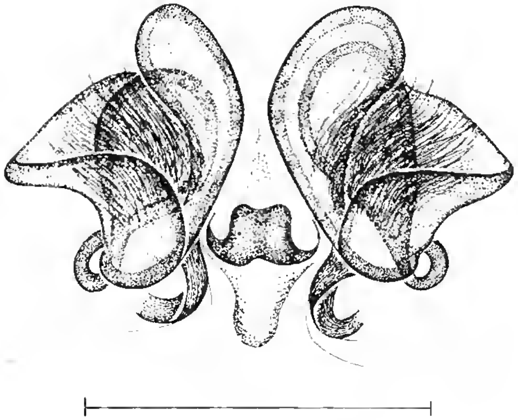

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Figures 15 and 16 *Tamopsis mainae* sp. nov. Female. 15. Epigyne. Scale: 0.5 mm. 16. Vulva. Scale: 0.25 mm.

near lateral and posterior borders light yellow, posteriorly of eyes with a whitish median stripe. Clypeus light yellow, a narrow median stripe dark. Chelicerae at base light, then darkened. Abdomen whitish, though rather strongly mottled, a wide, serrate, lancet-shaped median stripe, the wide lateral borders, and some transverse cross bars in posterior third dark piceous, colour of abdomen prevailing light. Legs, palpi, and PLS fairly conspicuously annulate. Ventral surface light.

Cephalothorax

Almost circular, much narrower than abdomen, fairly convex. Eye area rather depressed, clypeus c. half as high as eye area. PLE largest, PME much larger than AME, ALE fairly large. Distance AME/AME c. 2/3 of diameter of AME, distance AME/ALE c. diameter of AME, distance PME/PME <1/2 of diameter of PME, distance PME/PLE c. as long as diameter of PME. Chelicerae <2 x as long as wide. Sternum pentagonal, sparsely hirsute.

Abdomen

Slightly longer than wide, much wider than cephalothorax, markedly trapezoid, posteriorly widest. Dorsal surface with 5 pairs of rather circular to slightly elliptoid muscular pits, 1st and

3rd pits large. Ventral muscular pits in a wide, v-shaped arrangement. PLS considerably shorter than abdomen, tS comparatively short.

Legs

Measurements see above. Very short compared with body size. III comparatively elongate.

Epigyne

Without a pocket near lateral border.

Vulva

Small, compact, parts closely adjacent, medially with a narrow, transverse bar, with 2 receptaculi seminis, the ventral receptaculum much surpassing the dorsal receptaculum and both laterally glandulose. Vulva laterally with a large membraneous area partly covering the receptacula. Intraductory ducts short, directed posteriorly, but strongly curved outwards.

Male

Unknown.

Variation

Unknown.

Etymology

Named in honour of Barbara York Main, well known authority of Australian spiders.

Distribution

Inland southwestern Australia. Known only from type locality.

Habits

Unknown. Holotype collected in January.

Relationships

This species is rather isolated, but perhaps remotely related to eastern *T. brevipes* Baehr and Baehr, though certainly less closely than the following species.

Tamopsis triangularis sp. nov.

Figures 17, 18, 26

Holotype

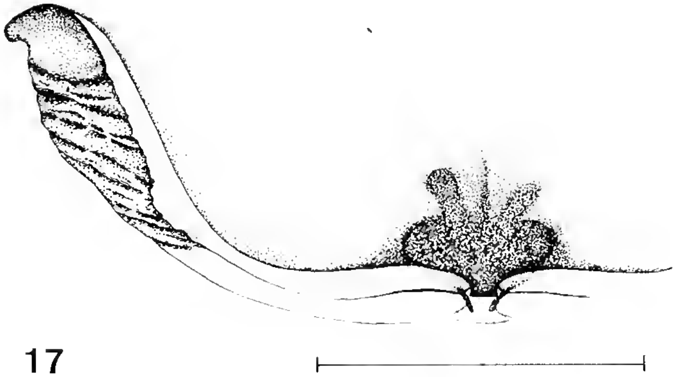
Female, NSW, Yanco Ck., 11 km SW. of Morundah 35.02S, 146.13E, 29 Dec. 1990, A. F. Longbottom S.654 (P46/4), River gums, "sandside" 50 km SW. of Narrandera (WAM 92/140).

Paratypes

2 females, same data (WAM 92/141-142, CBM).

Diagnosis

Species of the *queenslandica*-group, though most closely related to *T. brevipes* Baehr and Baehr. Distinguished from that species by the plate covering the lateral pocket in female epigyne having a very large medio-caudal part bearing conspicuous ridges.



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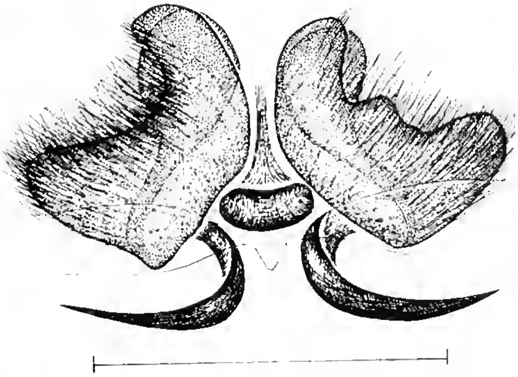

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Figures 17 and 18 *Tamopsis triangularis* sp. nov. Female. 17. Epigyne. Scale: 0.5 mm. 18. Vulva. Scale: 0.25 mm.

Description

FEMALE HOLOTYPE

Measurements

Length: 5.6 mm; cephalothorax length: 2.2 mm; width: 2.25 mm; abdomen length: 3.4 mm; width: 3.7 mm. Legs: I: 11.8 mm, II: 11.85 mm, III: 4.9 mm, IV: 11.7 mm; ratio: 1:1:0.41:0.99. Ratio LB/LL: 0.47. PLS length: 2.5 mm; bS: 0.5 mm; tS: 2.0 mm. Length ratio PLS/abdomen: 0.74. Eye ratio: 1:0.46:0.97:1.05.

Colour

Cephalothorax dark yellow to light brown, eye area and lateral border black, three radial spots near lateral border, and base conspicuously light yellow, posteriorly of eyes with a whitish median stripe. Clypeus at base more or less dark yellow, but with an oblique piceous stripe converging to lower border, face laterally of AME and PME with conspicuous yellow spot. Chelicerae light. Abdomen whitish, though rather strongly mottled, a wide, lancet-shaped median stripe, the wide lateral borders, and some transverse cross bars in middle and posterior third dark piceous, colour of abdomen prevailing light. Legs, palpi, and PLS fairly conspicuously annulate. Basal segment of palpi at outer and inner surface of apex with conspicuous black stripe. Ventral surface light.

Cephalothorax

Almost circular, even slightly wider than long, much narrower than abdomen, fairly convex. Eye area depressed, clypeus c. half as high as eye area. PLE but slightly larger than AME and PME, which are almost equal in size, ALE fairly large. Distance AME/AME <2/3 of diameter of AME, distance AME/ALE c. diameter of AME, distance PME/PME <1/2 of diameter of PME, distance PME/PLE c. as long as diameter of PME. Chelicerae <2 x as long as wide. Sternum pentagonal, sparsely hirsute.

Abdomen

Slightly wider than long, much wider than cephalothorax, extremely trapezoid, posteriorly widest. Dorsal surface with 5 pairs of rather circular to fairly elliptoid muscular pits, 1st and 3rd pits large, 3rd remarkably elliptoid. Ventral muscular pits in a wide, v-shaped arrangement. PLS considerably shorter than abdomen, tS comparatively short.

Legs

Measurements see above. Very short compared with body size. III comparatively elongate.

Epigyne

With a slit-like pocket near lateral border covered by a large sclerotized plate, medially of pocket with a large plate reaching halfways to middle and covered by several conspicuous ridges.

Vulva

Small, compact, parts closely adjacent, medially with a narrow, transverse bar, with 2 receptaculi seminis, ventral receptaculum laterally strongly excised and completely glandulose, covering completely the dorsal receptaculum. Intraductory ducts short, not crossing receptaculum seminis, posteriorly strongly curved laterally.

FEMALE PARATYPE 1 (WAM 92/141)

Measurements

Length: 5.95 mm; cephalothorax length: 2.2 mm; width: 2.25 mm; abdomen length: 3.75 mm; width: 4.1 mm. Legs: I: 11.7 mm, II: 11.45 mm, III: 4.75 mm, IV: 11.1 mm; ratio: 1:0.98:0.41:0.95. Ratio LB/LL: 0.51. PLS length: 2.6 mm; bS: 0.5 mm; tS: 2.1 mm. Length ratio PLS/abdomen: 0.69. Eye ratio: 1:0.45:0.99:1.04.

Male

Unknown.

Variation

Slight variation noted only in relative length of legs and PLS.

Etymology

Alludes to the striking triangular shape of abdomen.

Distribution

Riverina country in southern central New South Wales. Known only from type locality.

Habits

Largely unknown, type series collected in December on “river gums”.

Relationships

This species is certainly very closely related to *T. brevipes* Baehr and Baehr from eastern New South Wales. It is perhaps only a western transmontane subspecies. But any decision must await the discovery of the males of both species.

circumvidens-group

Tamopsis circumvidens Baehr and Baehr, 1987

Tamopsis circumvidens Baehr and Baehr, 1987: 378; 1992: 70.

New record: WA: 1 female, Gairdner Range 30.19S, 115.17E, Feb. 1990, G. Harold (WAM 92/124).

This very distinctive species was until now known from two localities in inland southwestern Australia and several localities in western Victoria. The new record enlarges the range slightly to the west and demonstrates that this species is distributed right through southern semiarid Australia.

tropica-group

Tamopsis leichardtiana Baehr and Baehr, 1987

Figure 26

Tamopsis leichardtiana Baehr and Baehr, 1987: 382.

New record: WA: 1 female, Tim Ealey Hill 21.35'20"S, 118.59'00"E, 22 April 1989, M. S. Harvey (WAM 92/144).

This species was hitherto known from a single female from northwestern Queensland. The new record enlarges the known range of this species right through northern Australia to the Pilbara region in northwestern Australia. This is evidence of an inland distribution in arid country of northern Australia. The specimen is fully coloured (better than the holotype which was moulting) and exhibits a striking pattern: the abdomen bears two large, conspicuous, white spots in posterior half around 3rd muscular pit, middle of clypeus and base of chelicerae are strikingly black, and legs, palpi, and PLS are conspicuously annulate.

Tamopsis gracilis sp. nov.

Figures 19, 20, 27

Holotype

Male, W. A.: Gorge SW. of Mt Robinson, 23.08S, 118.54E, 27 Aug. 1990, A. F. Longbottom S.474 (WAM 92/132).

Diagnosis

Small, very long-legged species of the *tropica*-group, very similar to *T. fickerti* (L. Koch), but distinguished from that species by much smaller size, less distinctive pattern, and male palpus with much wider excavate process at apex of median apophysis and straight instead of sinuate lateral apophysis which is less voluminous at apex.

Description

MALE HOLOTYPE

Measurements

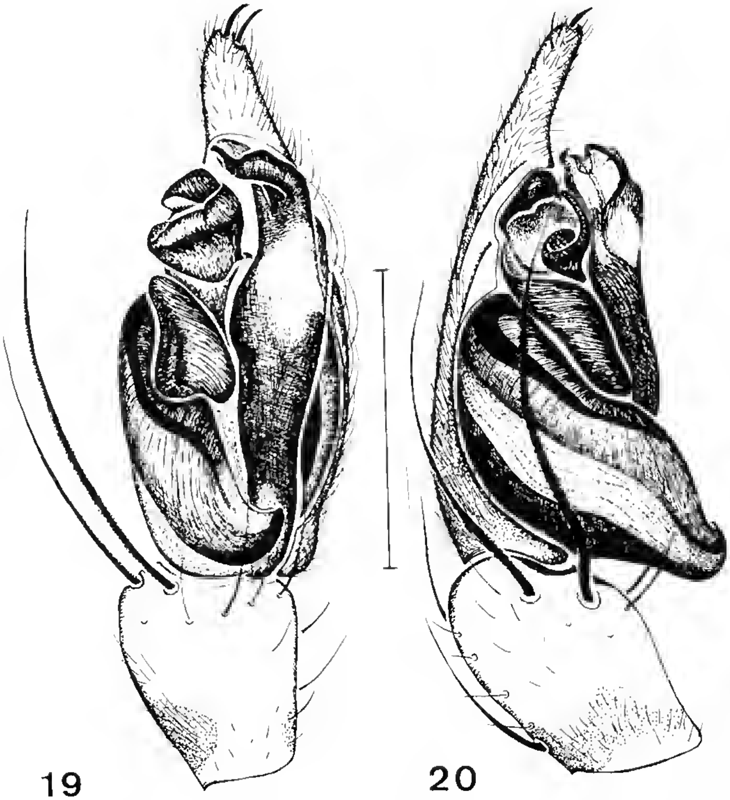
Length: 3.7 mm; cephalothorax length: 1.6 mm; width: 1.6 mm; abdomen length: 2.1 mm; width: 1.7 mm. Legs: I: 16.65 mm, II: 15.52 mm, III: 5.22 mm, IV: 14.64 mm; ratio: 1:0.93:0.31:0.88. Ratio LB/LL: 0.22. PLS length: 1.98 mm; bS: 0.48 mm; tS: 1.5 mm. Length ratio PLS/abdomen: 0.94. Eye ratio: 1:0.30:0.69:0.81.

Colour

Cephalothorax dark yellow, part of eye area and lateral borders narrowly black, some radial spots near lateral and posterior borders indistinctly ligther. Clypeus in middle basally with black stripe, ventrally white. Chelicerae and terminal segment of palpus black. Abdomen yellowish, pattern very indistinct (specimen in the course of shedding). Legs and PLS distinctly annulate. Ventral surface light.

Cephalothorax

Almost circular, almost as wide as abdomen, moderately convex. Eye area strongly raised, laterally not concave, clypeus c. as high as eye area. AME by far largest, PLE slightly larger than



Figures 19 and 20 *Tamopsis gracilis* sp. nov. Male palpus. 19. Ventral view. 20. Lateral view. Scale: 0.5 mm.

PME, ALE small. Distance AME/AME slightly >diameter of AME, distance AME/ALE c. 1/3 of diameter of AME, distance PME/PME slightly >1/3 of diameter of PME, distance PME/PLE slightly <diameter of PME. Chelicerae <2 x as long as wide. Sternum pentagonal, sparsely hirsute.

Abdomen

Distinctly longer than wide, slightly wider than cephalothorax, elliptoid, widest in middle. Dorsal surface with 5 pairs of rather circular muscular pits. Ventral muscular pits in a wide, v-shaped arrangement. PLS slightly shorter than abdomen, tS comparatively short.

Legs

Measurements see above. Very elongate, III comparatively short.

Palpus

Median apophysis rather short, contorted, apically wide, apex with a wide membraneous area and a scopula-like organ within. Lateral rim with sharp edge, anteriorly with a wide, excavate process, not hooked at tip. Lateral apophysis stout, strongly contorted, apex slightly excised.

Female

Unknown.

Variation

Unknown.

Etymology

Alludes to the smaller size compared with the closely related *T. fickerti*.

Distribution

Hamersley Ranges, northwestern Australia. Known only from type locality.

Habits

Unknown. Holotype collected in August "in gorge".

Relationships

This species is certainly closely related to southeastern *T. fickerti* (L. Koch) as can be seen by the very similar male palpus. For differences, see diagnosis. It may be the western vicariant of the widespread eastern species.

Tamopsis perthensis Baehr and Baehr, 1987

Tamopsis perthensis Baehr and Baehr, 1987: 386; 1989: 319; 1992: 75.

New record: WA: 1 female, Mt. Cooke, 32.25S, 116.18E, 25 February 1992, M. S. Harvey and J. M. Waldock (WAM 92/131); 1 male, WA: Yanchep, 7 Oct. 1992, M. S. Harvey (WAM 93/35).

The commonest species in southwestern Australia. The specimens were "hand collected" and captured "on *Melaleuca* trunk".

Tamopsis occidentalis Baehr and Baehr, 1987

Tamopsis occidentalis Baehr and Baehr, 1987: 387; 1989: 319; 1992: 76.

New records: WA: 1 female, Ashburton River, Near Urala Stn crossing, Aug. 1988, G. Crane; 1 female, Charlies Knob, Gibson Desert Nature Reserve, 25.03'S, 124.59'E, 18 Aug. 1990, A. E. de Jong (71494.9) (WAM 92/121).

This species is widespread in northwestern Australia between about Gascoyne River and the southern fringe of Great Sandy Desert (Baehr and Baehr 1987, 1992). The second new record, however, extends the known range far to the east deeply into the desert areas of central Western Australia.

Tamopsis marri Baehr and Baehr, 1989

Figure 27

Tamopsis marri Baehr and Baehr, 1989: 312; 1992: 75.

New record: WA: 7-8 km WNW. of Point Salvation, 28.12S, 123.36E, 8-10 Nov. 1990, E. R. Pianka (WAM 92/135).

This species is very closely related to *T. occidentalis* Baehr and Baehr and is presumably the southern vicariant of the latter. It was previously known from two localities in the southernmost part of southwestern Australia. The present record extends the known range somewhat to the northeast, but is still far outside the known range of *T. occidentalis*. The mentioned specimen was caught in "pitfall traps".

Tamopsis longbottomi sp. nov.

Figures 21, 22, 23, 24, 27

Holotype

Male, NT: Carpentaria H'way Rest area, 168 km E. of Stuart H'way, 13 Aug. 1991, A. F. Longbottom S.727 (WAM 92/136).

Paratype

Female, NT: Kakadu, Muirella Park, 16 Aug. 1980, H. Parnaby, ex Parnaby collection, *Tamopsis* sp. det. M Gray 1989 (AMS KS 20467).

Diagnosis

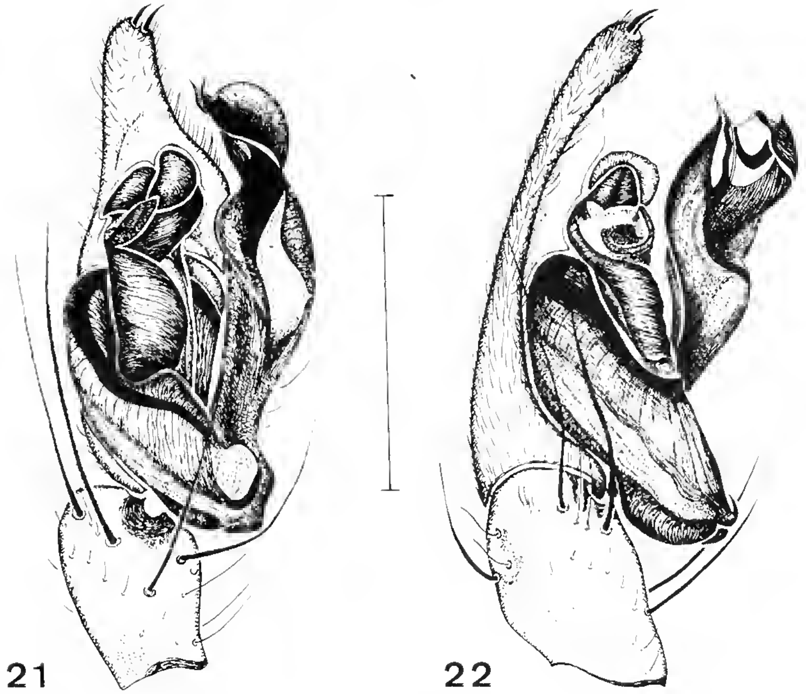
Very long-legged species of *tropica*-group, closely related to the *fickerti-fitzroyensis*-lineage, in shape of male palpus perhaps most similar to *T. marri* Baehr and Baehr and *T. fickerti* (L. Koch), in shape of female genitalia most resembling *T. leichardtiana* Baehr and Baehr and *T. rossi* Baehr and Baehr, but in view of the scapus in the epigyne also *T. fickerti* (L. Koch). Distinguished by very dark pattern of cephalothorax, especially eye area, clypeus, and chelicerae, apex of median apophysis with median excavate process triangular and very depressed and lateral process large and surpassing median process, and lateral apophysis strongly contorted and sinuate, apically wide, not excised, but bearing two short spines.

Description

MALE HOLOTYPE

Measurements

Length: c. 4.2 mm; cephalothorax length: 1.8 mm; width: 1.75 mm; abdomen length: c. 2.4 mm; width: 1.95 mm. Legs: I: 20.1 mm, II: 18.2 mm, III: 5.6 mm, IV: 16.4 mm; ratio: 1:0.91:0.28:0.82.



Figures 21 and 22 *Tamopsis longbottomi* sp. nov. Male palpus. 21. Ventral view. 22. Lateral view. Scale: 0.5 mm.

Ratio LB/LL: 0.21. PLS length: 2.5 mm; bS: 0.55 mm; tS: 1.95 mm. Length ratio PLS/abdomen: 1.05. Eye ratio: 1:0.25:0.66:0.70.

Colour

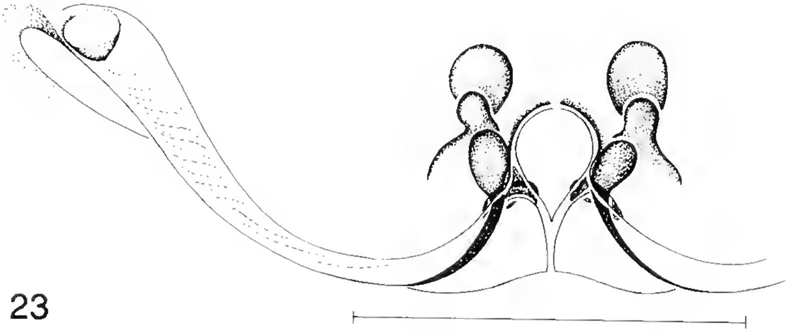
Cephalothorax dark yellow to piceous, anterior part of eye area and lateral borders black, some radial spots near lateral and posterior borders indistinctly lighter. Clypeus and base of chelicerae black. Posterior part of eye area conspicuously light, though with a dark median stripe. Basal segment of palpus with black stripe on inner and outer surfaces. Abdomen whitish, wide median lancet-shaped stripe and wide lateral borders conspicuously black, in posterior third with several dark transverse cross bars. Legs and PLS barely annulate, though dark on inner and outer surfaces. Ventral surface light.

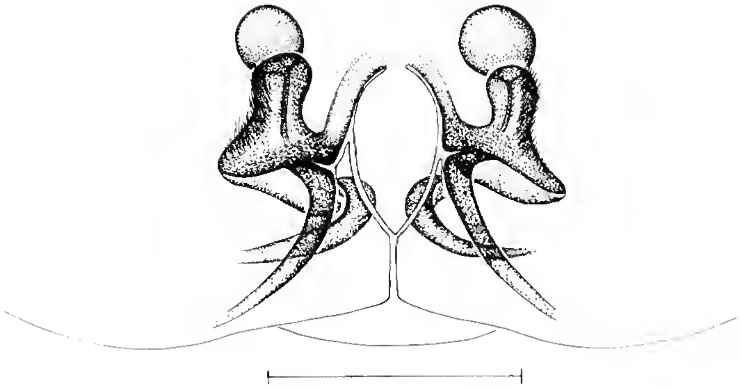
Cephalothorax

Almost circular, slightly narrower than abdomen, moderately convex. Eye area strongly raised, laterally not concave, clypeus c. as high as eye area. AME by far largest, PLE barely larger than PME, ALE small. Distance AME/AME c. 2/3 of diameter of AME, distance AME/ALE c. 1/3 of diameter of AME, distance PME/PME slightly >1/3 of diameter of PME, distance PME/PLE slightly <diameter of PME. Chelicerae <2 x as long as wide. Sternum pentagonal, sparsely hirsute.

Abdomen

Distinctly longer than wide, wider than cephalothorax, elliptoid, widest in middle. Dorsal surface with 5 pairs of rather circular muscular pits. Ventral muscular pits in a wide, v-shaped arrangement. PLS slightly longer than abdomen, tS comparatively short.





Figures 23 and 24 *Tamopsis longbottomi* sp.nov. Female. 23. Epigyne. Scale: 0.5 mm. 24. Vulva. Scale: 0.25 mm.

Legs

Measurements see above. Very elongate, III comparatively short.

Palpus

Median apophysis rather short, contorted, apically wide, apex with a wide membraneous area and a scopula-like organ within. Lateral rim with sharp edge, anteriorly with a wide, triangular, apically wide, very depressed, excavate process, not hooked at tip. Lateral part of apex with a large bulbous process distinctly surpassing median process. Lateral apophysis stout, strongly contorted, apex barely excised, though gently bisinuate, with two short spines at borders and a conspicuous, semicircular, sclerotized strap within apical membrane.

FEMALE PARATYPE

Measurements

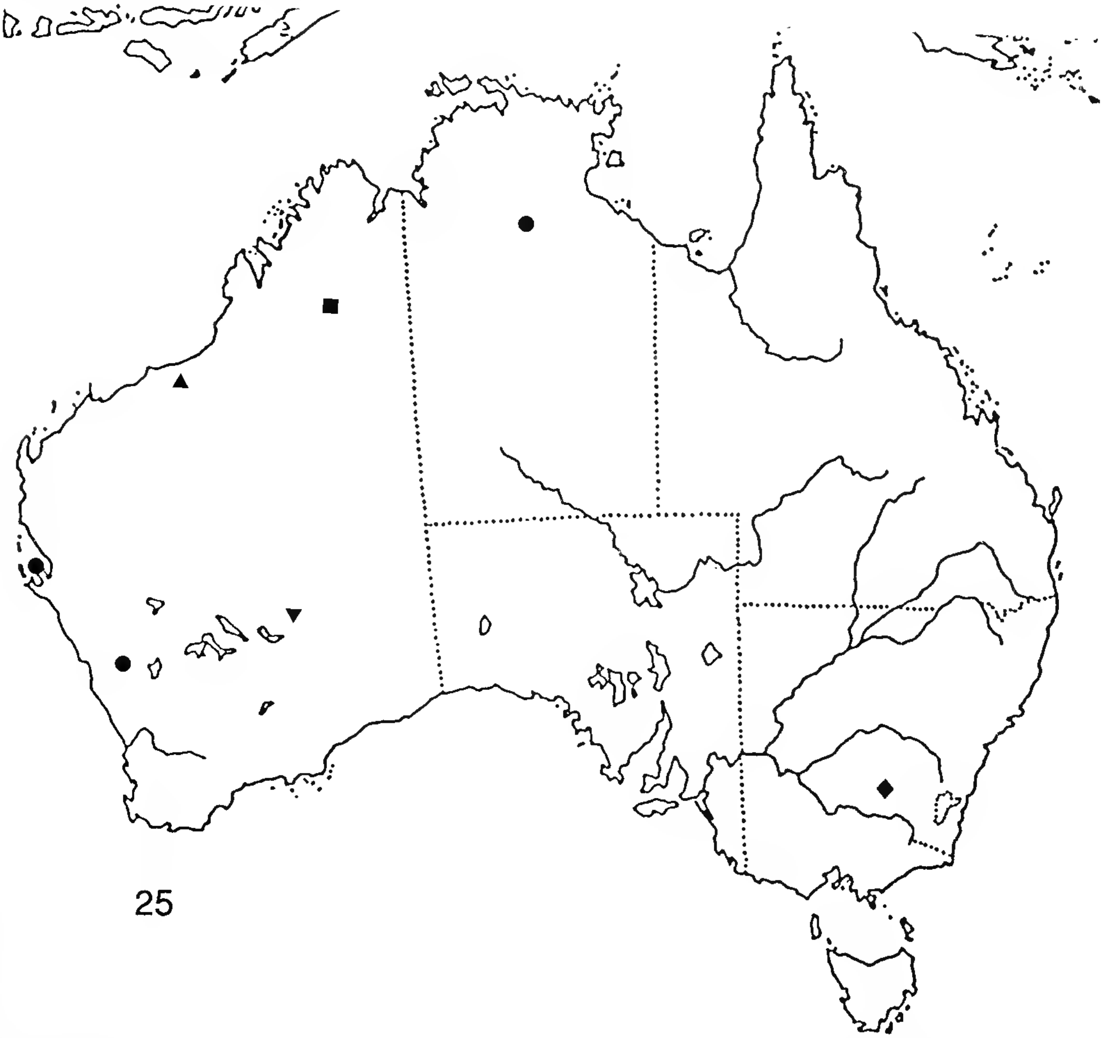
Length: 4.4 mm; cephalothorax length: 1.85 mm; width: 1.85 mm; abdomen length: 2.5 mm; width: 2.05 mm. Legs: I: 15.5 mm, II: 15.2 mm, III: 5.1 mm, IV: 13.7 mm; ratio: 1:0.92:0.31:0.83. Ratio LB/LL: 0.27 PLS length: 2.8 mm; bS: 0.65 mm; tS: 2.15 mm. Length ratio PLS/abdomen: 1.12. Eye ratio: 1:0.30:0.69:0.75.

Colour

Colour of cephalothorax rather similar to holotype, eye area dark. Abdomen almost uniformly dark, though with many yellow spots. Median lancet-shaped stripe and lateral borders barely marked, at apex with several dark transverse cross bars. Legs and PLS barely annulate, though dark on inner and outer surfaces. Ventral surface light.

Cephalothorax

Rather similar to male. Clypeus almost as high as eye area. AME by far largest, PLE slightly larger than PME, ALE small. Distance AME/AME c. 2/3 of diameter of AME, distance AME/ALE slightly >1/3 of diameter of AME, distance PME/PME slightly >1/2 of diameter of PME, distance PME/PLE slightly <diameter of PME.



25

Figure 25 Distribution of *Hersilia mimbi* sp. nov.: ■; *Tamopsis depressa* Baehr and Baehr: ●; *T. riverinae* sp. nov.: ◆ ; *T. facialis* sp. nov.: ▲ ; *T. piankai* sp. nov.: ▼ .

Figure 26 Distribution of *Tamopsis harveyi* sp. nov.: ▲ ; *T. gibbosa* sp. nov.: ● ; *T. mainae* sp. nov.: ◆ ; *T. triangularis* sp. nov.: ▼ ; *T. leichardtiana* Baehr and Baehr: ■ .

Abdomen

Rather similar to holotype. PLS distinctly longer than abdomen, tS comparatively short.

Legs

Measurements see above. Slightly shorter than in male, though still very elongate, III comparatively short.

Epigyne

With an opening immediately at lateral border covered by a plate. Medially with an elongate oval scapus.

Vulva

Apical part of dorsal receptaculum seminis circular, markedly separate, ventral receptaculum seminis horizontally bent, introductory duct conspicuously curved outside.

Variation

Due to limited material little variation noted.

Etymology

Named in honour of the collector of this as well as of several other interesting specimens.

Distribution

Northern half of Northern Territory.

Habits

Largely unknown. Holotype collected "dead in red-back web (*Latrodectus*)", paratype "on trunk of paperbark in swampy unburnt area". So far collected in August.

Relationships

This species belongs to the *fickerti-fitzroyensis*-lineage of the *tropica*-group that combines a group of at least 8 highly apomorphic and closely related species. In shape of palpus *T. longbottomi* resembles most *T. fickerti* (L. Koch) and *T. marri* (Baehr and Baehr), but this cluster of species is so similar that a reasonable decision, as to which species *T. longbottomi* is most closely related, is very difficult.

In shape of female genitalia *T. longbottomi* resembles *T. leichardtiana* Baehr and Baehr and *T. rossii* Baehr and Baehr, but it is distinguished from both, inter alia, by the median scapus in the epigyne. With regard to this scapus *T. longbottomi* resembled also *T. fickerti* (L. Koch), the single species having a comparable scapus. At the same time it is distinguished from *T. fickerti* by different shape of the scapus and by absence of the swollen introductory duct coiled around the base of the receptaculum seminis. In view of the female genitalia *T. longbottomi* may take an intermediate position between the three mentioned species. This position, however, will be only better understood, when males of both species, *T. leichardtiana* and *T. rossii* are known.

Tamopsis fitzroyensis Baehr and Baehr, 1987

Figure 27

Tamopsis fitzroyensis Baehr and Baehr, 1987: 389.

New records: WA: 1 male, 6 km E. of Mt. Talbot, Walcott Inlet, Site 19/2, 16°27'30"S, 124°50'30"E, B. Y. Main (FN/2) (BYM 88/K1041), 18 June 1988 (WAM 92/152); 1 female, 6 km E. of Mt. Talbot, Walcott Inlet, Site 19/2, 16°27'30"S, 124°50'30"E, B. Y. Main (FN/4) (BYM 88/K1085), 19 June 1988 (WAM 92/153); 1 female, Mt. Trafalgar, 15°16'50"S, 124°04'05"E, 16 June, 1988 Site 14/3, B. Y. Main (FN 5)(BYM 88/K923)(WAM 92/150); 1 female, 13.5 km NE. of Crystal Head, SW Osborne Island, 14°23'S, 125°57'E, N. Mc Kenzie (site 11/1) (BYM 88/K753), 10.6.1988 (WAM 92/151); 1 male, 1 female, WA. Manning Gorge 16°44'S, 125°57'E, 24 Dec. 1991, G. Harold (WAM 93/19-20).

This is a widespread species in the Kimberley Division. The mentioned specimens were caught in June and in December in "Rainforest", "on bark", "under cliffs, on *Terminalia* bark", and "on boab tree".

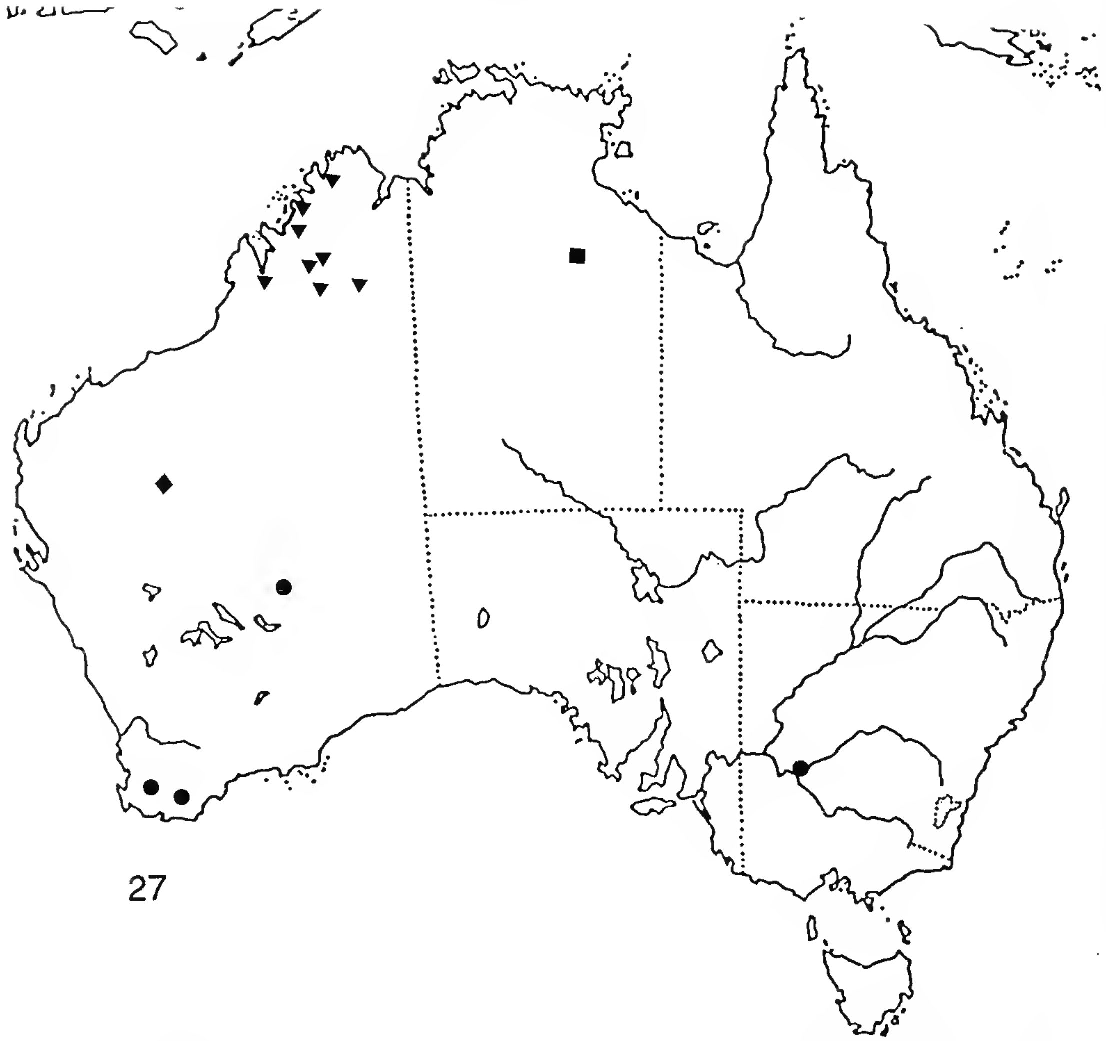


Figure 27 Distribution of *Tamopsis gracilis* sp. nov.: ◆ ; *T. marri* Baehr and Baehr: ● ; *T. longbottomi* sp. nov.: ■ ; *T. fitzroyensis* Baehr and Baehr: ▼ .

DISCUSSION

Biology

Even after some years of intensive work, both collecting and taxonomic, still rather little is known on the biology of the Australian Hersiliidae. Only a few observations have been made on hunting behaviour and prey, no observations at all are available on courtship and mating, and very little is known on propagation and development. And, surprisingly enough, even the simple habitat preference of most species is unknown, in spite of the knowledge of over 45 species.

The situation, however, is different according to the respective species-groups. Evidently the species of the genus *Tamopsis* are easily divided in two main groups: a group of high-eyed species that includes actually three presumably related species groups (*nanutarrae*-, *arnhemensis*-, *tropica*-groups), and a morphologically much more diverse group of more or less low-eyed species that comprises all other species groups.

From our own observations on several species of the high-eyed group and from label data and the few remarks in the very sparse literature, we are convinced that the high-eyed species live generally on the trunks of trees, preferably eucalypts but also other trees such as *Melaleuca, Ficus, Adansonia, Terminalia*, and certain other rain forest species. Sometimes they are found on boulders, walls, and fences. Generally they seem to prefer vertical structures, where they usually sit motionless head foremost in small fissures or depressions waiting for prey. It seems reasonable to assume that the strongly raised eye hill helps them to look over elevations or to obtain a larger visual field on the curved surface of tree trunks. These species are also usually very long-legged and they are extremely fast runners when disturbed, running around the trunk to reach a hiding place.

On the contrary, very little is known in these respects of the low-eyed species which have been thus far rarely collected in larger numbers. Most label records of collecting circumstances, where available, are rather curious and do not seem to give hints to the actual habitat. Specimens have been collected for example "active on ground", "in pitfall traps", "on rusty pipe ladder in house", "on diesel fuel tank", "on single thread on dead scrub", "inside a house", "on fern", "in mud wasp nest", "under wooden plank on beach", "while harvesting" etc. A better insight into the real habitats give perhaps the few observations of spiders collected by "beating foliage, shrubs, or twigs". We think that small branches and even twigs are perhaps the localities where the low-eyed species usually occur. This would explain the depressed eye area and the generally much shorter legs in these species. If this opinion would prove to be true, most low-eyed species are known from accidental collecting only and they have been hardly ever searched in their real habitat. We thus exspect that use of appropriate collecting methods in future will again considerably raise the number of species especially in the low-eyed group.

Distribution

The discovery of a second species of genus *Hersilia* in Australia enlarges the range of this genus to the west, but is not surprising. This genus is certainly a rather recent invader from the Oriental region into Australia. The two Australian species belong to the same apomorphic species-group within the diverse genus *Hersilia* like all species known from New Guinea (Baehr and Baehr, 1993). The slightly more apomorphic status of the Western Australian *H. mimbi* compared with the northern *T. australiensis* suggests that the original stock of *Hersilia* invaded Australia from the north, probably via Arnhem Land, and later split into another population in northwestern Australia.

The distribution patterns of the new species of the genus *Tamopsis* and of those species the ranges of which have been considerably enlarged in this paper, are more difficult to explain, especially with regard to the low-eyed species in view of the opinions expressed in the previous section.

In the light of the recent discoveries it turns out that the number of species in the western half of Australia is not perceptibly lower than in the east. On the contrary, in some groups (e.g. *queenslandica*-, *tropica*-groups) clusters of species apparently exist in Western Australia making its fauna even more diverse than that of eastern Australia, and thus compensating the majority of primitive, monotypic species-groups in the east. Moreover, it may be generally assumed that in most species-groups vicariants of eastern species exist in southwestern, northwestern, or central Australia. Certainly, the biogeographical history of most species-groups has been more complex than we assumed in our revision, although the general patterns are probably still true.

The additional, though still scanty material extends considerably the ranges of several species: In the north across most or the whole of the northern part of interior Australia *(T. depressa, T. leichardtiana)*, or at least far into the central arid regions *(T. occidentalis)*, and in the south through the mallee regions of southwestern Australia to western Victoria *(T. circumvidens, T. transiens, T. marri)* (Baehr and Baehr 1992). All those very widely ranging species, however, are adapted to arid or semiarid regions, where they perhaps live mainly on the widespread river gum (*Eucalyptus camaldulensis*), at least in the north, and in the south also on certain mallee species. Hence, their extensive ranges are easily understood.

In certain cases (e.g. in the *platycephala*-group), the range extension helps to clarify the difficult biogeographical situation. Here, the recently discovered wide range of *T. depressa* makes biogeographically much better sense, because this species is more closely related to eastern *T. platycephala* than to western *T. amplithorax*.

In the *eucalypti*-group and in the relationship of *T. brevipes* the distribution patterns are fairly simple. *T. riverinae*, and *T. mainae* and *T. triangularis*, respectively, are western, inland vicariants to an eastern species, namely *T. eucalypti* and *T. brevipes*, respectively. The western vicariants are generally more apomorphic, and they seem to have evolved by geographic expansion of an eastern stock and later isolated refugia.

In the rest of the *queenslandica*-group the situation is more difficult and the present knowledge should not regarded as conclusive, because certainly additional species will be discovered and may change the situation once more. However, western *T. facialis* and *T. harveyi*, respectively, are perhaps simply the western vicariants or sister species of the eastern *T. centralis* and *T. raveni*, respectively.

In the *tropica*-group the rather simple picture given in the revision has been altered even more due to the discovery of several new species in recent years. Thus, in the *fickerti-fitzroyensis*-lineage which comprises the most apomorphic species of the group, now 8 instead of 4 species are known (excluding species known only from females) and their phylogenetic relations are still rather obscure due to their very close relationships. As a consequence, our idea of a simple, clockwise pattern of range spreading and isolation with the result that the most plesiomorphic species lives in eastern Australia *(T. fickerti)* and the most apomorphic species in the northern part of northwestern Australia *(T. fitzroyensis)*, was certainly oversimplified, although the general trend seems still to be true. Especially in Western Australia the evolution apparently did not take place in a single-track direction; there must have been multiple events (Baehr and Baehr 1989, 1992).

To conclude, it becomes more and more evident that Western Australia has been a major centre of evolution within Hersiliidae. This might have been caused by the generally arid conditions in the whole of Western Australia where, however, some faunal refugia persisted. Diversification of taxa were thus promoted by even minor climatic changes. The generally more humid and better "buffered" climate in the east, on the other hand, apparently more or less prevented the development of such faunal refugia and speciation was more limited.

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A NEW TROGLOBITIC PLANTHOPPER SPECIES (HEMIPTERA: FULGOROIDEA: MEENOPLIDAE) FROM WESTERN AUSTRALIA

Hannelore Hoch*†

ABSTRACT

A new troglobitic meenoplid species, *Phaconeura proserpina* sp.nov., is described from a limestone cave in the Cape Range peninsula. This represents the second known cavernicolous meenoplid species from Western Australia. Notes on its ecology and generic position are given.

INTRODUCTION

Recent faunistic surveys of Australian caves have disproven the long-held belief of the continent's apparent paucity of terrestrial troglobites (obligate cavernicolous species). A remarkably rich obligate cavernicolous arthropod fauna has been discovered, especially in limestone caves and lava tubes of tropical North Queensland (Howarth 1988; Howarth and Stone 1990). As rhizophageous primary consumers (Howarth 1981), planthoppers (Hemiptera: Fulgoroidea) pose a significant element of this fauna. In the caves, they are represented by the families Cixiidae (genera *Undarana* Hoch and Howarth: two species, Hoch and Howarth 1989a, and *Solonaima* Kirkaldy: six species, Hoch and Howarth 1989b) and Meenoplidae (genus *Phaconeura* Kirkaldy: four species, Hoch 1990). From Western Australia another troglobitic meenoplid species has been described: *Phaconeura pluto* Fennah, Nambung National Park (Fennah 1973). In the epigean fauna of Australia, Meenoplidae are so far known with eight species and one subspecies of the genera *Phaconeura* and *Nisia* Melichar, both belonging to the subfamily Kermesiinae (Kirkaldy 1906; Woodward 1957; Fennah 1963).

Since 1987 intensive biological research has been conducted in Western Australia, in the Cape Range karst area (Humphreys 1991) and revealed the existence of a comparably diverse troglobitic fauna, as in Queensland. Among the many cave-adapted arthropod species is a previously unknown meenoplid species which is described here.

Outside Australia, cavernicolous Meenoplidae are so far known from Western Samoa (*Suva oloimoa*: Hoch and Asche 1988) and the Canary Islands (*Meenoplus cancavus*: Remane and Hoch 1988).

SYSTEMATICS

Family Meenoplidae
Genus *Phaconeura* Kirkaldy, 1906

Remarks

The monophyly of neither meenoplid genus occurring in Australia, *Phaconeura* and *Nisia*, has

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been discussed, and appears, at least for *Phaconeura*, questionable. *P. proserpina* is tentatively placed in *Phaconeura* although it lacks a diagnostic character of the genus, namely a median frontal carina. It cannot be decided yet, whether the lack of a median carina on the frons is a character shared with the ancestral species, or whether it has been lost during cave adaptation. The gradual reduction of carination of head and thorax as a result of the evolution of troglomorphies (e.g., reduction of compound eyes, and wings) has been observed in species of the cixiid genus *Solonaima* which display varying degrees of cave adaptation (Hoch and Howarth 1989b). Within the genus *P. proserpina* appears rather isolated. There is strong evidence that *P. proserpina* represents a separate evolutionary line that has adapted to caves, independently from the cavernicolous *Phaconeura* species of Queensland and from *Phaconeura pluto* from Western Australia. The configuration of its male and female genitalia vaguely resembles species of the *P. smithi* Woodward-group occuring in Queensland (Woodward 1957). However, the similarity does not seem sufficient to confirm a close phylogenetic relationship of *P. proserpina* with any other cavernicolous and surface dwelling *Phaconeura* species in Australia.

Phaconeura proserpina sp. nov.

Figures 1 - 13

Holotype

Male: Western Australia: North West Cape peninsula, Cave C-215 (22°01'40"S; 113°55'55"E), 31 May 1990, J. Waldock, Western Australian Museum (WAM 93/45).

Paratypes

One male: same data as holotype; one male, two females: same location as holotype, and 19 May 1991, R.D. Brooks, W.F. Humphreys and R.D. Brooks; one male, same location as holotype, and 5 July 1989, R. Wood, Western Australian Museum (WAM 93/46-50).

One male, same data as holotype, Zoological Institute and Zoological Museum, University of Hamburg.

Additional material

One nymph (V. instar): same location and data as holotype, three nymphs (V. instar): same location as holotype, and 15 July 1989, R.D. Brooks, R. Wood, and W.F. Humphreys, Western Australian Museum (WAM 93/51-54).

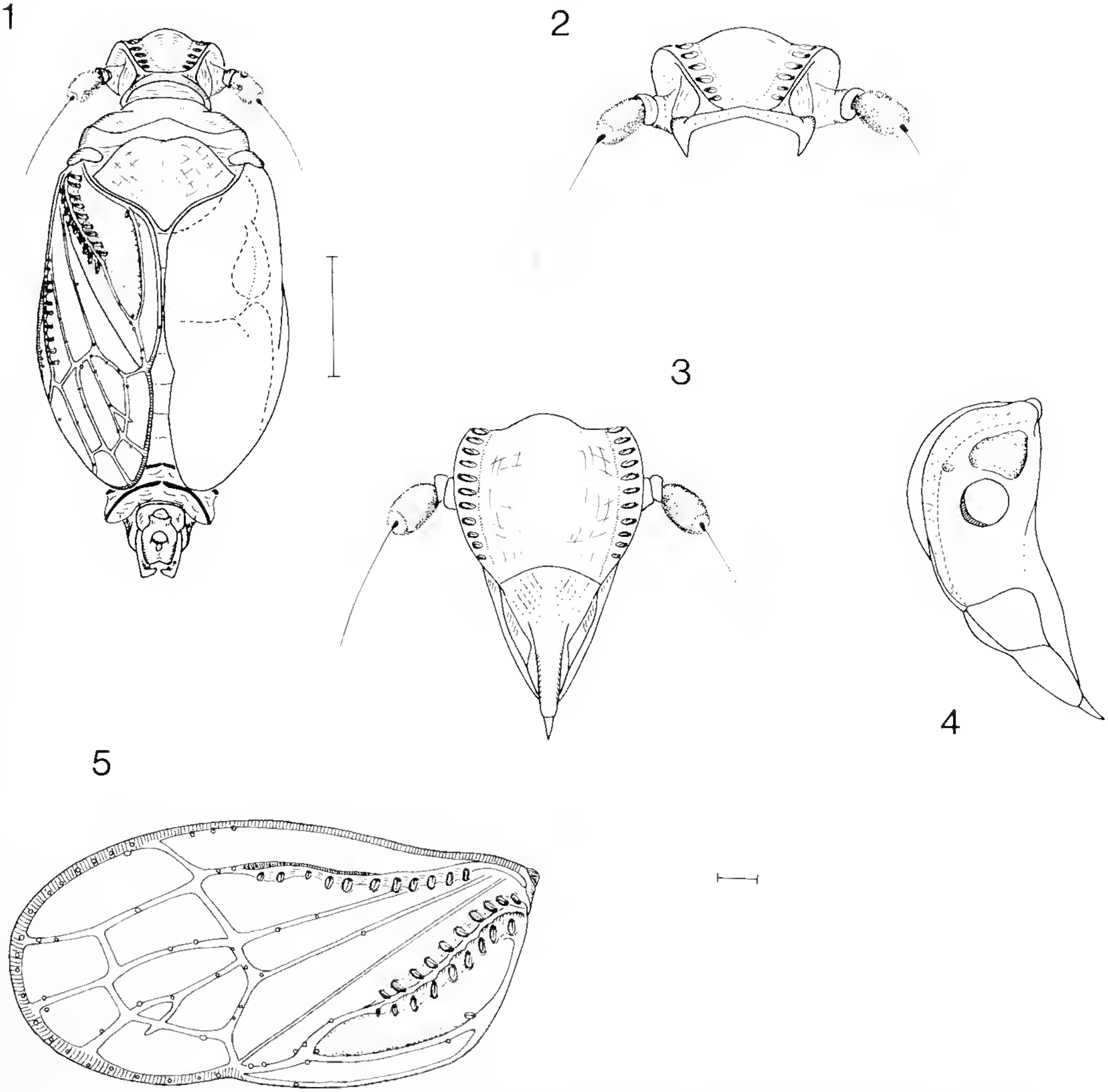
Diagnosis

Cavernicolous. In general appearance resembling the Western Australian *Phaconeura pluto* with eyes, tegmina and bodily pigmentation reduced, hind wings vestigial. Differing from this and the other congeners mainly by characters of the male and female genitalia. Male: aedeagus with 2 stout laterobasal spinose processes (Figures 10, 11, b), arising on each side of an unpaired dorsal projection. Female: ventral valvula globular bearing a short spine; anal segment laterally with an ear-shaped projection (Figures 12, 13).

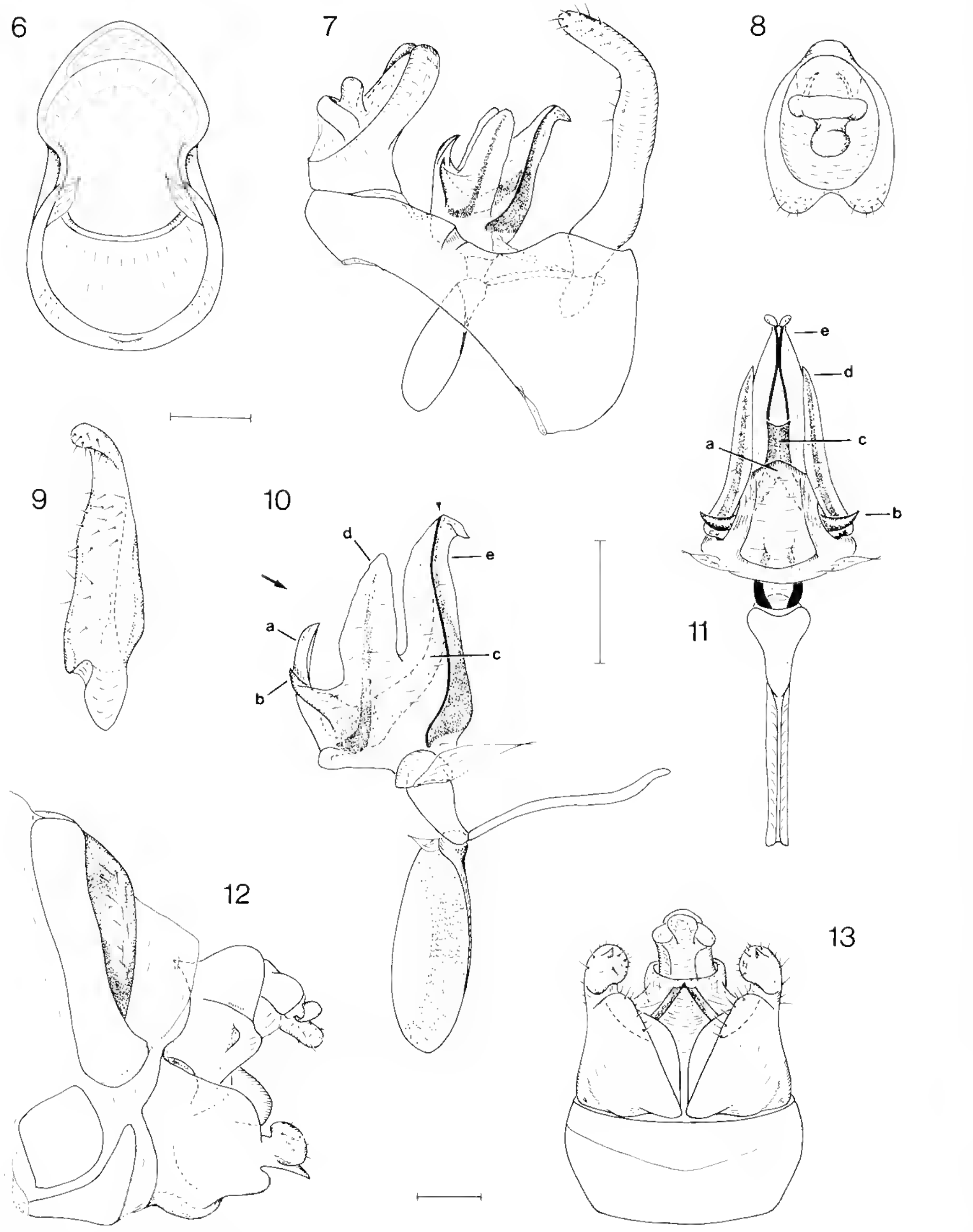
Description

Body length (equals distance between apex of head and tip of abdomen; measurements taken from specimens preserved in ethanol): male 2.0 - 2.25 mm (2.18 ± 0.103 mm; n=5); female 2.8 - 2.85 mm (n=2). Body and legs pale yellow; tegmina shallowly tectiform (Figure 1); tegmina translucent, yellowish, with venation pale yellow. Head (Figures 1-4): vertex slightly longer medially than wide at base (1.1-1.2 : 1), continuously rounded onto frons; posterolateral areolets indistinct. Compound eyes and median frontal ocellus absent, lateral ocelli strongly reduced. Former position of the compound eyes marked by a slightly vaulted area. Lateral margins of vertex and frons strongly ridged, produced laterad, each bearing a row of oval sensory pits which ends slightly above frontoclypeal suture. Vertex, frons and clypeus smooth, strongly vaulted, without median carina. Frons in frontal aspect with lateral margins shallowly convex (maximum width of frons at level of antennae), frons slightly wider than long medially (1.1-1.2 : 1), about as long as post- and anteclypeus together; transition frons-clypeus at frontoclypeal suture slightly notched (Figures 3, 4). Lateral carinae of postclypeus distinct. Rostrum elongate, slightly surpassing posttrochanters. First antennal segment short, ring-like, second antennal segment subcylindrical, ovoid, length ca. 1.2-1.3 x width; antennal sense organs indistinct, pustulate, irregular in number.

Thorax (Figures 1, 5): pronotum smooth, without distinct carination. Pronotum about half as



Figures 1-5 *Phaconeura proserpina,* holotype male: 1, habitus; 2, head, dorsal aspect; 3, same, ventral aspect; 4, same, lateral aspect; 5, tegmen. Scale line. Figure. 1: 0.5 mm, Figures 2-5: 0.1 mm.



Figures 6-11 *Phaconeura proserpina*, male genitalia, paratype: 6, genital segment, caudal aspect; 7, genital segment, anal segment, aedeagus, parameres, *in situ*, left lateral aspect; 8, anal segment, dorsal aspect; 9, left paramere, dorsal aspect; 10, aedeagus, left lateral aspect (arrow indicates aspect of Figure. 11); 11, same, dorsocaudal aspect. Figures 12-13. *Phaconeura proserpina*, female genitalia, paratype: 12, genital segment, anal segment, ventral valvifers and ventral valvulae, left lateral aspect; 13, same, ventral aspect. Scale line. Figures 6-9, Figures 10-11, Figures 12-13: 0.1 mm.

long as vertex medially, 2.6-2.9 times as wide as vertex at base; posterior margin shallowly excavated. Mesonotum nearly planate, with a faint median carina, lateral carinae reduced. Tegmina reduced in length, two times longer than maximum width (= slightly proximad of clavus), in repose reaching the anterior margin of genital segment; four to five apical cells; venation distad of nodal line individually variable; arrangements of sensory pits on tegmen as in other Kermesiinae. Hind wings strongly reduced, vestigial, not reaching the third abdominal segment. Posttibia as in other Meenoplidae laterally unarmed, distally with six to seven spines. Postbasitarsus distally with four to six, second posttarsal segment with four to five spines in a single row (partly individually asymmetrical). Postbasitarsus 2/3 the length of second and third posttarsal segments together. Pretarsal claws and arolia present.

Male genitalia (Figures 6-11): genital segment in caudal view figure-eight-shaped, in lateral aspect ventrally 2.75 times longer than dorsally. Anal segment in dorsal aspect longish ovate, apically produced into two bulbous lobes. Parameres longer than height of genital segment, in lateral aspect apical third bent dorsad, basal half slightly dilated; in ventral aspect inner margin smooth, shallowly convex. Aedeagus with sperm-conducting part directed straight caudad (Figure 10, 11, e), phallotrema apical, exposed to the dorsal side (Figure 10, e: small triangle); unpaired process dorsad of sperm-conducting part (Figure 10, a) flat, slightly curved ventrad, in dorsal view (Figure 11, a) apically obtusely triangular; two short and stout spines (Figure 10, 11, b) arising laterobasad of unpaired dorsal process, directed laterocaudad, their basal portions uniting to form a y-shaped structure (Figure 10, 11, c) thus connecting these laterodorsal spines (b) to sperm-conducting part (e). Ventrad of these spines (b), membrane connecting unpaired dorsal process (a) with sperm-conducting part (e) on each side produced in a tongue-shaped lobe: each directed caudad and supported by an integrated spinose sclerite (Figures 10, 11, d).

Female genitalia (Figures 12-13): as in other Meenoplidae strongly reduced; laterocaudal margin of ventral valvifer forming a distally rounded lobe, ventral valvula globular, apically with a short, minute spine (terminology *sensu* Woodward 1957). Laterobasal portion of anal segment with a small ear-shaped projection.

Etymology

The species is named from *Proserpina*, queen of the underworld in classical mythology.

DISTRIBUTION AND ECOLOGY

Phaconeura proserpina is known only from Cave C-215 in Cape Range on the North West Cape peninsula. Cave C-215 opens through Tulki Limestone just above the coastal plain and gives access to the coastal water table at a 24 m long stream passage (illustrated in Humphreys 1991). This cave is the only known location where elements of both the Cape Range terrestrial and the coastal aquatic fauna meet. Plant roots of an unidentified species hang from the roof of the stream passage into the water and *Phaconeura proserpina* specimens (adults and nymphs) were collected from the surface of the mud banks adjacent to the water. The collection point is in the (fresh air) dark zone, at an estimated altitude of 0.5 m (altitude of cave entrance is 21 m). The temperature is ca. 22.0°C, and the relative humidity ca. 89% (W.F. Humphreys, Western Australian Museum, pers. comm.). Due to its degree of troglomorphy (reduction of compound eyes, ocelli, tegmina, wings and pigment) *P. proserpina* is assumed to be restricted to underground habitats, and thus ecologically classifiable as obligate cavernicolous.

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TAXONOMIC STATUS OF *NYCTIMENE* (CHIROPTERA: PTEROPODIDAE) FROM THE BANDA, KAI AND ARU ISLANDS, MALUKU, INDONESIA - IMPLICATIONS FOR BIOGEOGRAPHY

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ABSTRACT

Nyctimene is recorded for the first time from the Aru and Banda island groups. The *Nyctimene* from Wokam, Aru island group, is morphologically close to *N. albiventer papuanus*. That from Kai Besar, Kai Kecil and Banda islands is described as a new subspecies of *N. albiventer*. The biogeographic relevance of this taxonomic separation is briefly discussed in the context of the mammal biogeography of these islands.

INTRODUCTION

Anderson (1912) first critically reviewed the genus *Nyctimene* Borkhausen and recognised 13 species. Since that time a further nine taxa have been described. These forms are distributed from the Philippines, Sulawesi, Maluku islands, Timor, north-east Australia, New Guinea and associated eastern islands.

As a consequence of the reviews and statements of Laurie and Hill (1954) Greig-Smith (1975), Koopman (1979,1982), Smith and Hood (1983), Petersen (1991), Corbet and Hill (1991, 1992) and Koopman *in* Wilson and Reeder (1993) the classification of these forms is generally considered to be as follows:

- *Nyctimene minutus* Andersen, 1910
  - *N. m. minutus* Andersen, 1910 - Sulawesi, Obi I.
  - *N. m. varius* Andersen, 1910 - W. Buru
- *Nyctimene albiventer* (Gray, 1863)
  - *N. a. albiventer* (Gray, 1863) - Morotai I., Halmahera I., Ternate I.
  - *N. a. papuanus* K. Andersen, 1910 - E. New Guinea, New Britain, Admiralty islands and Solomon islands.
- *Nyctimene draconilla* Thomas, 1922 - S. New Guinea
- *Nyctimene cephalotes* (Pallas, 1767)
  - *N.c. cephalotes* (Pallas, 1767) - Moluccas (fixed on Ambon I. by Andersen (1912), Sulawesi, Timor I., Timor Laut I., Tanimbar islands, Buru I., Seram I., N.W. Irian Jaya - Noomfor I. and southwest Papua)

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[*Vespertilio c. melinus* (Kerr, 1872)]

[*Cephalotes pallasi* (E. Geoffrey, 1810)]

- *Nyctimene major* (Dobson, 1877)

  N. m. major (Dobson 1877) - Duke of York I., Bismark Archipelago

  N. m. lullulae Thomas, 1904 - Woodlark I., Tobriand islands.

  N. m. geminus Andersen, 1910 - Tobriand and D'Entrecasteaux Archipelagos, Fergusson I., Kiriwia islands, Heath I., Goodenough I., Louisiade Archipelago.

  N. m. scitulus Andersen, 1910 - Solomon islands: Shortland, Alu, Florida, New Guinea, Guadalcanar; Choiseul and Malapa

- *Nyctimene cyclotis* Andersen, 1910 - Arfak Mountains, Irian Jaya

  N. c. certans Andersen, 1912 - S. New Guinea

- *Nyctimene aello* (Thomas, 1900) - E. New Guinea
- *Nyctimene celaeno* Thomas, 1922 - N.W. New Guinea
- *Nyctimene malaitensis* Phillips, 1968 - Malaita I., E. Solomon islands.
- *Nyctimene masalai* Smith and Hood, 1983 - New Ireland I..
- *Nyctimene rabori* Heaney and Petersen, 1984 - Negros I., Philippines
- *Nyctimene sanctacrucis* Troughton, 1931 - Santa Cruz I.
- *Nyctimene vizcaccia* Thomas, 1914

  N. v. vizcaccia Thomas, 1914 - Ruk I., Bismark Archipelago; Solomon islands.

  N. v. bougainville Troughton, 1936 - Bougainville I., Solomon islands.

  [*N. albiventer minor* Phillips, 1968] - Fauro, Choiseul and Santa Ysabel islands.

Recent expeditions to the Banda, Kai and Aru islands collected series of small *Nyctimene* with forearm measurements about 60 mm or less. The *Nyctimene* from Kai islands were considered by Andersen (1912) to be *N. albiventer papuanus*; he included several specimens from Kai islands in the measurements he presented for this form, including one specimen from Elat, Kai Besar I. Those collected from Banda Neira I., Banda islands and Wokam I., Aru islands are the first recorded from these island groups.

This paper presents the results of an examination of the taxonomic status of the forms of *Nyctimene* from Banda, Kai, and Aru by comparison with other small forms of *Nyctimene* with which they might be confused. These are the forms: *N. minutus, N. albiventer, N. cyclotis, N. cephalotes, N. masalai* and *N. vizcaccia.*

MATERIALS AND METHODS

A total of 62 adult specimens (listed in specimens examined section)was examined. These were from Banda Neira I. (2) Dullah I./Kai Kecil (7), Kai Besar I. (5) Wokam I./Aru islands (27), the Halmahera group (6) and Papua New Guinea (15). The locality of these specimens is listed in Figure 1. Apart from the Halmahera group specimens (Australian Museum, Sydney), all specimens are currently lodged in the Western Australian Museum. At the completion of this series of surveys half of the specimens from Banda I., Kai islands and Aru islands will be lodged in the Museum Zoologicum Bogoriense.

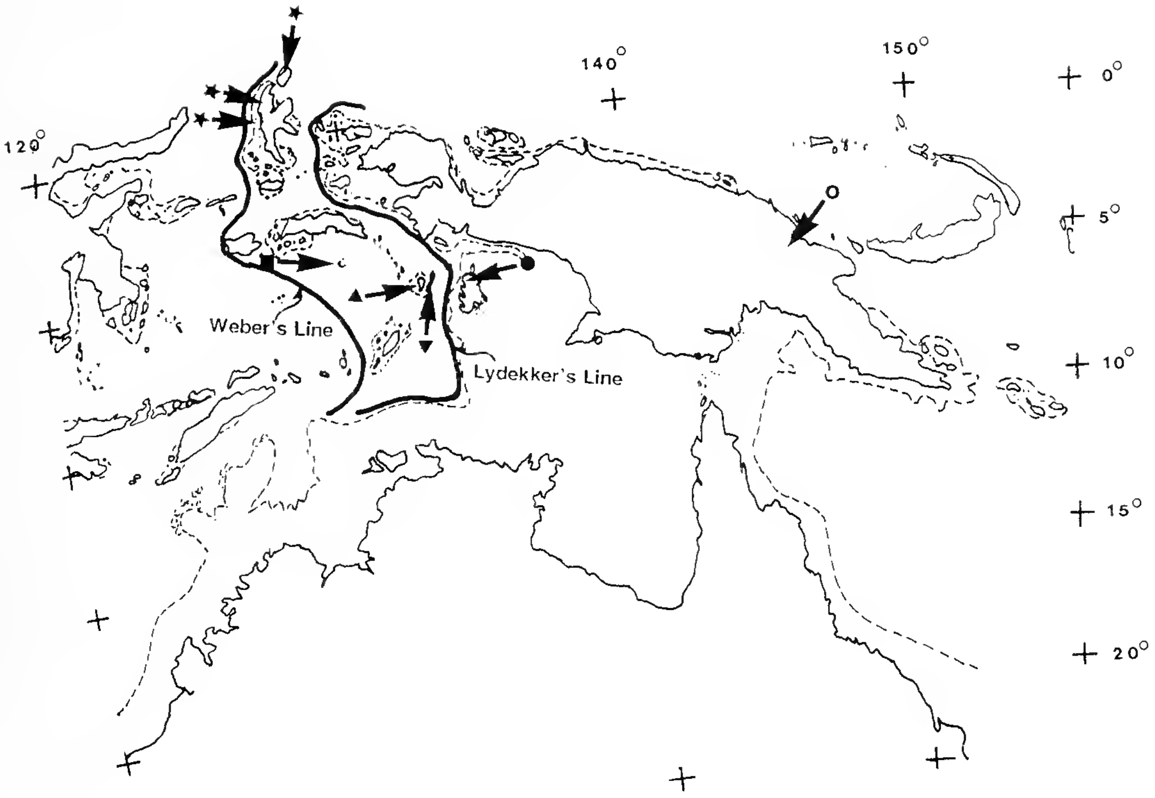

Figure 1 Locality of *Nyctimene albiventer* in this study. *N. albiventer keasti* subsp. nov. from Kai Kecil (▲), Kai Besar (▼) and Banda Neira (■); *N. albiventer albiventer* from Halmahera group (★); *N. albiventer papuanua* from Aru islands (●); and *N. albiventer papuanus* from Papua New Guinea (○). Also shown are the boundaries of the Sahul Shelf (dotted) and both Weber's and Lydekker's Biogeographic line (broad lines).

Seventeen measurements of skull, dentary and dental characters and 8 of external characters (all in mm) were recorded from adult specimens.

The measurements recorded were (all measurements involving teeth are to alveoli): GSL, greatest skull length; CBL, condylobasal length, PIF, minimum length from posterior margin of incisive foramen to margin of posterior palate; RL, rostrum length, from anteromost internal margin of orbit to nares; RH, rostrum height, from upper canine alveoli to level of dorsal surface of nasals; BB, braincase breadth above zygoma; ZW, zygomatic width; M^1M^1 and C^1C^1, width across M^1M^1 and C^1C^1 respectively, from the labial side; C^1M^1 and C_1M_2 upper and lower canine to last molar length; IOB, minimum interorbital breadth; POB, minimum postorbital breadth; MFW, mesopterygoid fossa width, at the widest point of the palatal flange; P^4P^4, palatal width between the lingual aspect of P^4P^4; ML, mandible length, from condyle to anteromost point of dentary; CH, dentary coronoid height; SV, tip of rhinarium between nostrils to anus length; TV; tail to anus length; EAR, basal notch to apex length; PES, length of pes, angle joint to tip of finger, excluding claw; FA, forearm length; MC3-5, metacarpal 3,4 and 5 length.

Table 1 Measurements, in mm, for skull, dentary, dental and external characters (see Material and Methods for explanation of character codes) of adult *Nyctimene albiventer albiventer* (Morotai I; Ternate islands and Halmahera I.), *N.a. papuanus* (Wokam islands, Aru; Papua New Guinea) and *N. a. keasti* subsp. nov. (Dullah I., Kai Kecil I. Kai Besar I. and Neira Banda I., Banda islands). N, sample size; $\bar{X}$, mean; SD, standard deviation; Min, minimum; Max., maximum.

		GSL	CBL	PIF	RL	RH	BB	ZW	M^{1}M^1	C^{1}C^1	C^{1}M^1	IOB
Nyctimene a. keasti	N	7	7	7	7	7	7	7	7	7	7	7
Kai Kecil I.	$\bar{X}$	28.81	27.37	12.09	5.46	6.49	12.17	19.02	8.13	5.48	9.50	5.69
(Pulau Dullah)	SD	0.50	0.42	0.28	0.34	0.36	0.31	0.36	0.28	0.26	0.26	0.28
	Min	28.04	26.56	11.58	4.96	5.98	11.64	18.63	7.66	5.21	8.98	5.29
	Max	29.38	27.88	12.47	5.90	6.96	12.56	19.71	8.45	5.78	9.80	6.12
Nyctimene a. keasti	N	5	5	5	5	5	5	5	5	5	5	5
Kai Besar I.	$\bar{X}$	28.71	27.15	12.01	5.60	6.17	12.56	19.11	8.19	5.44	9.67	5.68
	SD	0.54	0.67	0.26	0.35	0.34	0.09	0.31	0.18	0.23	0.17	0.20
	Min	28.22	26.02	11.72	5.05	5.75	12.44	18.88	7.91	5.18	9.36	5.50
	Max	29.36	27.69	12.42	6.00	6.66	12.68	19.60	8.40	5.80	9.77	5.98
Nyctimene a. keasti	N	2	2	2	2	2	2	2	2	2	2	2
Banda I.	$\bar{X}$	29.05	27.84	11.99	5.67	6.40	12.61	19.38	8.50	5.24	9.46	5.31
	SD	0.27	0.28	0.03	0.18	0.02	0.43	0.12	0.11	0.38	0.13	0.03
	Min	28.86	27.64	11.97	5.54	6.39	12.30	19.30	8.42	4.97	9.37	5.29
	Max	29.24	28.04	12.01	5.80	6.42	12.91	7	8.58	5.51	9.55	5.33
Nyctimene a. keasti	N	14	14	14	14	14	14	14	14	14	14	14
(Total)	$\bar{X}$	28.81	27.36	12.05	5.54	6.37	12.37	19.10	8.21	5.43	9.56	5.63
	SD	0.47	0.53	0.24	0.32	0.35	0.32	0.33	0.25	0.26	0.22	0.26
	Min	28.04	26.02	11.58	4.96	5.75	11.64	18.63	7.66	4.97	8.98	5.29
	Max	29.38	28.04	12.47	6.00	6.96	12.91	19.71	8.58	5.80	9.80	6.12
Nyctimene a. albiventer	N	6	6	5	6	6	6	6	6	6	6	6
Moratai I. Ternate I.	$\bar{X}$	25.68	24.55	10.27	4.83	5.80	11.36	17.01	7.32	4.82	8.49	4.90
Halmahera I.	SD	0.60	0.60	0.43	0.10	0.20	0.15	0.29	0.19	0.12	0.17	0.28
	Min	24.67	23.75	9.83	4.69	5.57	11.10	16.55	7.02	4.68	8.24	4.47
	Max	26.39	25.17	10.93	4.97	6.02	11.54	17.36	7.50	5.01	8.69	5.27
Nytcimene a. papuanus	N	13	13	13	13	13	13	13	13	13	13	13
Papua New Guinea	$\bar{X}$	26.82	25.69	10.57	4.60	6.41	12.00	18.27	7.98	5.17	8.63	5.21
	SD	0.50	0.53	0.45	0.27	0.23	0.35	0.44	0.25	0.11	0.21	0.24
	Min	25.86	24.73	9.77	4.08	5.94	11.40	17.40	7.46	5.03	8.20	4.83
	Max	27.41	26.37	11.25	5.02	6.73	12.60	19.18	8.28	5.41	9.02	5.51
Nyctimeme a. papuanus	N	26	26	26	26	26	26	26	25	26	26	26
Aru islands	$\bar{X}$	27.35	26.06	10.72	4.79	6.26	12.03	18.22	8.23	5.35	8.99	4.99
	SD	0.68	0.70	0.48	0.27	0.36	0.34	0.53	0.34	0.26	0.28	0.33
	Min	25.84	24.45	9.74	4.37	5.48	11.55	17.46	7.69	4.97	8.43	4.48
	Max	28.45	27.40	11.68	5.38	7.00	13.06	19.69	9.22	6.10	9.51	5.73

The skull, dentary and dental characters were measured to 0.01, while the external characters were measured to 0.1. Terminology used in the description of skull, dentary, dental and external characters follows Hill and Smith (1984). Pelage description follow the colour terminology of Smithe (1975).

Table 1 (cont.)

POB	MFW	P^4P^4	ML	CH	C_1M_2	SV	TV	EAR	PES	FA	MC3	MC4	MC5
7	7	7	7	7	7	7	7	7	7	7	7	7	7
5.88	4.70	5.18	21.38	12.80	10.81	74.5	21.4	15.3	12.5	58.4	42.0	38.6	4.08
0.37	0.15	0.09	0.42	0.28	0.32	3.1	1.6	0.3	0.8	0.8	1.0	0.9	0.9
5.21	4.50	5.03	20.69	12.42	10.27	69.9	19.9	14.8	11.6	57.1	40.7	37.5	39.4
6.27	4.96	5.29	22.03	13.22	11.18	78.7	24.1	15.6	13.9	59.4	43.2	39.6	41.8
5	5	5	5	5	5	5	5	5	5	5	5	5	5
6.20	4.84	5.22	21.64	12.94	10.89	73.8	19.7	14.4	13.4	57.9	42.4	38.4	40.5
0.24	0.17	0.13	0.63	0.37	0.16	5.6	0.8	0.3	0.3	1.8	1.4	0.6	1.5
5.83	4.69	5.06	20.58	12.33	10.75	69.7	18.6	14.2	13.1	55.1	40.9	37.7	38.7
6.44	5.05	5.38	22.11	13.32	11.10	83.3	20.9	14.8	13.8	59.7	44.5	39.4	42.7
2	2	2	2	2	2	2	2	2	2	2	2	2	2
5.89	4.78	5.37	21.13	12.42	10.88	69.8	22.6	14.9	12.5	60.6	42.2	38.6	39.9
0.17	0.14	0.25	0.19	0.25	0.2	0.6	3.1	0.1	1.7	2.6	2.4	2.6	1.8
5.77	4.68	5.19	20.99	12.24	10.76	69.3	20.4	14.8	11.3	58.7	40.5	36.7	38.6
6.01	4.88	5.55	21.26	15.59	11.00	70.2	24.8	14.9	13.7	62.4	43.9	40.4	41.2
14	14	14	14	14	14	14	14	14	14	14	14	14	14
6.00	4.76	5.22	21.44	12.80	10.85	73.5	20.9	14.9	12.8	58.5	42.2	38.5	40.5
0.33	0.16	0.14	0.49	0.34	0.24	4.1	1.8	0.5	0.9	1.6	1.2	1.0	1.2
5.21	4.50	5.03	20.58	12.24	10.27	69.3	18.6	14.2	11.3	55.1	40.5	36.7	38.6
6.44	5.05	5.55	22.11	13.32	11.18	83.3	24.8	15.6	13.9	62.4	44.5	40.4	42.7
6	5	6	6	6	6	6	6	6	6	6	6	6	6
5.33	4.64	4.65	18.97	10.31	9.52	69.8	20.9	12.7	11.0	51.2	36.1	33.8	35.1
0.27	0.22	0.14	0.55	0.54	0.13	2.0	2.2	0.4	0.7	1.2	0.8	0.8	0.9
4.96	4.27	4.50	18.07	9.56	9.31	67.5	19.3	12.1	10.3	49.9	35.0	32.4	34.3
5.64	4.82	4.83	19.50	10.78	9.69	73.6	25.2	13.3	12.1	53.1	37.2	34.5	36.5
13	13	12	13	13	13	15	15	15	15	15	15	15	15
5.76	4.66	5.24	19.76	11.22	9.61	70.6	20.7	12.8	10.7	54.6	39.2	36.2	38.7
0.34	0.19	0.26	0.41	0.29	0.37	3.3	1.5	0.8	0.6	1.2	1.2	0.7	1.1
5.14	4.37	4.71	19.14	10.74	9.01	64.2	19.1	11.7	9.9	52.7	37.4	35.0	36.5
6.38	4.95	5.58	20.53	11.70	10.17	74.7	23.4	14.2	12.2	56.8	40.9	37.7	4.03
26	26	25	25	26	25	27	27	27	27	27	27	27	27
5.54	4.48	5.36	20.26	11.69	9.99	65.8	22.3	13.6	12.2	55.8	39.8	36.1	39.0
0.36	0.27	0.24	0.67	0.73	0.36	5.4	2.5	0.8	0.7	1.6	1.6	1.4	1.4
4.92	4.06	4.97	18.09	10.32	9.43	57.9	17.9	11.7	11.2	53.4	35.5	33.5	36.0
62.5	5.35	5.87	21.30	12.69	10.67	77.6	30.1	14.7	13.3	59.2	42.8	39.2	41.3

Adults were diagnosed as those specimens with the following sutures fused: basioccipital - basisphenoid, basisphenoid - presphenoid and palatine - maxillary (these sutures are illustrated in Heaney and Peterson 1984: Figure 4).

The effect of sex and island for all characters was examined by multiple regressions for the six

Table 2 Multiple regressions on sex and island populations of *Nyctimene albiventer* (Halmahera group, Kai Kecil, Kai Besar, Banda, Aru and Papua New Guinea) for skull, dentary, dental and external characters. F values are presented for the main effects and their interaction. For explanation of character codes see Material and Methods section. Significance levels are *, $0.05 > p > 0.01$, ** $0.01 > p > 0.001$, *** $p < 0.001$

CHARACTER	MAIN EFFECTS SEX	 ISLAND	INTERACTION SEX. ISLAND
GSL	0.389	13.842***	1.076
CBL	1.394	8.652***	1.086
PIF	0.769	12.721***	1.153
RL	0.074	8.775***	1.050
RH	0.001	2.784*	0.436
BB	1.092	3.914**	0.673
ZW	2.627	10.046***	0.360
M^1M^1	0.005	5.203***	0.550
C^1C^1	0.587	4.251**	2.027
C^1M^1	1.382	15.180***	0.200
IOB	0.010	5.912***	0.986
POB	0.001	1.671	1.937
MFW	0.007	1.752	0.181
P^4P^4	0.101	6.404***	0.236
ML	0.146	10.302***	0.799
CH	1.344	10.850***	0.567
C_1M_2	2.071	13.018***	0.737
SV	0.008	5.682***	1.486
TV	1.080	1.228	1.384
EAR	0.659	11.114***	0.336
PES	0.101	13.893***	0.237
FA	0.113	13.042***	0.208
MC3	0.941	11.676***	0.311
MC4	0.456	8.204***	0.307
MC5	2.475	10.962***	0.529

islands/island groups: Banda, Kai Kecil, Kai Besar, Aru, Halmahera group and Papua New Guinea. Examination of the residuals from regression analyses gave no indication of heteroscedasticity.

Stepwise canonical variate (discriminant) analyses were run for skull, dentary and dental characters and external characters using all characters and a reduced set of these characters. This reduced set of characters was selected because they provided values that minimise Wilks Lambda.

STATISTICS: RESULTS AND DISCUSSION

Univariate statistics

Mean, standard deviation, minimum and maximum values and sample size for each island or island group are presented in Table 1 for all characters examined.

Multiple regressions

Multiple regressions were run for skull, dentary and dental and external characters on sex and island populations for the groups: Kai Besar, Kai Kecil, Banda, Aru, Halmahera and Papua New Guinea (Table 2).

Sex

No character showed a significant relationship with sex alone or with the interaction between sex and island (Table 2).

Island

Only postorbital breadth (POB), mesopterygoid fossa width (MFW) and tail to vent (TV) were not significantly related to island. Rostrum height (RH) was also probably not significantly related to island because $P>0.01$ might be expected to occur by chance alone, considering the number of interactions being tested. The 21 other characters, most of which were significant at $P<0.001$, indicated that there were considerable differences in morphology between these island populations.

Multivariate analyses

Because the multiple regression analysis indicated no sexual dimorphism, males and females are combined in the subsequent analyses.

The DFA was first run using the islands Aru, Kai Besar, Kai Kecil, the Halmahera group (Halmahera, Ternate and Morotai), Papua New Guinea and Banda. Banda was ungrouped because there was only two individuals. Kai Besar, Kai Kecil and Banda clustered closely together, as did Aru and Papua New Guinea. The DFA was then run using the following island groupings representative of putative taxa: Kai Besar/Kai Kecil/Banda, Aru/Papua New Guinea and the Halmahera group, for skull, dentary and dental characters and externals characters separately. These analyses used the complete set of 17 skull, dentary and dental characters and 8 external characters.

However, because the number of individuals in the island group with the smallest sample size (the Halmahera group, N=6) was less than the number of characters measured, fewer characters were used in the analysis. Only the DFA based on these reduced character sets are presented below. This was because both for the skull, dentary and dental and external characters, the reduced set of characters produced very similar DFA plots to those using the full set of characters.

Skull, dentary and dental characters

The DFA was run using the following characters: greatest skull length (GSL), inside P^4P^4 breadth (P^4P^4) lower C_1M_2 length (C_1M_2) and rostrum length (RL). The DFA produced two significant functions. Function 1 explained 63.4 percent of the variance and function 2, 36.6 percent. A total of 98.3 percent of individuals were correctly classified to their appropriate island group. The misclassified animal was from Aru; it was placed in the Halmahera group. the plot of functions 1 and 2 (Figure 2a) indicates that the island groups were approximately equidistant in discriminant function space. The Kai islands/Banda group separated from both the other two island groups on function 1 and from the Halmahera group on function 2. The Halmahera group also separated from the Aru/Papua New Guinea group on function 2.

The characters loading most heavily (>0.6) on function 1 were C_1M_2 and RL (Table 3a). Characters loading heavily (>0.6) on function 2 were GSL and P_4P_4 (Table 3a).

External characters

The DFA was run using the following characters: forearm length (FA) ear length (EAR), snout to vent length (SV) and pes length (PES). The DFA produced two significant functions. Function

Table 3 Canonical variate function coefficients for the *Nyctimene albiventer* subspecies (*albiventer, papuanus* and subsp. nov.). Standardised values, followed by (in brackets) unstandardised values. (a) skull and dental characters and (b) external characters. For explanation of character codes see Materials and Methods section.

Table 3a

CHARACTER	FUNCTION 1	FUNCTION 2
GSL	-0.1618 (-0.2569)	1.0604 (1.6839)
P^4P^4	-0.4071 (-1.8559)	0.6624 (3.0199)
C_1M_2	0.8256 (2.3241)	-0.2980 (-0.8388)
RL	0.7687 (2.7696)	-0.5667 (-2.0418)
CONSTANT	-20.3478	-43.4262
VARIANCE EXPLAINED (%)	63.4	36.6

Table 3b

CHARACTER	FUNCTION 1	FUNCTION 2
FA	0.6331 (0.4091)	-0.8306 (-0.5367)
EAR	0.1260 (0.1385)	0.3754 (0.4125)
PES	0.3406 (0.0708)	0.7559 (0.1571)
SV	0.5169 (0.6720)	0.4953 (0.6439)
CONSTANT	-38.4503	5.3860
VARIANCE EXPLAINED (%)	84.9	15.1

1 explained 84.9 percent of the variance and function 2, 15.1 percent (Table 3b). A total of 91.9 percent of individuals were correctly classified to their appropriate island group. The misclassified animals were as follows: two Aru/Papua New Guinea animals were classified to the Halmahera group and two to the Kai islands/Banda group. The plot of functions 1 and 2 shows that all three groups cluster separately, with the Kai islands/Banda group forming the most distinct cluster. The Kai islands/Banda group separated from both the other island groups principally on function 1. The Aru/Papua New Guinea group separates from the Halmahera group principally on function 2 (Figure 2b). The character that loads most heavily (>0.6) on function 1 is FA and those that load most heavily (>0.6) on function 2 are FA and PES.

The above DFA indicates that Kai Besar, Kai Kecil and Banda islands have a population of *Nyctimene* that differs in morphology from that on the Aru islands. The *Nyctimene* from the Kai islands were considered by Andersen (1912) and Laurie and Hill (1954) to be *N. albiventer papuanus* (Andersen 1912 examined at least one specimen from Elat, Kai Besar in his critical revision). Our comparison with *N. a papuanus* from Papua New Guinea indicates that it is the Aru population that is most similar to *N. a. papuanus*, and not the Kai islands/Banda populations. Further, comparison with topotypical specimens of *N. a. albiventer* from Morotai and the other islands on which this form is distributed (Halmahera and Ternate) indicates that the Kai islands/Banda population is not representative of *N. a. albiventer*. Comparison of the Kai islands/Banda I. population with the other small forms of *Nyctimene*, indicates that is an undescribed subspecies of *Nyctimene albiventer* which is described below.

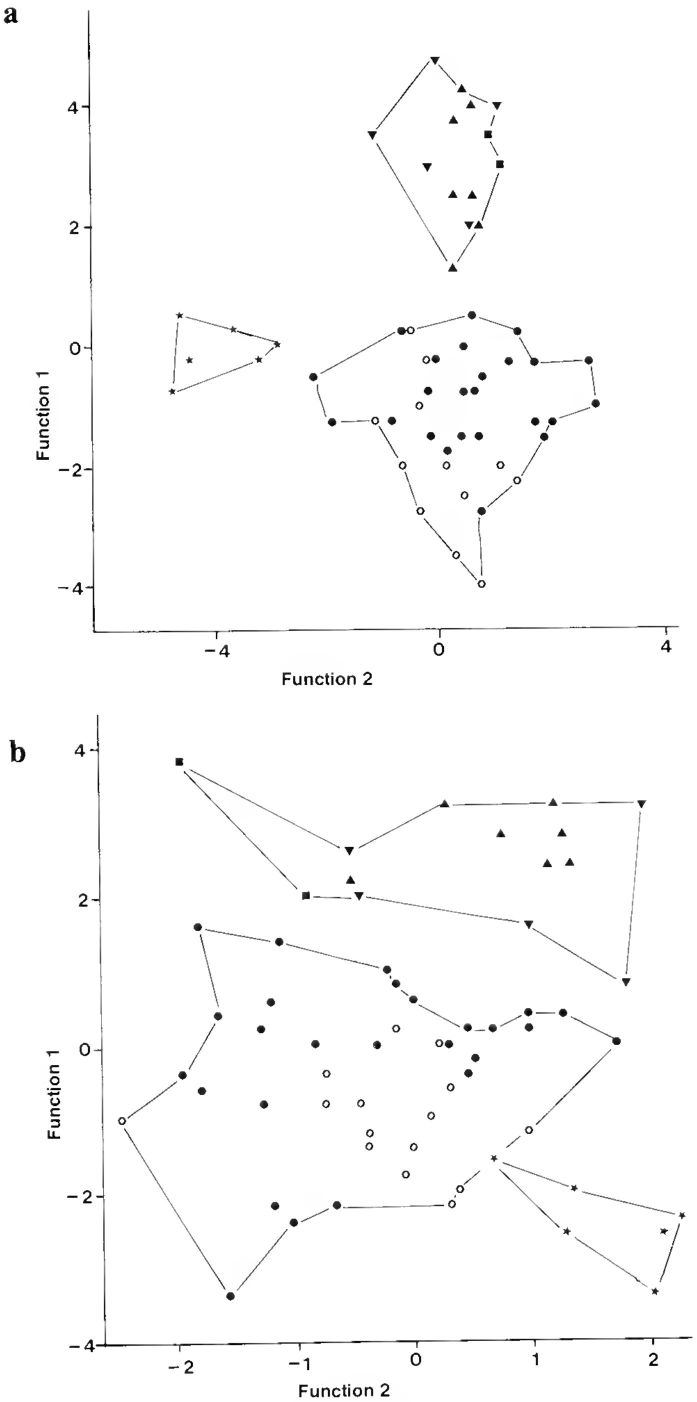

Figure 2 Canonical variate analysis based on three island groupings of (Kai islands/Banda group, Halmahera/Morotai/Ternate group and Aru/Papua New Guinea group) based on (a) skull, dentary and dental characters and (b) external characters, for functions 1 and 2. Symbols for *N. albiventer* subspecies as for Figure 1 caption.

SYSTEMATICS

Nyctimene albiventer keasti Kitchener, subsp. nov.

Holotype

Museum Zoologicum Bogoriense No. MZB 15300; adult male; weight 30 gm; carcase fixed in 10 percent formalin, preserved in 75 percent ethanol; skull separate; collected by D.J. Kitchener and R.A. How on 22 October 1992.

Type locality

Near Taman Anggrek, 12 km N. Tual, Pulau Dullah, closely associated with Pulau Kai Kecil, (5°38'S,132°44'E), collected in a mist net from mixed lowland evergreen rainforest bordering a lake, at sea level.

Paratypes

Kai islands, Dullah I., (nr. Kai Kecil), Nr Taman Anggrek (05°03'S, 132°44'E.): WAM M42141-2, M42144-5, M42649, M42651 (5♂♂, 1♀); Kai islands, Kai Besar, Desa Mun (05°26'S, 133°04'E.): WAM M42054, M42090 (1♂, 1♀); Elat (05°39'S, 132°59'E.): WAM M42686 (1♂); 3 km W Fakoi (05°36'S,133°06'E.) WAM M42699-700 (2♂♂); Banda islands, Banda Neira I. (04°33'S, 129°55'E.): WAM M42006, M42375 (2♀♀).

Diagnosis

Nyctimene albiventer keasti is compared directly with *N.a albiventer, N. a. papuanus* and *Nyctimene cephalotes* (WAM specimens from Ambon and Seram). It is compared with *N. minutus, N. cyclotis, N. masalai* and *N. vizcaccia* through the excellent description of these forms in Andersen (1912), Smith and Hood (1983), and Heaney and Petersen (1984), and also utilising Corbet and Hill (1992).

Nyctimene albiventer keasti differs from *N. a. albiventer* in having females that have a considerably paler dorsal pelage (Fawn Color) than males (Buff Yellow). In averaging larger in all measurements, except tail to vent length (Table 1). It is absolutely larger in the following characters: greatest skull length 28.81 (28.04-29.38) *v.* 25.68 (24.67-26.39), zygomatic width 19.10 (18.63-19.71) *v.* 17.01 (16.55-17.36); mandible height 12.80 (12.24-13.32) *v.* 10.31 (9.56-10.78), C_1M_2 length 10.85 (10.27-11.18) *v.* 9.52 (9.31-9.69), forearm length 58.5 (55.1-62.4) *v.* 51.2 (49.9-53.1) and ear length 14.9 (14.2-15.6) *v.* 12.7 (12.1-13.3).

It differs from *N. a papuanus* from Papua New Guinea by averaging larger in most measurements and having the following measurements absolutely larger: greatest skull length, palate to incisor foramen length, mandible length, mandible height, C_1M_2 length and metacarpal 4 length (Table 1).

It differs from *N. a. papuanus* from Aru islands in averaging larger in all measurements except P^4P^4 length and tail to vent length. For example: greatest skull length 28.81 (28.04-29.38) *v.* 27.35 (25.84-28.45), zygomatic width 19.10 (18.63-19.71) *v.* 18.22 (17.46-19.61), mandible height 12.80 (12.24-13.32) *v.* 11.69 (10.32-12.69), C_1M_2 10.85 (10.27-11.18) *v.* 9.99 (9.43-10.67), forearm length 58.5 (55.1-62.4) *v.* 55.8 (53.4-59.2) and ear length 14.9 (14.2-15.6) *v.* 13.6 (11.7-14.7)

It further differs from *N. a. papuanus* from Aru (generally) and Papua New Guinea (absolutely) in having the greatest skull length larger relative to P^4P^4 breadth (Figure 3a); rostrum length generally longer relative to P^4P^4 breadth (Figure 3b) and ear length generally longer relative to forearm length in both the Aru and Papua New Guinea populations (Figure 4).

It differs from both *N. a albiventer* and *N. a. papuanus* by clustering distinctly from them in discriminant function space for both skull, dentary and dental characters and external characters. (Figures 2a, b).

It differs from *N. cephalotes* in having dorsal stripe less obvious, particularly on anterior one-

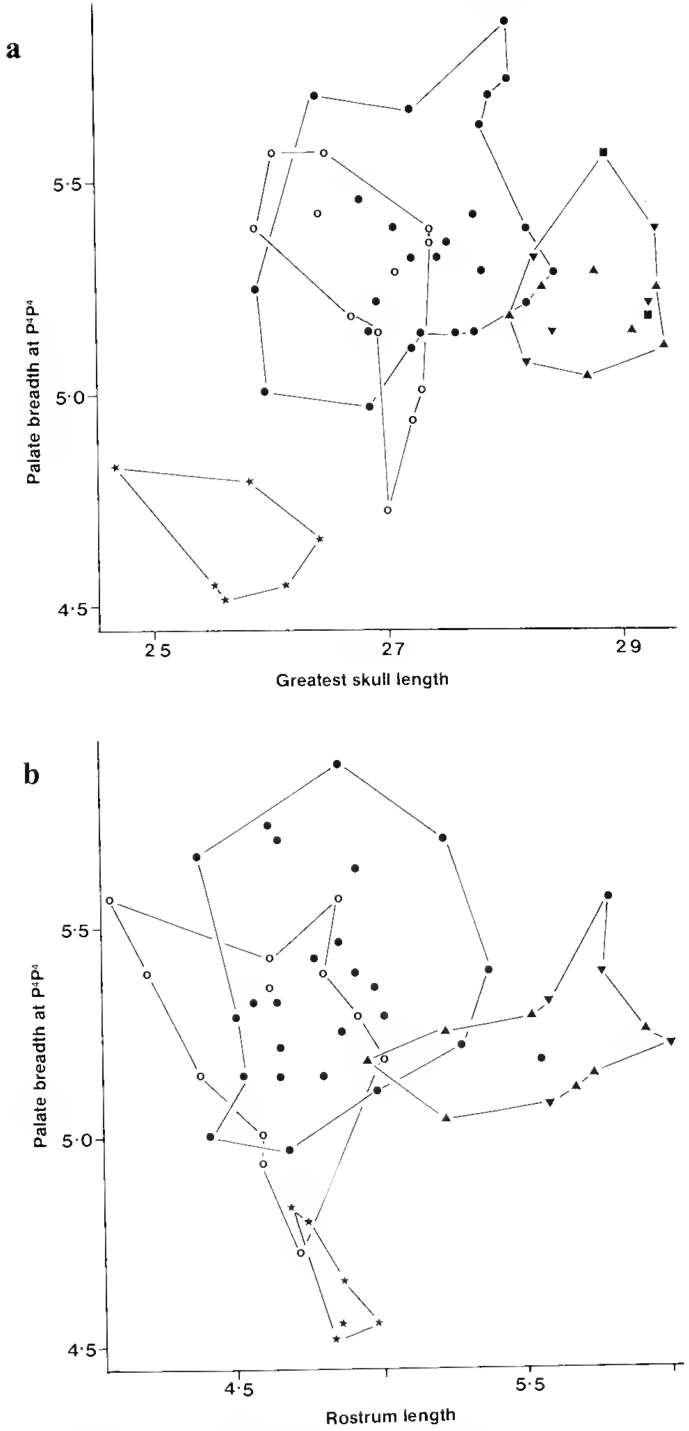

Figure 3 Plot of palatal width at P^4P^4 versus (a) greatest skull length and (b) rostrum length for subspecies of *Nyctimene albiventer*. Symbols as for Figure 1 caption.

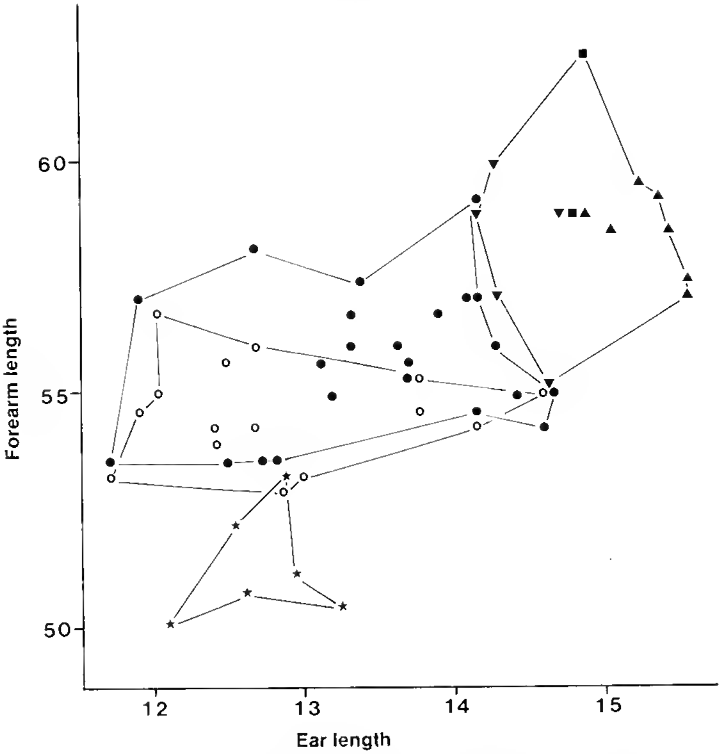

Figure 4 Plot of forearm length *versus* ear length for subspecies of *Nyctimene albiventer*. Symbols as for Figure 1 caption.

third of back, and narrower 1.0-3.5 *v.* 3.5-5.0; generally smaller in overall size, for example: condylobasal length 27.36 (26.02-28.04) *v.* 28.1-32; braincase breadth 12.37 (11.64-12.91) *v.* 13.2-13.8; M^1M^1 breadth 8.21 (7.66-8.58) *v.* 9-10; C^1C^1 breadth 5.43 (4.92-5.80) *v.* 5.8-6.2; mandible length 21.44 (20.58-22.11) *v.* 23.0-24.8; forearm length 58.5 (55.1-62.4) *v.* 60-71 (only one specimen from Banda I., had a forearm in excess of 60).

It differs from *N. minutus* in having dorsum generally a uniform colour, except for the presence of a thin dorsal stripe, rather than a conspicuously mottled dorsum with darker tips to the hairs; forearm longer 58.5 (55.1-62.4) *v.* 51-55; metacarpal 3 longer 42.2 (40.5-44.5) *v.* 35.5-38.5; M^1M^1 width larger 8.21 (7.66-8.58) *v.* 7.5; interorbital breadth larger 5.63 (5.29-6.12) *v.* 4.8-5.2; palatal breadth between P^4P^4 5.22 (5.03-5.55) *v.* 4.2-4.4.

It differs from *N. cyclotis* in having ears unmodified rather than unusually broad, semicircularly rounded above; colour of dorsum uniform, except for the presence of a thin dorsal stripe rather than mottled with darker tips to the hairs, pelage not long and woolly; M^1 subequal in size rather than noticeably smaller than P^4; premolars and molars rectangular rather than round; premolars have two strong cusps not three; palate frequently with round fenestrations; forearm longer, averages 58.5 *v.* *ca.* 53; metacarpal 5 longer 40.5 (38.6-42.7) *v.* 36.5; and interorbital breadth larger 5.63 (5.29-6.12) *v.* 4.5.

It differs from *N. masalai* in having general colour of dorsum uniform rather than mottled dark reddish brown; dark mid dorsal stripe narrower, *ca.* 1.5-3.5 *v.* 5; frontal sinuses converging in supraorbital region rather than parallel; maxillary toothrow slightly to moderately arched rather than straight; bony palate only slightly domed; no marked reduction of coronial cusps; labial cusps present on C^1 rather than absent; generally smaller in overall size, for example: condylobasal length 27.36 (26.02-28.04) *v.* 29.7-30.7; zygomatic width 19.1 (18.63-19.7) *v.* 20.4-20.9; C^1M^1 length 9.56 (8.98-9.80) *v.* 10.4-10.9; C_1M_2 length 10.85 (10.27-11.18) *v.* 12.1-12.5; and length of forearm 58.5 (55.1-62.4) *v.* 63.5-67.5.

If differs from *N. vizcaccia* in having colour of dorsum generally uniform rather than mottled, cranium squarish rather than rectangular; braincase globose rather than elongate, rostrum shorter (Smith and Hood 1983: figures 1,2); P3 with distinct internal cusp teeth, usually shorter.

Description

Skull, dentary and dentition

Rostrum of skull short, nasal dorsal surface almost horizontal, premaxillary part of nares terminates directly above incisors or projects slightly anterior to them; braincase typical of *N. albiventer* with cranium inflated to level of frontal dorsal inflation, or just above that level, generally less inflated than in *N. albiventer*; zygoma wide; intraorbital foramen suboval and traverse lower half of zygomatic arch; frontals low to arched, depending on age, occasionally with pronounced frontal sulcus, converging slightly posteriorly; sagittal and lambdoidal crests moderately high, the junction of these crests projects posteriorly to a point approximately level with supraoccipital; posterior palate extends well beyond M^1, its margin varies from U-shaped to sharply rectangular; basi-and presphenoid median ridge prominent; pterygoid process low and slightly arched ventrally towards the mesoptergoid fossa.

Upper toothrows gently curved; upper incisors in contact, sited posterior of line joining C^1C^1 anteriormost face, except for Banda specimens which approach this line; C^1 with moderate secondary labial cusp, this cusp not apparent in some old specimens with worn teeth, prominent cusp with gentle lingual ridge connecting to lingual and posterior cingulum. P^2 subcircular, buccal area half to three-quarters that of incisors; P^3 occlusal view shape rectangular with a prominent labial cusp and much lower separate lingual cusp; posterior basal shelf well defined and forms slight basin, occlusal area slightly larger than P^4; P^4 occlusal view subrectangular with posterolingual salient from basal shelf, labial cusp lower than that of P^3, lingual cusp less clearly defined than that of P^3 with longer posterior ridge that reaches almost to posterolingual edge of posterior basal shelf, lingual cusp closer in height to labial cusp than is case in P^3, M^1 subrectangular, labial cusp low and only slightly taller than lingual cusp, posterior basal shelf definition similar to that of P^3 and P^4. C_1 not in contact with each other or with P_2; P_2 suboval, slightly taller than C_1 cingulum; P_3 with tall labial cusp with gently sloping anterior and posterior flanges in line of toothrow, shorter labial cusp distinct; P_4 considerably shorter than P_3, labial cusp taller than lingual cusp but less so than in P_3. These cusps connected by commissure that arcs around the anterior face of tooth; M_2 longer and narrower than P_4 but with both labial and lingual cusps much reduced on those of P_4; M_2 small, about half area of M_1 when viewed from occlusal aspect, posterior basal shelf slightly smaller than that of P_4 and M_1.

Pelage

In males, dorsal pelage considerably darker than that of females. In males, dorsal fur predominantly Fawn Color, ca 10.5 long, with basal one-third of hairs Drab. A moderately wide dorsal stripe of Olive Brown begins thinly (0.5-1.5 wide) at the neck and widens to 3.5 in region of lower back; fur on dorsal proximal surface of uropatagium Fawn Color. Throat, chest and abdomen Buff Yellow, ca 5.5 long; underside of shoulder Cinnamon; ears not furred, distal three-quarters Burnt Umber and remainder Cinnamon.

In females, dorsal fur predominantly Buff Yellow with basal one-third of hairs Drab; dorsal median stripe as for males and Olive Brown; fur on dorsal proximal surface of uropatagium Raw Umber. Throat, chest and abdomen Buff Yellow; Ears not furred, distal half Burnt Umber and remainder Clay Color.

Both sexes have wings and ears with yellow spots of varying size, these spots are generally confined to skin of forearm and digits and occasionally tibia and tail. The wing patagia have darker spots of irregular size.

Distribution

Banda and Kai Island groups.

Etymology

Named after Mr Colin Keast, Western Australian Museum, who has assisted in an honorary capacity over a period of three years with laboratory aspects of the research in the Indonesian mammals. These animals were collected as a consequence of the joint Western Australian Museum and Museum Zoologicum Bogoriense expeditions to Eastern Indonesia.

GENERAL DISCUSSION

Simpson (1977) reviewed the biogeography of Wallacea (incorporating the Maluku islands) and concluded that it was not a region of intergradation between the faunas on the Sahul Shelf to the east and the Sunda Shelf to the west. Rather, he considered it to be a region with a considerable extent of endemicity and possessing its own unique fauna. Recent studies on mammals in Nusa Tenggara on the southern edge of Wallacea support this view (Kitchener *et al.* 1993).

It appears from the detailed critique offered by Simpson (1977) on the biogeography of this broad region, that the eastern boundary for mammals between Wallacea and the Australian Biogeographic region is placed somewhere between Lydekker's (1896) Line and Weber's Line as defined by Mayr (1944) (see Figure 1). Lydekker's Line follows the western boundary of the Sahul Shelf whereas Weber's Line lies considerably to the west, between Babar and Tanimbar islands north to the western side of Buru I. and the Halmahera group of islands.

As noted by Simpson (1977) Lydekker's Line, readjusted to coincide with the edge of the Sahul Shelf, is a "clear cut boundary". All faunas and islands to east of that line definitely belong to the Australian Region. However, Mayr (1944) proposed, based on "faunal balance", that Weber's Line represented the boundary where the Oriental and Australian fauna meet. Although this view was criticised by Simpson (1977), it does indicate that a considerable number of Australian animal species reach Weber's Line. Clearly, then, the zone between Lydekker's and Weber's Lines represent a zone of interface between the Australian Region and the regions to the west. Further, this interface zone would appear to offer considerable opportunities for research as to the possible mechanisms (morphological, genetic and ecological) at play that restrict the distribution westwards of the Australian fauna.

This study of the morphological variation within *Nyctimene albiventer* indicates that while the population on Aru is similar to that of Papua New Guinea (*N. a. papuanus*), the populations on Kai Besar, Kai Kecil and Banda islands are morphologically distinct (*N. a. keasti* subsp. nov.) as are those of the Halmahera group (*N. a. albiventer*). Other species of mammals which have forms on both Aru and Kai islands that have been recognised as taxonomically distinct are: *Syconycteris australis* Peters, 1867; *Rhinolophus euryotis* Temminck, 1834; *Hipposideros ater* Templeton, 1848; *Pteropus melanopogon* Peters, 1867; *Phalanger orientalis* (Pallas, 1766) and *Thylogale brunii* (Schreber, 1778) (see Appendix). Both the Kai islands forms of *Syconycteris australis* and *Thylogale brunii* were considered by van Strien (1986) to be the same subspecies as those on Aru islands. However, the form of *Syconycteris australis*, *Phalanger orientalis* and *Thylogale brunii* on Aru islands was considered the same as those in New Guinea, while the Kai islands form was distinct. (The Kai islands form of *P. orientalis* also occurs on Banda islands.).

During the last major glaciation (17000-20000 yr BP), the sea levels in the northern Australasian region were 120-145 m lower than at present (Chappell 1982: 69). This resulted in the exposure of the Sahul Shelf, including the area of the Arafura Sea. Such exposure of the Sahul Shelf has occurred for extensive periods of the geological history of this region since the Triassic (Doutch 1972). Thus the Aru islands were connected by dry land to New Guinea intermittently throughout the Pleistocene. However, during this period, the Aru islands were separated from Kai islands and Banda islands by a water gap similar in width to the present one (see Figure 1). As a consequence of past connections, the mammal fauna of the Aru islands has been greatly influenced by that of New Guinea, as suggested by the distribution pattern of subspecies cited above. Reference to the Appendix, which lists the species on Aru, Kai and Banda islands, with each species categorised as being essentially Australian (A), Oriental (O), endemic (E) or of uncertain origin (U), further attests to this association.

On Aru islands, all 16 marsupial and rodent species, including a suite of New Guinea lowland murids recorded there for the first time by us (*Rattus steini*, *R. leucopus*, *Melomys rufescens* and *M.* sp. cf. *M. levipes*), are New Guinea in origin - as are three of the six bat species. The two shrews and the civet cat are Oriental. There are no endemic species. Thus of the 25 mammal species on Aru that can be categorised, 76% are Australian and 24% are Oriental in origin.

On Kai islands, six of the seven marsupial and rodent species and five of the ten bat species are Oriental. The shrew and the civet cat are Oriental. Two and possibly three species are endemic including a newly described *Melomys* (Kitchener and Maryanto 1993). The taxonomic situation with *Rhinolophus keyensis* is still unclear. Thus of the 19 mammal species on the Kai islands that can be categorised 58% are Australian and 42% are Oriental.

On the Banda islands only two of the eight species (25%) that could be categorised are Australian.

Of particular interest biogeographically was the discovery of the shrew species *Suncus murinus* (Linnaeus, 1766) on Banda Neira I.; Kai Besar I. and Wokam I., Aru islands and *Crocidura maxi* (Sody, 1936) on Wokam I., Aru I. These are the most eastern records of shrews reported in the Indo-Malayan region (see Corbet and Hill 1992) and are the first records of shrews on the Sahul Shelf. The specimens of *Crocidura maxi* vary slightly both genetically and morphologically, from *C. maxi* reported elsewhere in the Lesser Sunda islands. (Kitchener *et al*. 1993). This finding is of interest because it is the only known location where shrews coexist with a small Australopapuan carnivorous marsupial (*Sminthopsis virginiae rufigenis*).

In summary, for mammals the Aru and Kai islands lie in the Australian Biogeographic region, while the situation with Banda islands is less clear. Either the deep water gap between oceanic Kai islands and the continental Aru islands, or their different environments or habitats, have been a major impediment to the western movement of the mammal fauna of the Australian region (New Guinea), and possibly to gene flow within species. This is indicated by three situations: first by the proportions of Australian region mammal species on these islands, which falls from 76% of the fauna on Aru to 58% on Kai islands and 25% on the Banda islands (these values are very slightly increased if *Suncus, Paradoxurus* and *Cervus* are removed from the analysis because they may have been transported around by humans - see Laurie and Hill 1954 and Corbet and Hill 1992); secondly, by the association of subspecies; those on the Aru islands associate with New Guinea, while those on Kai islands associate with the Banda and Maluku populations; and thirdly, Aru islands have no known endemic species, whereas Kai islands have two and possibly three.

SPECIMENS EXAMINED

Nyctimene albiventer papuanus

Aru islands, Wokam I., Kampong Karangguli (05°48'S, 134°15'E.) WAM M42467, M42486, M42498-501, M42556-9, M42605-6, M42562-4, M42577-8, M42585-9, M42590, M42602, M42607-8, M42609 (17♂♂, 10♀♀).

Papua New Guinea

Sempi (5°40'40"S, 145°46'40"E): WAM M 427391; Usino (5°33'50"S, 145°21'20"E): WAM M27401-6 (3♂♂, 3♀♀); Baiteta (5°00'20"S, 145°44'40"E): WAM M27398-400 (3♂♂) and Baumina (5°29'00"S, 145°43'00"E): WAM M27392-4, M27397 (3♂♂, 1♀).

Nyctimene albiventer albiventer (All specimens from Australian Museum)

North Halmahera I., Goal area (1°15'N, 127°32'E): M25078, M25080, M25086 (3♂♂); Ternate I., Ayr Tege Tege (0°48'N, 127°20'E): M25085 (1♀); Morotai (20°20'N, 128°20'E): M26457-8 (1♂, 1♀).

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APPENDIX

List of mammal species from Aru, Kai and Banda island groups. N, new records from the Western Australian Museum - Museum Zoologicum Bogoriense survey of October-November, 1992. A, Australian; O, Oriental; U, Biogeographic region not clearly Australian or Oriental; E, endemic.

		ISLAND GROUP		
	SPECIES	ARU	KAI	BANDA
	MARSUPIALIA			
A	*Murexia longicaudata longicaudata* (Schlegel, 1866)	x		
A	*Sminthopsis virginiae rufigenis* Thomas, 1922	x		
A	*Myoictis melas wallacii* Gray, 1858	x		
A	*Echymipera rufescens rufescens* (Peters and Doria, 1875)	x	x	
A	*Phalanger gymnotis* (Peters and Doria, 1875)	x		
A	*P. maculatus chrysorrhous* (Temminch, 1824)	x	x	x
A	*P. orientalis mimicus* Thomas, 1922	x		
U	*P. orientalis amboinensis* (Lacepede, 1801)		x	x
A	*Petaurus breviceps flavidus* Tate and Archbold, 1935	x	xN	
A	*Dactylopsila trivirgata trivirgata* Gray, 1858	x		
A	*Thylogale brunii brunii* (Schreber, 1778)	x		
A	*T. brunii gracilis* Miklouho-Macleay, 1884		x	
	RODENTIA			
A	*Uromys caudimaculatus aruensis*	x	x	
A	*Hydromys chrysogaster beccarii*	x	x	
U	*Rattus rattus septicus* Sody, 1933	x	x	x
O	*R. exulans* (Peale, 1848)		xN	xN
A	*R. leucopus* (Gray, 1867)	xN		
A	*R. steini* Ruemmler, 1935	xN		
U	*Mus musculus castaneus*		xN	xN
A	*Melomys rufescens* (Alston, 1877)	xN		
A	*M. sp. cf. M levipes* (Thomas, 1897)	xN		
E	M. sp. nov		xN	
	SORICIDAE			
O	*Suncus murinus* Linnaeus, 1766	xN	xN	xN
O	*Crocidura maxi* Sody, 1936	xN		
	VIVERRIDAE			
O	*Paradoxurus hermaphroditis setosus* Jaquinot and Pucheran, 1853	x	x	
	CERVIDAE			
O	*Cervus timorensis moluccensis* Quoy and Gaimard, 1830			x
	PTEROPODIDAE			
O	*Pteropus melanopogon melanogogon* Peters, 1867			x
O	*P. melanopogon aruensis* Peters, 1867	x		
O	*P. melanopogon keyensis* Peters, 1867		x	
A	*P. macrotis macrotis* Peters, 1867	x	?	
O	*P. griseus* (E. Geoffroy, 1810)			x
O	*Dobsonia viridis viridis* Heude, 1897		x	x
O	*D. moluccense* Quoy and Gaimard, 1830	x		
A	*Nyctimene albiventer keasti* subsp. nov.		x	xN
A	*Nyctimene albiventer papuanus* Andersen, 1910	xN		
U	*Macroglossus minimus lagochilus* Matschie, 1899	x	x	x
A	*Syconycteris australis papuana* (Matschie, 1899)	x		
A	*S. australis keyensis* Andersen, 1911		x	

		ISLAND GROUP		
	SPECIES	ARU	KAI	BANDA
	EMBALLONURIDAE			
O	*Taphozous achates* Thomas, 1915		x	
A	*Emballonura beccarii clavium* Thomas, 1915		x	
A	*E. nigrescens nigriscens* Gray, 1832		x	
	RHINOLOPHIDAE			
U	*Rhinolophus euryotis aruensis* Andersen, 1907	x		
U	*R. euryotis praestans* Andersen, 1905		x	
U	*R. philippinensis achilles* Thomas, 1900	?	x	
E	*R. keyensis keyensis* Peters, 1871		x	
	HIPPOSIDERIDAE			
U	*Hipposideros ater saevus* Andersen, 1918		x	
U	*H. ater aruensis* Gray, 1858	x		
U	*H. cervinus cervinus* (Gould, 1854)	x	x	
O	*H. bicolor* Temminck, 1834		xN	
U	*H. diadema custos* Andersen, 1918		x	
A	*Aselliscus tricuspidatus* Temminck, 1834		x	
	VESPERTILIONIDAE			
U	*Miniopterus australis tibialis* (Tomes, 1858)		x	
O	*M. pusillus macroneme* Revilliod, 1914		x	
U	*M. schreibersii oceanensis* Maeda, 1982		x	
U	*Myotis adversus moluccarum* Thomas, 1915		x	
E	*M. stalkeri* Thomas, 1910		x	
U	*Pipistrellus tenuis papuanus* (Peters and Doria, 1888)	x	x	x
O	*P. javanicus javanicus* (Gray, 1838)	?		
O	*Scotophilus kuhlii temmincki* (Horsfield, 1824)	x		

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NOTES ON THE BIOLOGY OF THE GENUS *PLETHOLAX* COPE (SQUAMATA: PYGOPODIDAE)

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ABSTRACT

Pletholax is a monotypic genus of pygopods, with two subspecies recognised. The nominate subspecies is an inhabitant of heaths and woodlands, particularly *Banksia*-dominated associations, on sandy substrates, while *P. gracilis edelensis* inhabits heaths and tussock grasslands on sandy substrates. *Pletholax* is active both above and below the soil surface. Size at maturity, sexual dimorphism in adult size and adult sex ratio are documented. The gonadal cycles of both sexes peak in Spring. Clutch size is two. Diet remains unknown, but the species may feed predominantly on termites. Predation by birds is reported. Neither subspecies appears to be endangered.

INTRODUCTION

Pletholax Cope is a monotypic genus of pygopodid lizard restricted to the lower/mid west coasts of Western Australia. Morphologically, it is one of the most divergent of the pygopodids, with an extremely slender elongate body, a depressed pointed head and strongly bicarinate scales on all surfaces (dorsal, lateral, ventral) of body and tail. Internally, it is unique amongst pygopodids in possessing an interclavicle (Stephenson 1962), although the homology of this element remains contentious (Kluge 1976).

Although several authors have commented on habitat preferences and other aspects of the biology of *Pletholax* (Mertens 1965; Kluge 1974; Storr and Harold 1978; Davidge 1979, 1980; Wilson and Knowles 1988; Greer 1989; How and Dell 1990; Storr *et al.* 1990; Turpin 1990, 1991; Ehmann 1992; Maryan 1993), much of this literature is in the form of broad unsubstantiated statements, or of very limited circulation. There are few specific details published on the ecology of this genus. Accordingly, we take this opportunity to review the literature and provide additional data on the ecology of *Pletholax*, based on the dissection of museum specimens (n = 66), field and captive observations, and collection data associated with museum material.

HABITAT PREFERENCES

Two subspecies of *Pletholax* are recognised: *P. g. gracilis* Cope from predominantly coastal areas between Geraldton and the Perth region, and *P. g. edelensis* Storr from the Kalbarri-Shark Bay region (Storr 1978; Storr *et al.* 1990). The nominate subspecies has been reported from *Banksia*/*Eucalyptus* woodlands or heaths on sandy soils (Kluge 1974; Davidge 1979, 1980;

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Wilson and Knowles 1988; How and Dell 1990; Storr *et al.* 1990; Turpin 1990; Ehmann 1992; Maryan 1993). Kluge (1974) trapped six specimens from a mixed *Banksia/Eucalyptus* coastal woodland community on stationary dunes and protruding limestone ridges, but on the basis of specimens recorded from Red Hill and Coomberdale, inferred that the taxon was not restricted to such habitats. Wilson and Knowles (1988) state that this subspecies occasionally occurs on lateritic soils. Specific habitat data are available for museum specimens from six localities: Koondoola, Mooliabeenee, Murdoch, North Lake, Victoria Park and Willeton. In all cases the habitat consisted of *Banksia* dominated woodland or heath on sand (white or grey when specifically noted). The Jandakot series was also taken from *Banksia* woodland on deep sands (Davidge 1979, 1980). An additional specimen, from 30km WSW of Badgingarra, was reported from mid-high heath. Although specific habitat data are unavailable for all other specimens (see "Material Examined"), we are aware of sandy substrates (often with *Banksia* communities) in the vicinity of all localities, with the possible exception of 13km WSW Winchester, which we have not visited. At Karawara (originally Manning/South Perth, 32°00'S 115°51'E) one of us (MP) observed and collected *Pletholax* in a *Banksia* woodland over heath understory on white siliceous Bassendean sands with *Banksia menziesii* R.Br. (dominant), *B. attenuata* R.Br. and *B. ilicifolia* R.Br., *Eucalyptus todtiana* F.Muell., *Allocasuarina fraseriana* (Miq.)L.Johnson, *Pattersonia occidentalis* R.Br., *Daviesia triflora* M.D. Crisp and *Stirlingia* sp. In contrast, a single specimen was found at Green Head (30°04'S 114°58'E) in low coastal heath (lacking *Banksia* spp.) on white calcareous sand.

Pletholax g. edelensis is also known from sandy substrates (Storr and Harold 1978; see also Wilson and Knowles 1988; Storr *et al.* 1990), although *Banksia*s are not present. Instead, specimens have been taken from *Spinifex longifolius* R.Br. on coastal dunes, low open *Triodia plurinervata* N. Burb. under low *Acacia* on light pink-brown sandy loam and very sparse *Acacia* shrubs over dense low heath on grey loamy sand (MP *pers. obs.*; data accompanying type series and WAM R103978, R104259-60).

HABITS

The earliest published observations on the habits of *Pletholax* (Kluge 1974:38,148) noted that six individuals of *P. g. gracilis* held in captivity habitually burrowed into sand, and described the species as "an extremely rapid sand swimmer". Kluge (*in* Gans 1975) similarly describes the species as a sand swimmer. In contrast, Bamford (*in* Greer 1989) observed individuals leaping between shrubs to escape capture, and Wilson and Knowles (1988) and Ehmann (1992) respectively suggest that the species is occasionally/mostly active above ground, gliding through dense vegetation, and basking in shrubs. Davidge (1979), although lacking specific field observations (all her material was pit-trapped) suggested that the species was arboreal, on the basis of the keeled scales, "cautious movements .... [when] .... hooked over a slippery rod" (Davidge 1979:65), prehensile tail and "stick-like rigidity" (Davidge 1979:95). She reported that "the body and most of the tail of *Pletholax* were held rigid so that individuals curled the tip of the tail around a finger when held but rarely curled the whole body" (Davidge 1979:54). However, such behaviour could also be explained as an adaptation to pushing through dense low vegetation such as tussock grasses, through the meshwork formed in leaf litter mats, or to facilitate fossorial activity.

It is clear from the collection of many specimens in pit-trap lines (Mertens 1965; Kluge 1974; Davidge 1979, 1980; Turpin 1990, 1991; Maryan 1993; data accompanying WAM R42955, R78091, R83188, R89379, R94496, R94649) that *P. g. gracilis* is often active on the surface. However, Kluge's observations of fossorial activity are supported by the collection of one specimen in a dead rotting stump (Wilson and Knowles 1988; data accompanying WAM R85383) and our observations (MP). One individual captured at Karawara was placed overnight in a bucket with approximately 16cm of sand. When the bucket was examined the following morning, the lizard had burrowed to the very bottom of the sand layer. The depth to which the lizard had burrowed in loose sand suggests that fossoriality is more than simply occasional, although the extent of subsurface activity remains to be determined.

BODY SIZES

Davidge (1979, 1980) reported a minimum mature SVL of 60mm for *P. g. gracilis* and did not identify any sexual dimorphism in adult size. A gravid female with SVL 75mm was reported by Mertens (1965). Our data indicate that, as for other pygopodids for which data are available (Kluge 1974; Patchell and Shine 1986; Webb and Shine, in press), female *Pletholax* of both subspecies are larger than males. Mature female *P. g. gracilis* had SVL 67.5-83.0mm ($\bar{x} = 75.2$, sd = 4.07, n = 22), while mature males were significantly smaller, with SVL 56-69.5mm ($\bar{x} = 62.4$, sd = 3.09, n = 30; Mann-Whitney U test, $z = 6.075$, $p < 0.001$). For *P. g. edelensis*, which attains greater sizes, the direction of the sexual dimorphism was the same (mature females: SVL 79.0-88.0mm, $\bar{x} = 83.0$, sd = 3.81, n = 4; mature males: SVL 67.5-80.0mm, $\bar{x} = 72.6$, sd = 5.65, n = 4; Mann-Whitney U test, $U = 1$, $p < 0.05$). Minimum mature size was determined by the presence of yolking ovarian follicles in females, and enlarged turgid testes accompanied by opaque deferent ducts in males.

Of 66 individuals, representing both subspecies, only four were immature: one subadult female (WAM R80937; SVL = 67.5mm) and three very small unsexed juveniles (WAM R62577-78, R85383; SVL range 29.0-36.5mm), the latter collected in February and March. A similar paucity of juveniles (2 of 25 captures) was reported by Davidge (1979).

SEX RATIO

Davidge (1980) reported a significant excess of adult males in the material she examined (17 adult males:6 adult females), although she did not provide any analysis of seasonal variation in sex ratio. From the material examined here, there was some evidence for seasonal variation in adult sex ratio. In *P. g. gracilis*, adult females outnumbered adult males in the cooler months (March-August; 7:2) while the reverse was true in Spring (September-November; 10:15) and Summer (December-February; 5:11). Pooling Spring and Summer samples, these differences are almost statistically significant ($\chi^2 = 3.43$, 1 d.f., $0.10 < p < 0.05$). Davidge's sample was mostly collected between September and January, with fewer than two captures in each of March, April and May, and no captures in other months over a 16 month period (Davidge 1979).

REPRODUCTIVE CYCLE

Male

Davidge (1979, 1980) reported an October peak in testis size in *P. g. gracilis*, with reduced testes in January. In the material we examined, mature-sized males of this subspecies collected in December/January (n = 12) and March (n = 1) had small flattened testes and transparent deferent ducts. A single male collected in May had moderately enlarged testes but transparent deferent ducts. September (n = 3) and October (n = 9) males had enlarged turgid testes and opaque deferent ducts. Of three males collected in November, one had enlarged turgid testes and opaque ducts while the others were similar to December males. Males of *P. g. edelensis* were only available for August/ September (n = 3) and January (n = 1). The former specimens had enlarged testes while the latter had small testes. These data are consistent with a Spring peak in the male cycle in both subspecies.

The only other published data on the timing of the male reproductive cycle in pygopodids are for populations of *Delma fraseri* and *Pygopus lepidopodus* sympatric with *P. gracilis* (Davidge 1979, 1980), and for *Lialis burtonis* (Saint Girons *et al.* 1992). All three taxa similarly show a Spring/early Summer peak in testis size and spermiogenesis, although later in the season than in *Pletholax* (November in *Pygopus* and possibly *Lialis*, December in *Delma*). A Spring peak in testis size has also been reported in other southern Australian gekkonoids (How and Kitchener 1983; How *et al.* 1986).

Female

Davidge (1979, 1980) reported an October peak in "egg" size for *P. g. gracilis*, although she did not indicate whether this referred to ovarian follicles or oviducal eggs. Ehmann (1992) similarly reports oviposition in October (subspecies not identified) while Mertens (1965) reports an ovigerous *P. g. gracilis* collected 15 November. Of our material, mature-sized females of *P. g. gracilis* collected in March (n = 5), April (n = 1) and July (n = 1) showed no follicular activity. A single September female (11 September) had slightly enlarged follicles beginning to develop yolk. Of six October females, one (collected 2 October) showed no follicular activity, three (one from 23 October, others without precise date) had enlarged yolking follicles (6.3-9.3mm long), one (31 October) carried shelled oviducal eggs and one (no precise date), although showing little follicular activity, had grossly dilated oviducts suggesting recent oviposition. Of three November specimens, one (22 November) carried shelled oviducal eggs, while the others showed no follicular activity. Of five specimens collected December/January, one (19 December) carried shelled oviducal eggs, while the remainder were reproductively inactive.

Only four female *P. g. edelensis*, all collected in August, were examined and all lacked follicular development.

The pattern of Spring vitellogenesis and oviposition in *Pletholax* is consistent with data on other pygopodids (Davidge 1979, 1980; Patchell and Shine 1986).

CLUTCH SIZE AND EGG SHAPE

In all cases, *Pletholax* clutch size was two, one in each ovary/oviduct (n = 3 with enlarged ovarian follicles; n = 3 with oviducal eggs). A clutch size of two has also been reported for *Pletholax* by Mertens (1965), Davidge (1979, 1980), Bamford (*in* Greer 1989) and Ehmann (1992), and for other pygopodids by Patchell and Shine (1986).

Both enlarged yolking follicles and shelled oviducal eggs were extremely elongate, with straight sides and rounded ends. Davidge (1979, 1980) reports maximum egg dimensions of 13 x 4mm, while Mertens (1965) reports two eggs of 16-17 x 5mm. The elongate egg shape probably reflects anatomical contraints imposed by the slender body.

DIET

Almost nothing has previously been reported on the diet of *P. gracilis*. Davidge (1979:96), although finding no identifiable material in the stomachs of her material, observed captives readily lapping honey/water mixtures, and, combined with her assumption of arboreality for the species, suggested that the species may feed primarily on nectar or pollen of *Banksias*. However, she was unable to obtain support for this view by direct evidence, with no identifiable pollen in stomach content smears, and a lack of interest by captive *Pletholax* in freshly picked *Banksia* inflorescences. Greer (1989), quoting Ehmann (*pers. comm.*), states that captive *Pletholax* were "seen to lick sweet fruit (apple and banana) and to lap honey water". Ehmann (1992) states that *Pletholax* "licks nectar from heath flowers, and the body fluids of small, soft insects and spiders that abound near the flowers. The spiders are grasped by the body, the abdomen is broken, and the juices are licked up".

Stomach contents were lacking from most preserved specimens we examined (unfortunately the stomachs had previously been removed from most of the large Jandakot series, which comprises about half the available specimens), while the colon mostly contained only small amounts of indeterminate faecal material. The stomach of one specimen (WAM R23918) contained approximately 60 short segments of vegetable matter (2-2.5x0.5mm) with striate surface, with a similar number in the colon. The colon of a second specimen (WAM R61907) contained an insect head-capsule (1.5x1.6mm), possibly of a termite worker. A small section of tough, smooth arthropod chitin, possibly part of another insect head-capsule, was found in AM R13815.

While these data are insufficient to definitively identify the dietary preferences of *Pletholax*, several comments are possible. Firstly, the paucity of digesta in the gut of *Pletholax* contrasts markedly with most other pygopodids. Patchell and Shine (1986) reported stomach contents from 47-89% of *Lialis*, *Pygopus* and *Delma* species they examined, while we have observed large amounts of chitinous arthropod remains in the stomach and/or colon of the majority of specimens of *Delma* and *Aclys* that we examined. The myrmecophagous *Aprasia*, on the other hand, resemble *Pletholax* in the paucity of food items across samples (Webb and Shine, in press). The lack of food in *Aprasia* has been attributed to infrequent "binge-feeding" in local food-rich microenvironments (ant nests) (Webb and Shine, in press).

Secondly, the short segments of vegetable matter present in one *Pletholax* specimen appeared to be fine stem segments (possibly grass) rather than floral elements. Further, their even length suggests cropping by insect mandibles, rather than the masticating teeth of *Pletholax* (Rieppel 1984; M. Hutchinson, *pers. comm.*). The combination of these data, with the possible identification of isopteran material, leads us to tentatively suggest that *Pletholax* may feed predominantly on termites. This suggestion is consistent with the general absence of identifiable gut contents in the specimens examined, which were mostly pit-trapped or surface collected in other ways (hence away from feeding sites), and with the collection of a single individual in a dead stump. The plant material may have been secondarily or accidentally ingested within or near a termite colony.

Finally, we note that although nectivory could also explain the lack of gut contents in the specimens, there is a paucity of near-ground-level nectar-bearing plants at several of the known localities for *P. g. edelensis*. This observation is inconsistent with the conclusions presented by Ehmann (1992), although we do not exclude the possibility that occasional nectivory could occur.

PREDATION

One specimen (WAM R12687; collected 19 December) was noted as being "caught by Kestrel [*Falco cenchroides*] nesting in cave". Two specimens (AM R13815, R26628; collected 11 September) were taken from the stomach of a magpie (*Cracticus tibicen dorsalis*). In both cases it is probable that the lizards were taken when active on the surface.

CONSERVATION STATUS

It has been suggested that *Pletholax* may be at risk due to land clearing within its range (Ehmann 1992). Certainly, original native vegetation is now rare or absent at many of the localities in the Perth metropolitan area from which the species was formerly collected, and there would appear to have been a reduction in distribution in this region. However, the nominate subspecies is known from a number of reserves, and has an extensive distribution outside the Perth region, while the known localities for *P. g. edelensis* remain little disturbed, with the southernmost occurring within Kalbarri National Park.

MATERIAL EXAMINED

P. g. gracilis

Australian Museum (AM): R13815, R26628, Mandurah (32°32'S 115°43'E)

Western Australian Museum (WAM): R4212, R104374, Victoria Park (31°59'S 115°53'E); R9697, Coomberdale (30°27'S 116°02'E); R11150, South Perth (31°59'S 115°51'E); R13682, R23918, Dianella (31°54'S 115°53'E); R16886, Red Hill (31°23'S 116°06'E); R12687, Jurien Bay (30°15'S 115°01'E); R25071, Eneabba (29°49'S 115°16'E); R36172, Bentley (32°01'S 115°55'E); R42955, Sorrento (31°48'S 115°44'E); R60017, 30km WSW Badgingarra (30°28'S 115°12'E); R61895-98, R61900, R61902-03, R61905-11, R62577-81, R64723-25, Jandakot (32°06'S 115°53'E); R60940, 13km WSW Winchester (29°49'S 115°49'E); R78091, R82912, R93004, Mooliabeenee (31°20'S 116°01'E); R80932, R80934-38, R83188, Murdoch (32°04'S 115°49'E); R82856, Wireless Hill (32°01'S 115°49'E); R85383, Koondoola (31°50'S 115°51'E); R88063, Cottesloe (31°59'S 115°45'E); R89379, R96195, Willeton (32°02'S 115°52'E); R94496, North Lake (32°04'S 115°49'E); R94649, Boonanarring Nature Reserve (31°13'S 115°50'E); R97606, Perth airport (31°56'S 115°58'E); R106108, R106171-72, Marangaroo (31°50'S 115°51'E)

P. g. edelensis

WAM: R54755, 5km S Useless Loop (26°10'S 114°24'E); R54814, R54863, 4km S Useless Loop (26°10'S 114°24'E); R55085, 10km NW Useless Loop (26°05'S 113°19'E); R97304, 13km E Kalbarri (27°41'S 114°17'E); R103978, Edel Land (26°17'S 113°19'E); R104259-60, Edel Land (26°16'S 113°16'E)

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A NEW SPECIES OF *MELOMYS* (RODENTIA: MURIDAE) FROM KAI BESAR ISLAND, MALUKU TENGAH, INDONESIA

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ABSTRACT

Four specimens of *Melomys* recently collected from Kai Besar Island, eastern Indonesia, are herein described as a new species.

INTRODUCTION

The genus *Melomys* Thomas, 1922 is currently in a state of considerable taxonomic confusion, despite several attempts to review the group (Rümmler 1938; Tate 1951) and several other pertinent taxonomic considerations (Laurie and Hill 1954; Menzies and Dennis 1979).

In particular, there is great taxonomic uncertainty relating to the group of smaller *Melomys* with: head and body length usually less than 120mm; white or pale coloured abdominal fur; moderately long anterior palatal foramen; and with three or occasionally two or three hairs/ tail scale in the mid tail region. This group is usually taken to represent *Melomys lutillus*, a species considered to have as many as 11 subspecies by Tate (1951) or as few as 5 subspecies by Rümmler (1938).

In October 1992, a team of vertebrate biologists from the Western Australian Museum and the Museum Zoologicum Bogoriense collected four specimens of *Melomys* from Kai Besar Island (Figure 1) that were most allied to *Melomys lutillus*. In this paper we detail a comparison of these Kai specimens with all 11 forms that have been placed in *M. lutillus* by previous workers at some time, as well as with several other species that could conceivably be confused taxonomically with the Kai Besar *Melomys*. As a consequence of these comparisons we conclude that the Kai Besar *Melomys* are a new species which we herein describe.

METHODS

Weight of the Kai Besar specimens was recorded in the field prior to their fixation. External measurements were all recorded from the specimens following their fixation and preservation. All measurements (in mm) were taken with digital dial calipers: external to 0.1 mm; skull and dental to 0.01 mm. Measurement points follow Tate (1951). Pelage and colour descriptions follow Smithe (1975). Comparison of the Kai specimens with other forms with which they might be confused depended on descriptions of these other forms in Rümmler (1938), Tate (1951), Menzies and Dennis (1979) and the original type descriptions (referenced

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in Tate 1951)). Adult condition was judged on the basis of fused basioccipital and basisphenoid suture and appearance of reproductive organs.

TAXONOMY

Melomys bannisteri sp. nov.

Figures 2-4

Holotype

Western Australian Museum specimen number (WAM) M42669; adult female carcass fixed in 10% formalin

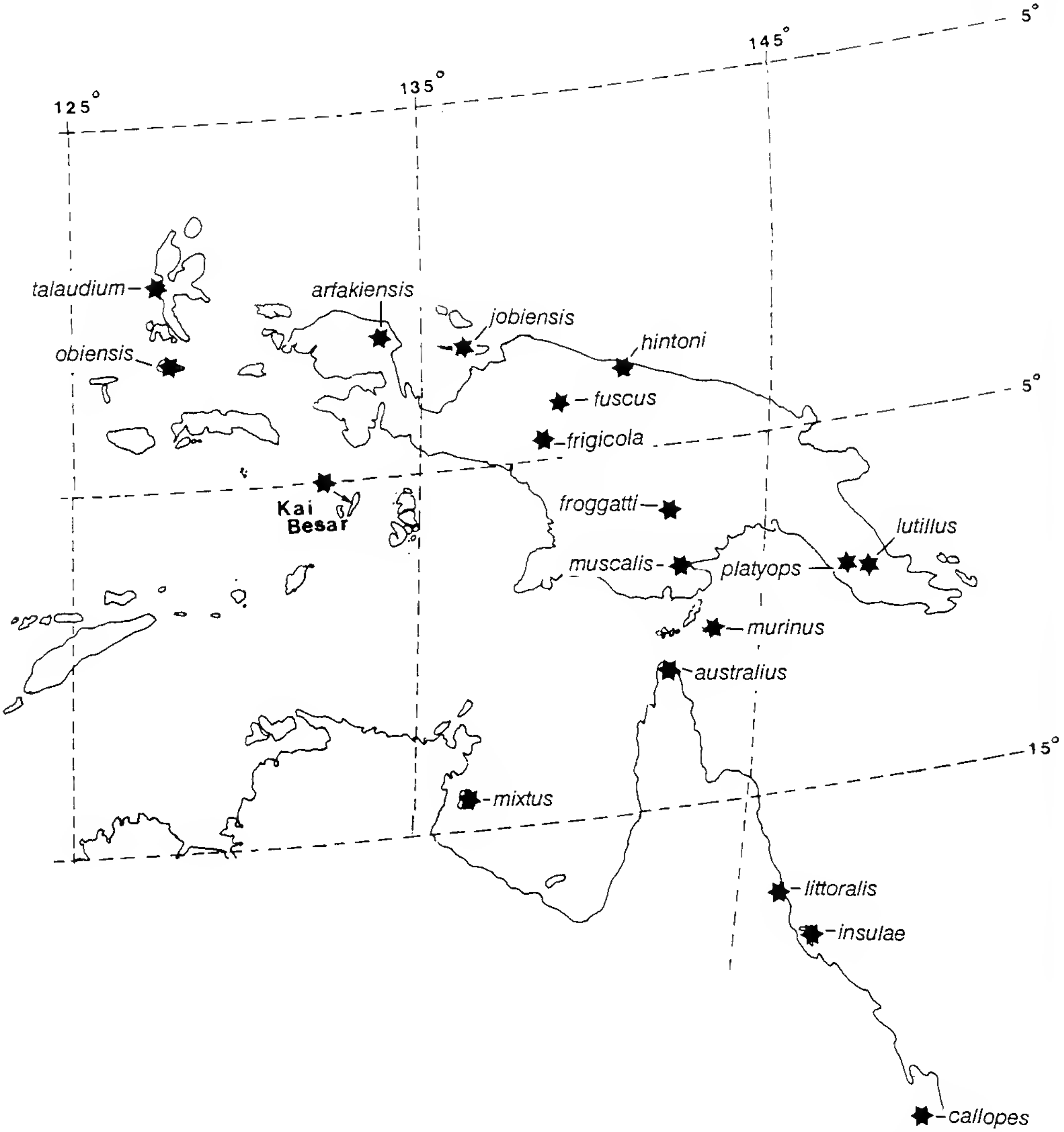

Figure 1 Type locality of *Melomys bannisteri* sp. nov. and of other forms of *Melomys* referred to in text.

and preserved in 70% ethanol; skull separate; liver preserved in ultrafreeze. Collected in break-back trap on 13 October 1992 by D.J. Kitchener and Island Maryanto.

Type locality

2km west Fakoi, Kai Besar Island, Maluku Tengah, Indonesia (5°38'50"S, 133°02'00"E); altitude 200m; in disturbed partially open low evergreen rainforest with a ground cover of bracken fern and low sedges.

Paratypes

WAM 42132, adult female, collected at Desa Mun (5°26'50"S, 133°03'50"E), Kai Besar Island, by R.A. How and R.E. Johnstone on 15 October 1992.

WAM M42678 and WAM M42689 (both adult males), collected 2 km. west of Desa Fakoi, Kai Besar Island, by D.J. Kitchener and Island Maryanto on 14 and 15 October 1992. All specimens preserved as holotype.

Diagnosis

Melomys bannisteri is distinguished from all other small or moderate sized *Melomys* with pale coloured underfur; and moderate length anterior palative foramina by the following combination of characters: head to body length <120; tail to vent length <120; pes length <27; pes broad (Figure 4); tail hairs 2-3/scale; tail scales large <13/cm at mid point of tail; tail hairs very short, <30% length of tail scales; belly fur pure white; C^1-M^3 tooth row length >5.8; anterior palatal foramen does not reach posteriorly to M^1 anterior alveolus margin; moderate supraorbital ledges; M^1 and M^2 posterior cingulum broad and prominent; zygomatic plate breadth >3.7.

It differs from *Melomys lutillus lutillus* (Thomas, 1913), which has similar external measurements, in having ventral hairs generally pure white rather than white hairs restricted to "border spots in the neck and inguinal region," and "irregularly distributed along the belly midline" (Rümmler 1938); tail scales larger 11-12 *v.* 15 scales/cm; skull generally larger: e.g., zygomatic width 15.8-16.6 *v.* 14.6-14.7; nasal length 10.6-11.5 *v.* 9.8-10.1; zygomatic plate breadth 4.0-4.6 *v.* 2.9-3.1; palatal length 15.7-16.2 *v.* 14.5-14.7; tooth row longer: e.g., C^1-M^3 length 5.9-6.2 *v.* 5.2-5.3 and teeth broader: e.g., M^1 breadth 1.8-1.9 *v.* 1.6-1.7; anterior palatal foramen relatively shorter, terminates posterior to M^1 anterior face rather than at or slightly posterior to M^1 anterior face; and posterior margin of palate terminates at M^3 mid-point rather than at M^3 posterior face.

It differs from *Melomys lutillus australius* Thomas, 1924, in having external measurements generally slightly smaller: e.g., head to vent length 111.6-114.5 *v.* 123, tail to vent length 106.4-117.6 *v.* 125, pes length 23.2-25.5 *v.* 27; larger tail scales 11-12 *v.* 16 scales/cm; tail hairs shorter 20-30% *v.* 75% of tail scale length; belly fur white rather than generally strongly buffy except for mid-line where it is pure white or pale fawn; palate posterior margin terminating at mid point rather than posterior edge of M^3; anterior palatal foramen shorter (4.8-5.0 *v.* 5.4) and does not extend to M^1 anterior face.

It differs from *Melomys lutillus callopes* Finlayson, 1942, which has similar external measurements, in having larger scales on tail 11-12 *v.* 15 scales/cm; shorter anterior palatal foramen (4.8-5.0 *v.* 5.1-6.1) which does not reach M^1 anterior alveolus; supraorbital ledges moderate and that region not with smoothly rounded edges; anterior edge of zygomatic plate slopes posteriorly and not anteriorly from anterodorsal aspect; interorbital breadth larger relative to condylobasal length 0.162-0.176 *v.* 0.156; ear shorter 12.8-15.1 *v.* 18.0; bulla shorter 4.5-4.6 *v.* 4.7-4.8.

It differs from *Melomys lutillus frigicola* Tate, 1951, in having head to vent smaller 111.6-114.5 *v.* 130; tail to vent length smaller 106.4-117.6 *v.* 142 and pes length smaller 23.2-25.5

v. 29; dorsal pelage with shorter hair 11 *v*. 15-17; tail scale hairs shorter; anterior palatal foramen shorter (4.8-5.0 *v*. 5.1) and not reaching M^1 anterior alveolus; bulla shorter 4.5-4.6 *v*. 4.8; zygomatic plate broader 4.0-4.6 *v*. 3.5; mastoid narrower relative to condylobasal length 0.378-0.397 *v*. 0.424.

It differs from *Melomys lutillus froggatti* Troughton, 1937, which has similar external measurements, in having tail hairs shorter 20-30% *v*. 50-100% of tail scale length; larger scales 11-12 *v*. 13/cm; pelage of undersurface contrasts, rather than toning in with that of flanks; belly fur white not grey; interorbital region not broadly concave; cranium not abruptly rounded anteriorly.

It differs from *Melomys lutillus hintoni* Rümmler, 1935, in having external measurements slightly larger: e.g., tail to vent length 106.4-117.6 *v*. 100; pes length 23.2-25.5 *v*. 22. Skull generally larger; e.g., condylobasal length 28.8-30.6 *v*. 26.8; zygomatic plate broader 4.0-4.6 *v*. 3.2, but zygomatic width narrower relative to condylobasal length 0.535-0.548 *v*. 0.567. Teeth larger: e.g., C^1-M^3 length 5.9-6.2 *v* 5.2

It differs from *Melomys lutillus insulae* Troughton and le Souef, 1929, in having a tail that is not markedly bicoloured and subequal to rather than shorter than head to vent length; tail scales larger 11-12 *v* 13-14 cm; belly fur white rather than pale grey base tipped with light pinkish cinnamon; pes white not pinkish cinnamon. Skull generally larger: e.g., greatest skull length 32.7-32.8 *v* 30.2 and zygomatic width 15.8-16.6 *v* 15.4. However the holotype of *insulae* may not be an adult (Rümmler 1938).

It differs from *Melomys lutillus littoralis* (Lönnberg 1916) in having pes length shorter 23.2-25.5 *v*. 28; belly fur pure white and not light buff; tail scales larger 11-12 *v*. 18-19 scales/cm; larger body and tail measurements: e.g., head to vent length 111.6-114.5 *v*. ±90 and tail to vent length 106.4-117.6 *v*. ± 90; zygomatic plate broader 4.0-4.6 *v*. 3.6; anterior palatal foramen does not extend to M^1 anterior face. Teeth slightly shorter: e.g., C^1-M^3 length 5.9-6.2 *v*. 6.3.

It differs from *Melomys lutillus mixtus* Troughton, 1935 which, based on the holotype which Rümmler (1938) considered is probably subadult, has similar external measurements. Tail hairs much shorter 20-30% *v*. 100% of scale length. Skull larger; e.g., greatest skull length 32.4-32.8 *v*. 28.6; anterior palatal foramen does not extend to M^1 anterior face; teeth both longer: e.g., C^1-M^3 length 5.9-6.2 *v*. 5.5 and broader, e.g., M^1 breadth 1.8-2.0 *v*. 1.6.

It differs from *Melomys lutillus murinus* (Thomas, 1930), which has similar external measurements, in having larger tail scales 11-12 *v*. 14-15 cm; skull generally larger: e.g., condylobasal length 28.8-30.6 *v*. 25.5-27.0, zygomatic width 15.8-16.6 *v*. 14.8; supraorbital ridge absent but a horizontal ledge present in older specimens; palate posterior margin terminates at M^3 mid point rather than level with M^3 posterior face; anterior palatal foramen relatively shorter, does not reach posterior to M^1 anterior alveoli; and teeth much larger: e.g., C^1-M^3 length 5.9-6.2 *v*. 5.1-5.3.

It differs from *Melomys lutillus muscalis* (Thomas, 1913), which has similar body measurements, in having larger tail scales 11-12 v. 15/cm; slightly larger skull measurements: e.g., condylobasal length 28.8-30.6 *v*. 26.2-27.9; zygomatic width 15.8-16.6 *v*. 13.9-15.0, interorbital breadth 4.9-5.1 *v*. 4.2-4.7; zygomatic plate breadth 4.0-4.6 *v*. 3.2-3.4; anterior palatal foramen posterior edge much closer to M^1 rather than terminating nearly half their length anterior of M^1 anterior edge, and teeth much larger: e.g., C^1-M^3 length 5.9-6.2 *v*. 4.5-5.3.

It differs from *Melomys platyops* (Thomas, 1906) in having 2-3 rather than 1 hair/tail scale although Tate (1951:284) states that "occasional specimens of northern *platyops* (*M. p. mamberanus*) specimens having some scales one-haired and others three-haired can be noted, as well as individuals having three-haired tail scales and other individuals with one-haired tail scales". It differs also in having larger tail scales 11-12 *v.* 13-19 scales/cm and ventral fur pure white rather than grey black based fur tipped with greyish white or yellow brown colour.

It also differs from *M. platyops platyops* and *M. p. fuscus* Rümmler, 1935 in having external and skull measurements much smaller: e.g., head to vent length 111.6-114.5 *v.* >135, pes length 23.2-25.5. *v.* >28, condylobasal length 28.8-30.6 *v.* >34, zygomatic width 15.8-16.6 *v.* >17.5.

Table 1 Measurements (in mm) of the skull, dentition, and externals and weight of *Melomys bannisteri* sp. nov., holotype and paratypes.

CHARACTER WAM NUMBER / SEX	HOLOTYPE M42669 ♂	PARATYPES M42689 ♂	 M42678 ♂	 M42132 ♀	MEAN (RANGE)
Age	Young adult	Adult	Adult	Adult	
Greatest skull length	32.76	-	-	32.74	32.75 (32.74-32.76)
Condylobasal length	30.62	30.01	28.80	30.45	29.97 (28.80-30.62)
Condyloincisive length	30.22	29.79	28.71	30.16	29.72 (28.71-30.22)
Zygomatic width	16.54	16.06	15.79	16.61	16.25 (15.79-16.61)
Interorbital breadth	4.89	5.10	5.05	5.06	5.03 (4.89-5.10)
Interparietal breadth	9.67	9.63	-	10.22	9.84 (9.63-10.22)
Braincase breadth	13.62	13.79	13.83	13.94	13.80 (13.62-13.94)
Mastoid width	11.58	11.45	11.44	11.93	11.60 (11.44-11.93)
Nasal length	10.61	-	-	11.46	11.04 (10.61-11.46)
Nasal breadth	4.35	-	-	3.58	4.00 (3.58-4.35)
Zygomatic plate breadth	4.44	4.12	3.98	4.57	4.28 (3.98-4.57)
Diastema length	8.80	8.44	7.88	8.38	8.38 (7.88-8.80)
Height muzzle (behind ant. pal. for.)	8.22	8.13	7.84	8.35	8.14 (7.84-8.35)
Palatal length	16.23	16.20	15.74	16.22	16.10 (15.74-16.23)
Ant. palatal foramen length	4.90	4.96	4.83	4.82	4.88 (4.82-4.96)
Ant. palatal foramen breadth	1.80	1.85	1.87	1.80	1.83 (1.80-1.87)
Mesopterygoid fossa breadth	2.86	2.83	-	2.37	2.69 (2.37-2.86)
M^1-M^1 breadth (inside)	2.48	2.70	2.57	2.77	2.61 (2.48-2.77)
Bulla length	4.59	4.64	4.45	-	4.56 (4.45-4.64)
M^1-M^3 crown length	5.86	6.20	5.90	6.02	6.00 (5.86-6.20)
M^1-M^3 alveoli length	6.08	6.38	6.06	6.33	6.21 (6.06-6.38)
M^1 crown length	3.01	3.34	3.14	3.10	3.15 (3.01-3.34)
M^1 crown breadth	1.92	1.96	1.84	1.79	1.88 (1.79-1.96)
M^2 crown length	2.02	2.20	2.10	2.03	2.09 (2.03-2.20)
M^2 crown breadth	2.04	1.89	1.75	1.81	1.87 (1.75-2.04)
M^3 crown length	1.15	1.29	1.23	1.18	1.21 (1.15-1.29)
M^3 crown breadth	1.33	1.28	1.28	1.16	1.26 (1.16-1.33)
Head to vent length	111.7	114.5	113.1	111.6	112.7 (111.6-114.5)
Tail to vent length	117.6	113.7	110.3	106.4	112.0 (106.4-117.6)
Ear length (from basal notch)	15.1	-	12.8	13.3	13.7 (12.8-15.1)
Pes length (without claw)	25.0	24.3	25.5	23.2	24.5 (23.2-25.5)
Tibia length	32.9	32.9	31.1	31.3	32.1 (31.1-32.9)
Weight (gms)	61.5	56.0	48.8	45.0	52.8 (45.0-61.5)

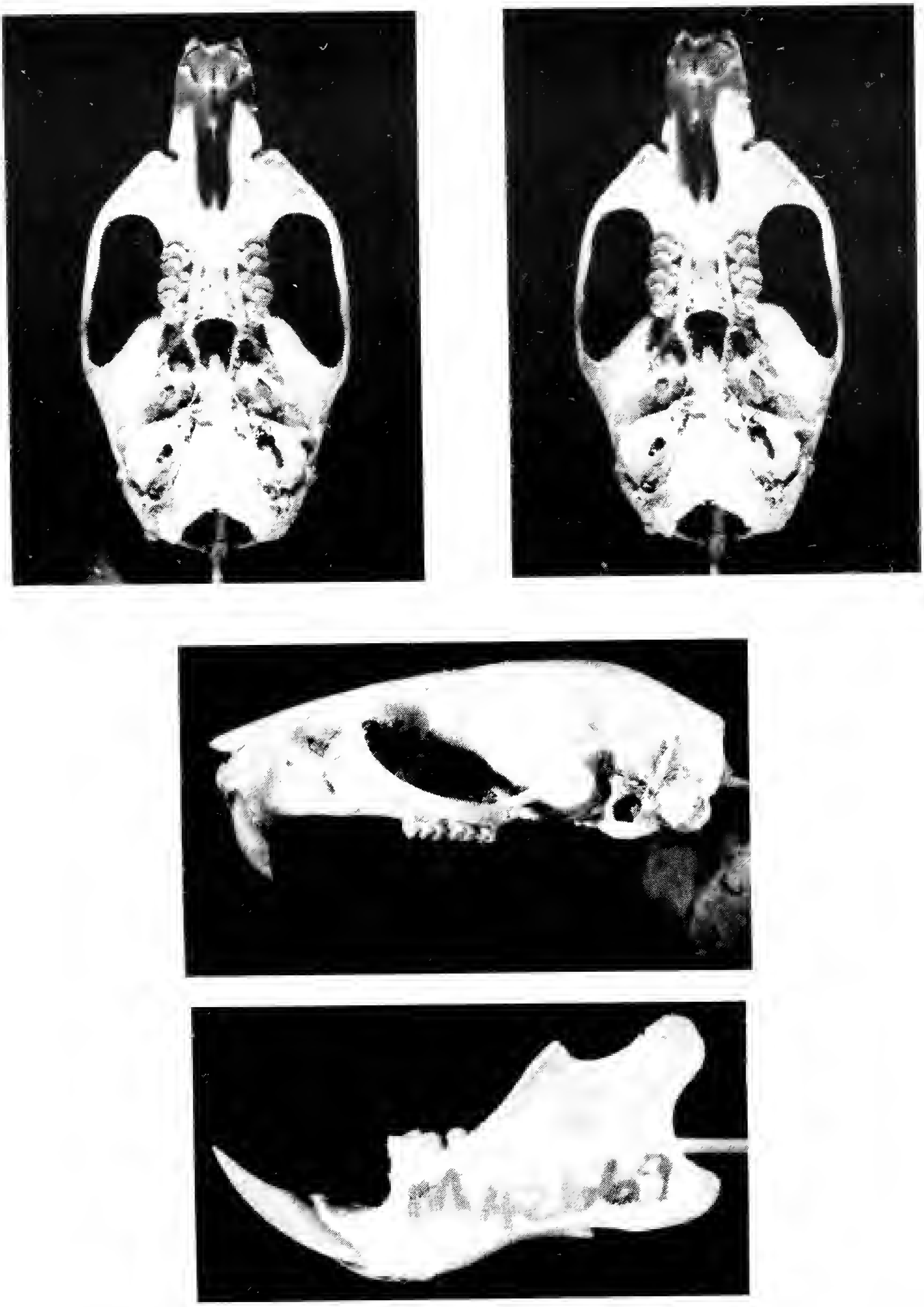

Figure 2 Plates of ventral (as stereopairs) of the skull and lateral surface of the skull and dentary of holotype of *Melomys bannisteri* sp. nov.

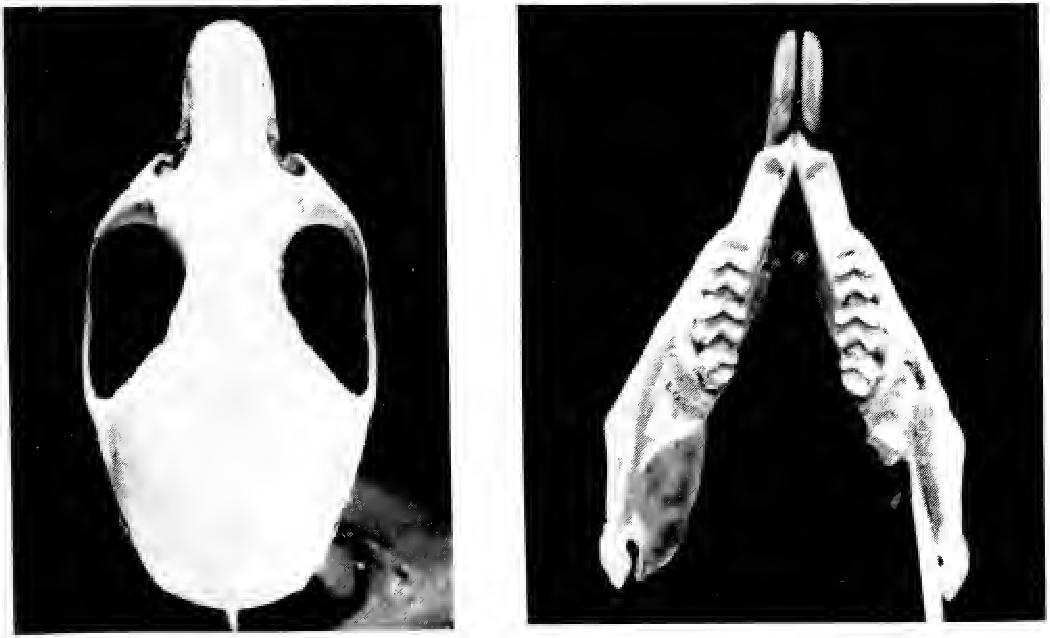

Figure 3 Plates of dorsal of the skull and dentary of holotype of *Melomys bannisteri* sp. nov.

It also differs from *M. p. arfakiensis* Rümmler, 1935, which is similar in general body and skull dimensions, in having tail subequal in length to head and body rather than 18% longer, pes shorter 23.2-25.5 *v.* 27-29 and bulla longer relative to condybasal length 0.150-0.154 *v.* 0.140.

It also differs from *M. p. jobiensis* Rümmler, 1935 which has similar external dimensions, in having zygomatic width greater 15.8-16.6 *v.* 14.7, narrow interorbital breadth 4.9-5.1 *v.* 5.7; shorter palatal length 15.7-16.2 *v.* 16.7-17.3, much longer anterior palatal foramen 4.8-5.0 *v.* 4.1; narrower between M^1M^1 internal surfaces 2.5-2.8 *v.* 3.1; C^1-M^3 crown length longer 5.9-6.2 *v.* 5.6-5.7; M^3 not as reduced; M^3 anteriolingual cusp separate.

It differs from *Melomys obiensis* (Thomas, 1911) and *M. fulgens* (Thomas, 1920) (including *talaudium* (Thomas, 1921)) in being much smaller overall; e.g., head to vent length $<<140$, tail to vent length $<<150$, pes length <28, greatest skull length $<<38$, interorbital breadth $<<5.6$, anterior palatal length $<<5.7$, C^1-M^3 length <6.4.

Description

Measurements of skull, dentition and externals presented in Table 1.

Skull (Figures 2-3)

Skull small, dorsal outline gently curved in lateral profile from nasal distal tip to parietal mid point, which is moderately inflated; interparietal not inflated, lambdoidal crest slight; interorbital region very slightly concave, moderately wide; nasal moderately narrowed posteriorly; rostrum short; zygomatic arch moderately wide, squamosal part narrowed; zygomatic plate broad, leading edge slopes slightly posterior from anterior apex; infraorbital foramen moderately wide; lachrymal bones moderate, post squamosal hook not well developed posteriorly, forms a vertical ridge with lateral occipital and mastoid; supraorbital lateral shelf posterior from mid constriction of interorbital region, also a slight vertical beading on this shelf which is perceptible to one third length of parietal; anterior palatal foramen moderately long and elongate, does not reach M^1 alveolus; mesopterygoid fossa moderately wide, pterygoid bones narrow slightly posteriorly; parapterygoid fossa narrow but deep; bulla moderately long and little inflated.

Dentition (Figures 2-3)

Molars large, M^3 not noticeably reduced for *Melomys*; M^1 anterior and posterior lamellae with well developed lophs; posterior lamella without lingual loph but with well developed and spacious posterior cingulum with the appearance of a central vestigial cusp; M^2 with only large anterolingual cusp remaining of anterior lamella, second lamella well developed, approximates that of M^1 but again with a well developed posterior cingulum with vestigial cusp; M^3 with anterolingual cusp well developed, separate from posterior lamella; molar rows diverge slightly posteriorly from each other; incisors opisthodont.

Externals (Figure 4)

A small to moderate sized *Melomys*: head and body length (112.7) subequal with tail length (112.0); ears moderately long (13.7); and pes broad, length moderate (24.5).

Pelage

Dominant colour of dorsal surface Cinnamon Brown resulting from Cinnamon Brown and/ or Black tipping to the Medium Neutral Gray colour of basal three-quarters of hairs. Hairs in mid dorsum 11mm long while those in mid forehead 5mm long; flanks Buffy Yellow tipping to the Medium Neutral Gray colour of basal one-half of hairs. Lips, throat, chest, abdomen to anus, inside of thigh and pes upper surface White, hairs 5-6mm long, outer leg surface, manus upper surface and cheeks Cream Colour. Distal half of ear pinna lightly furred inside

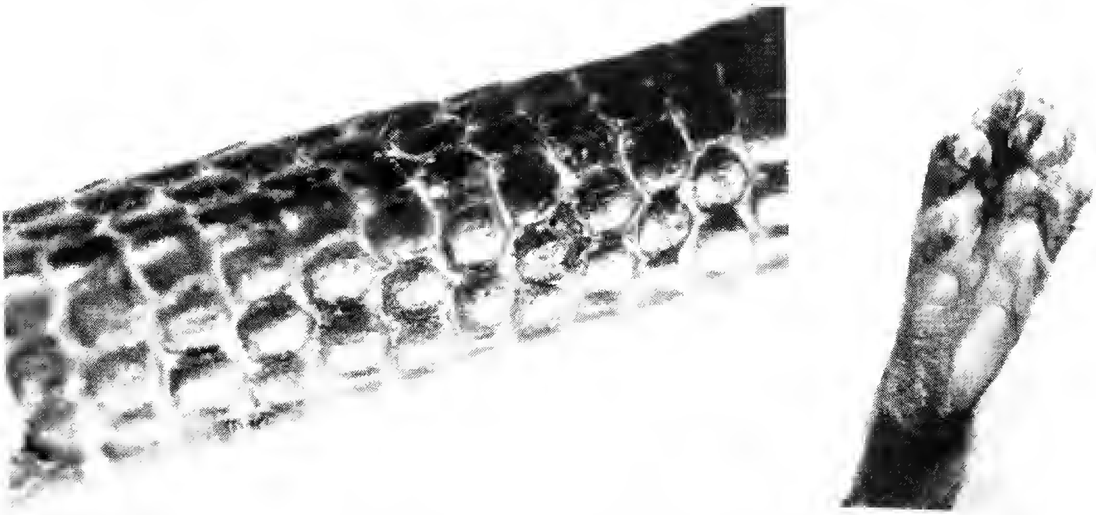

Figure 4 Plate of tail and pes plantar surface of holotype of *Melomys bannisteri* sp. nov.

and outside with Cinnamon Brown, external basal half well haired with Cinnamon Brown. Tail dorsal and lateral surface Greyish Brown, undersurface a paler Dark Neutral Gray.

Hairs on dorsal surface of tail usually 3, frequently 2 and occasionally 1 per scale; on ventral and lateral surfaces 3 per scale; tail hairs short, less than 30% scale width. Scales typical of *Melomys* of the *lutillus* group (Figure 4). On head numerous Black mystical vibrissae up to 40 long; numerous short (up to 12mm) White submental vibrissae; two moderately long (up to 7.5) White interramal vibrissae; a single long (up to 22) Black genal vibrissa; several long (up to 23) Black supraorbital vibrissae and 2-3 long (up to 10) Black with White tipped ulnar vibrissae.

Reproduction

Only one male (WAM M42678), weighing 45gm, had scrotal testes; these were large and 12.6mm long, with well developed caudal epididymis and considerable fat deposits surrounding the caput epididymis. The other two males were heavier. The larger of these (WAM M42669, holotype) weighing 61.5gm, had inguinal testes that were slightly smaller (10.5mm long) than WAM M42678. The other, WAM M42689, had large (12.6mm long) abdominal testes.

The female, WAM M42132, weighing 45gm, had recently given birth and was lactating. Its four inguinal teats were enlarged, 3.8mm long, and with enlarged mammary glands. The uterine horns had recently involuted; the left uterine horn had two implantation scars.

Etymology

Named after Mr John Bannister, recently retired after 17 years as the Director of the Western Australian Museum, in recognition for his continued interest and support of research in Nusa Tenggara, Indonesia, and for his efforts over many years towards improving the collections of the mammal section, Western Australian Museum.

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EARLY ORDOVICIAN GASTROPODS FROM THE CANNING BASIN, WESTERN AUSTRALIA

Yu Wen*

ABSTRACT

Fossil gastropods collected from the Lower Ordovician Emanuel Formation and Gap Creek Formation, Canning Basin, Western Australia, comprise eight species in seven genera, including two new species. The most common gastropods of the Emanuel Formation are *Peelerophon oehlerti* (Bergeron), *Ecculiomphalus* cf. *abendanoni* (Frech), *Pararaphistoma (Pararaphistoma) qualteriatum* (Schlotheim), *Pararaphistoma (Climacoraphistoma) vaginati* (Koken and Perner) and *Seelya emanuelensis* sp. nov. This gastropod fauna shows strong resemblances to those of southeastern Asia including China and to those of South America and Western Europe, ranging in age from Tremadocian to early Arenigian. Two species of Lower Ordovician gastropod, *Teiichispira kobayashi* Yochelson and Jones and *Oriostoma? canningense* sp. nov., are described from the Gap Creek Formation.

INTRODUCTION

The material utilized in the present paper were mainly collected by B.F. Glenister, A.W. Lindner and W.S. Johnson, all then of the University of Western Australia from the Emanuel Formation and Gap Creek Formation of Emanuel Creek, Canning Basin in 1957, 1958 and 1987 respectively. It also includes part specimens procured by D. Merrilees of the Western Australian Museum and J. Pas from the Emanuel Formation and Gap Creek Formation in 1960 and 1991 respectively (Figure 1).

The Lower Ordovician strata are extensively developed in the Canning Basin, but nearly all occur in the subsurface. The outcrop of the type section is along the Emanuel Creek. The Lower Ordovician in the Canning Basin has been divided in ascending order into Emanuel Formation and Gap Creek Formation (Guppy *et al.* 1958; Playford *et al.* 1975; McTavish and Legg 1976; Legg 1976; Forman and Wales 1981).

The Emanuel Formation is chiefly composed of light grey, nodular limestone and green-grey calcareous shale with a basal bed of sandy dolomite and arkose, about 594m in thickness (Playford *et al.* 1975). The formation yields various groups of fossils, such as conodonts, graptolites, trilobites, brachiopods, gastropods and cephalopods. More than 130 specimens of gastropods belonging to six species in five genera, were mainly obtained from the limestone, including *Peelerophon oehlerti* (Bergeron), *Bucania* sp., *Ecculiomphalus* cf. *abendanoni* (Frech), *Pararaphistoma (Pararaphistoma) qualteriatum* (Schlotheim), *Pararaphistoma*

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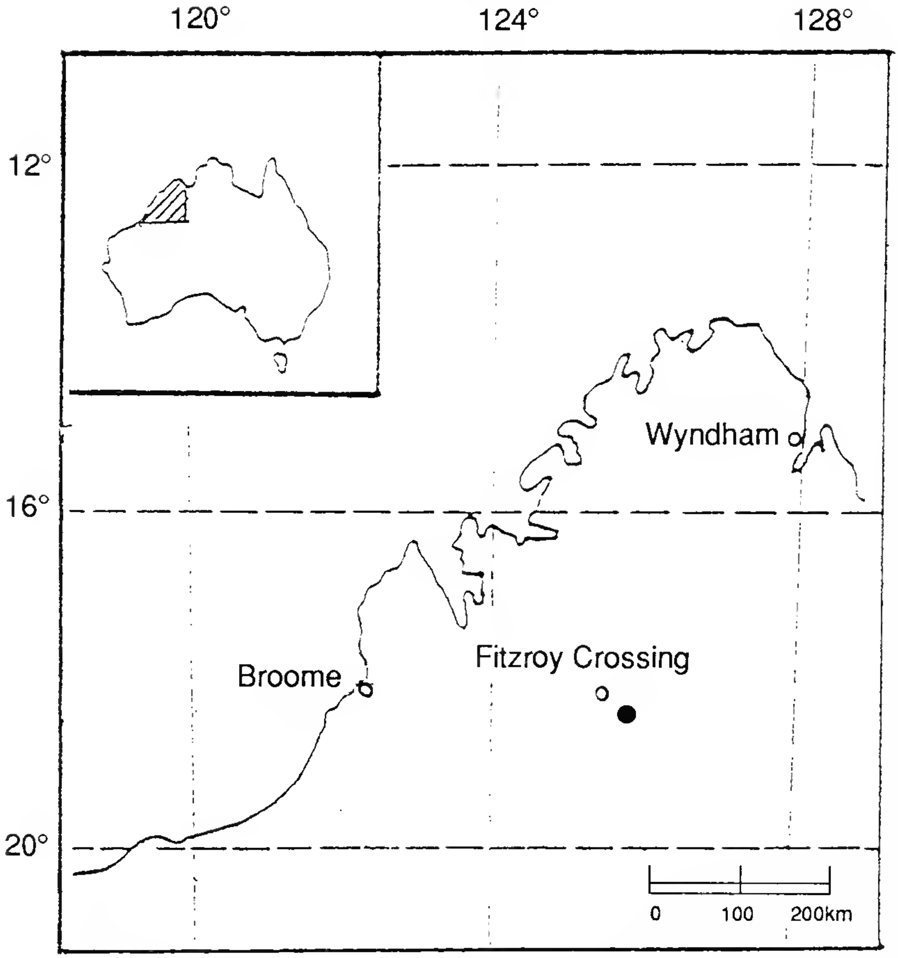


Figure 1 Map showing the locality of Early Ordovician gastropods in Canning Basin, Western Australia.

(Climacoraphistoma) vaginati (Koken and Perner) and *Seelya emanuelensis* sp. nov. The characteristic elements of this assemblage are *Peelerophon oehlerti, Pararaphistoma (Pararaphistoma) qualteriatum, P. (Climacoraphistoma) vaginati* and *Ecculiomphalus abendanoni*. The *Peelerophon oehlerti* assemblage has been found widely distributed in South America, Western Europe, Southeast Asia and Australia, from the Tremadocian to early Arenigian.

The Gap Creek Formation is about 192m (Playford *et al.* 1975) thick and consists mainly of light-brown dolomite with interbedded dolomitic sandstone and shale, which conformably overlie the Emanuel Formation and is overlain with angular unconformity by the Upper Devonian Pillara Limestone. The common Lower Ordovician fossils of the Gap Creek Formation are the brachiopod *Spanodonta hoskingiae* Prendergast, the gastropod *Teiichispira kobayashi* Yochelson and Jones and *Oriostoma? canningense* sp. nov. The associated conodonts which have been referred to Zone OCE by McTavish and Legg (1976), indicating a late Arenigian age.

DISCUSSION

The species *Peelerophon oehlerti* (Bergeron) is a characteristic form in the Emanuel Formation. The geographical and stratigraphical distribution as well as ecology of *Peelerophon oehlerti* have been discussed in detail by Jell *et al.* (1984). This species proves to be a common form in Argentina, southwestern France, western Australia, Tasmania and southern Thailand from the Tremadocian to early Arenigian. Subsequently, this species has been reported from the Ordovician of Bolivia (Babin and Branisa 1987) and southeast China

Table 1 Geographic and stratigraphic distribution of the Lower Ordovician gastropods in the Canning Basin of Western Australia.

				Formations			
Species	Western Australia		Queensland	Tasmania	Malaysia	Thailand	N.China
	Emanuel	Gap Creek	Coolibah	Florentine Valley	Setul	Thung Song	Liangchiashan
Peelerophon oehlerti (Bergeron)	X			X		X	
Bucania sp.	X						
Teiichispira kobayashi Yochelson and Jones		X	X		X		
Ecculiomphalus cf. *abendanoni* (Frech)	X						
Pararaphistoma (Pararaphistoma) qualteriatum (Schlotheim)	X						X
Pararaphistoma (Climacoraphistoma) vaginati (Koken and Perner)	X						
Oriostoma? canningense sp. nov.		X					
Seelya emanuelensis sp. nov.	X						

				Formations			
Species	S. China		SW France		Baltic region	Argentina	Bolivia
	Yinchupu	Dawan	St Chinian	La Maurerie		Cardonal	
Peelerophon oehlerti (Bergeron)	X		X	X		X	X
Bucania sp.							
Teiichispira kobayashi Yochelson and Jones							
Ecculiomphalus cf. *abendanoni* (Frech)		X					
Pararaphistoma (Pararaphistoma) qualteriatum (Schlotheim)					X		
Pararaphistoma (Climacoraphistoma) vaginati (Koken and Perner)					X		
Oriostoma? canningense sp. nov.							
Seelya emanuelensis sp. nov.							

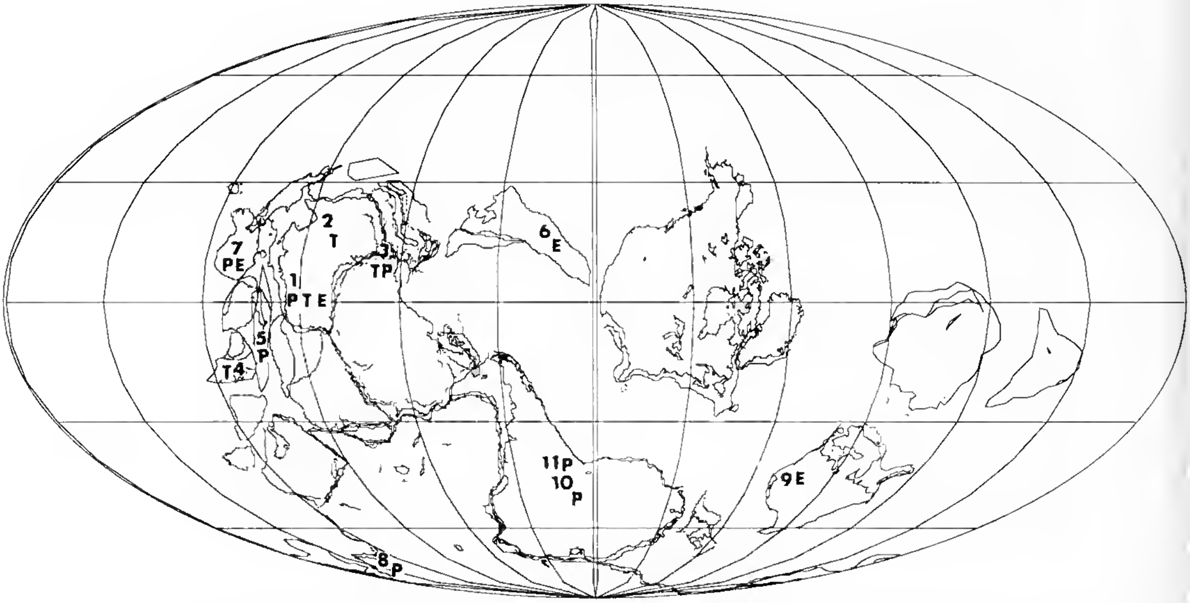


Figure 2 Paleogeographic distribution of Early Ordovician gastropod *Peelerophon* (P), *Teiichispira* (T), and *Bucania, Ecculiomphaus, Pararaphistoma* and *Seelya* (E). Continent reconstruction after Li *et al.* in Long (1993). (1) W. Australia, (2) Queensland, (3) Tasmania, (4) Malaysia, (5) Thailand, (6) N. China, (7) S. China, (8) SW France, (9) Baltic Region, (10) Argentina and (11) Bolivia.

(Yu 1989). In Bolivia, this species has been found from the Middle Ordovician (upper Llanvirnian) and in association with *Ribeiria, Ekaterodonta* and Endoceratoidea (Babin and Branisa 1987). In China, *Peelerophon oehlerti* has been recorded from the Lower Ordovician Liuxia Formation of Yuhang County, Zhejiang Province (Yu 1989). Five specimens of this species occur in the dark-grey nodular limestone, in association with the trilobites *Asaphopsis, Symphysurus, Geragnotus* and *Shumadia* and nautiloids *Ellesmeroceras* and *Proendoceas. Asaphopsis* is widely distributed in the Lower Ordovician in Himalaya, southwestern France, Argentina and Tasmania. *Geragnotus* and *Shumadia* are also reported from the Emanuel Formation.

Ecculiomphalus abendanoni (Frech) was first described from the Lower Ordovician Dawan Formation of Hubei, China (Frech 1911). Nine specimens of this species were procured at Emanuel Creek.

Of special interest is the occurrence of *Pararaphistoma (Climacoraphistoma) vaginati* (Koken and Perner) in the Emanuel Formation. This species was originally described from the Lower Ordovician of the Baltic Region (Koken and Perner 1925; Vostokova 1955) and subsequently from the Lower Ordovician La Maurerie Formation of the Montagne Noire, southwestern France (Yochelson 1982). *Pararaphistoma (Pararaphistoma) qualteriatum* (Schlotheim) is also a common form from the Lower Ordovician in the Baltic Region (Lindström 1884; Koken 1897; Koken and Perner 1925; Vostokova 1955), south Xinjiang and Hebei of China (Yu 1961), Norway (Yochelson 1962).

The gastropods of the Gap Creek Formation in the Canning Basin include *Teiichispira kobayashi* Yochelson and Jones and *Oriostoma? canningense* sp. nov. The macluritacean genus *Teiichispira* was erected by Yochelson and Jones from the Lower Ordovician Setul Formation of Langkawi Island, Malaysia in 1968, with *Teiichispira kobayashi* as its type species. This genus has been found in the Lower Ordovician of Alabama and Utah, U.S.A.; western Newfoundland of Canada (Yochelson and Jones 1968; Yochelson 1992) and Australia (Gilbert-Tomlinson in Hill *et al.* 1969; Gilbert-Tomlinson 1973; Laurie 1991) (Table 1).

Oriostoma is one of the common fossils in the Silurian and Lower Devonian, but currently, two Ordovician species have been reported from North America, these are *Oriostoma? cf. angulatum* (Wahlenberg) from the Upper Ordovician of Alaska (Rohr and Blodgett 1985) and *Oriostoma bromidensis* Rohr and Johns (1990) from the Middle Ordovician Bromide Formation of Oklahoma.

To summarize what has been mentioned above of the gastropod genera described in this paper, *Peelerophon* is only distributed around the periphery of the Early Ordovician Gondwana Supercontinent (Jell *et al.* 1984), *Teiichispria* is restricted to the tropical zones (Yochelson 1979), while *Bucania, Ecculiomphalus, Pararaphistoma* and *Seelya* may be a group of cosmopolitan genera, widespread in Europe, North America and Asia (Figure 2).

Peelerophon, Ecculiomphalus, Pararaphistoma and *Seelya* are the common gastropods in the Emanuel Formation. Among them, *Peelerophon* has coarsely lamellose growth lines and Yochelson (1982) speculated that these prominently ornamented gastropods may be shallow water dwellers. The openly coiled euomphalariacean *Ecculiomphalus* is the predominant member of this gastropod assemblage, but most specimens are poorly preserved and about 70% of the individual shells are broken, suggesting a turbulent intertidal or subtidal taphonomic environment. The turbiniform murchisoniacean *Seelya* is the largest form in the Emanuel Formation, attaining a maximum height of 37.70 mm, and well developed slit and selenizone; the morphological characters are comparable with those modern epifaunal gastropods which live on hard substrates (Peel 1977). This thick-shelled form is generally considered to have lived as benthonic creeping form within subtidal or intertidal zone. As a whole, the gastropod assemblage of the Emanuel Formation indicates a subtidal or intertidal environments. It is interesting that sedimentological evidence appears to tend to the same conclusion (McTavish and Legg 1976, p. 460).

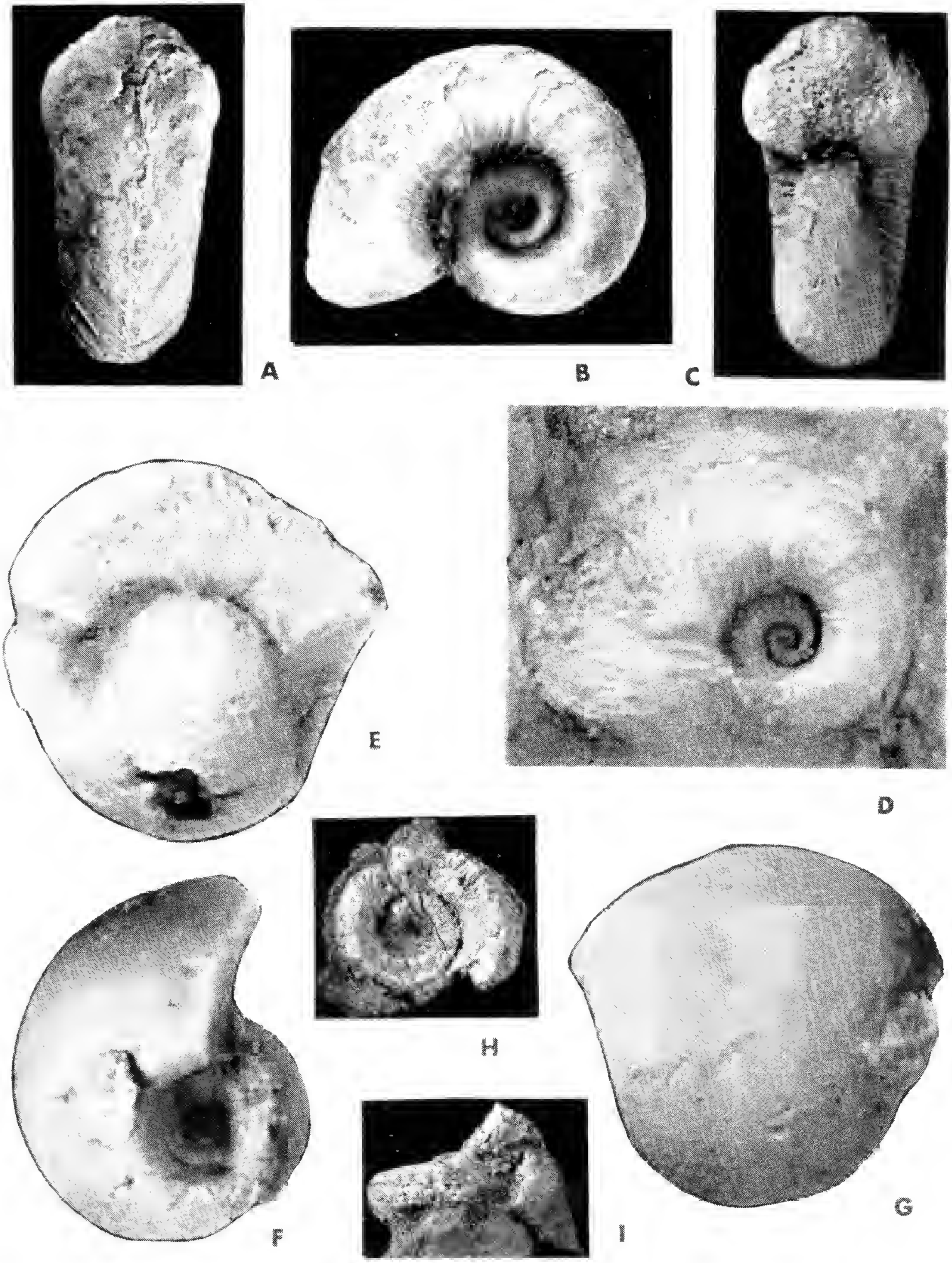
The Ordovician gastropod opercula have been widely recorded (Salter 1859; Billings 1865; Ulrich 1911; Yochelson 1957, 1966, 1975, 1979, 1986 1992; Yochelson and Jones 1968; Yochelson and Wise 1972; Rohr and Blodgett 1985; Rohr and Johns 1990), and some of them prove to be good environmental indicators. As Yochelson (1979) noted, provided with a heavy calcarous operculum, *Ceratopea* might have been an inhabitant of shallow, subtropical to tropical water. Recently, four opercula of *Teiichispira* have been obtained from the Gap Creek Formation. The operculum is heavy and elongate, and may add weight to the animal and allow it to live in more agitated water (Yochelson 1992). According to McTavish and Legg (1976), the Gap Creek Formation was formed under a predominantly intertidal or supratidal environment, as indicated by the development of desication cracks, algal lamenae, intraclastic beds, small scale crossbedding, fossil trails, erosinal truncation, scour-and-fill, abundant vertical burrows and some horizontal burrows.

SYSTEMATIC PALAEONTOLOGY

Class Gastropoda Cuvier, 1797

Subclass Prosobranchia Milne Edwards, 1848

Order Archaeogastropoda Thiele, 1925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Suborder Bellerophontina Ulrich and Scofield, 1897
Superfamily Bellerophontacea M'Coy, 1851
Family Bellerophontidae M'Coy, 1851
Genus *Peelerophon* Yochelson, 1982

Peelerophon oehlerti (Bergeron, 1889)
(Figures 3 A-D)

Bellerophon oehlerti Bergeron, 1889: 343, pl. 4, figs 10-11; Throal, 1935: 149, pl. 12, figs 4a, 4b, 5.

Oxynodiscus keideli Kobayashi, 1935: 63, pl. 11, figs 19, 20.

Oxydiscus keideli Kobayashi: Harrington, 1937: pl. 7, fig. 6.

Bucania mudanensis Kobayashi, 1937: 424, pl. 1, fig. 30.

Bucania cyrtoglypha Harrington, 1938: 136, pl. 3, figs 8, 10, 11, 13, 15, 16.

Peelerophon oehlerti (Bergeron): Yochelson, 1982: 57, pl. 14, figs 1-3, 10-14; Jell, Burett, Stait and Yochelson, 1984: 169, fig. 1; Babin and Branisa, 1987: 121, pl. 1, figs 4-6; Yu, 1989: 679, fig. 1.

Material

This species is represented by four specimens. WAM 92.285 was collected by A.W. Lindner of the University of Western Australia from the Emanuel Formation at the Emanuel Creek of West Kimberley in 1958. WAM 92.286, 92.287 and 92.288 were collected by B.F. Glenister of the University of Western Australia in 1957 from the same locality and horizon.

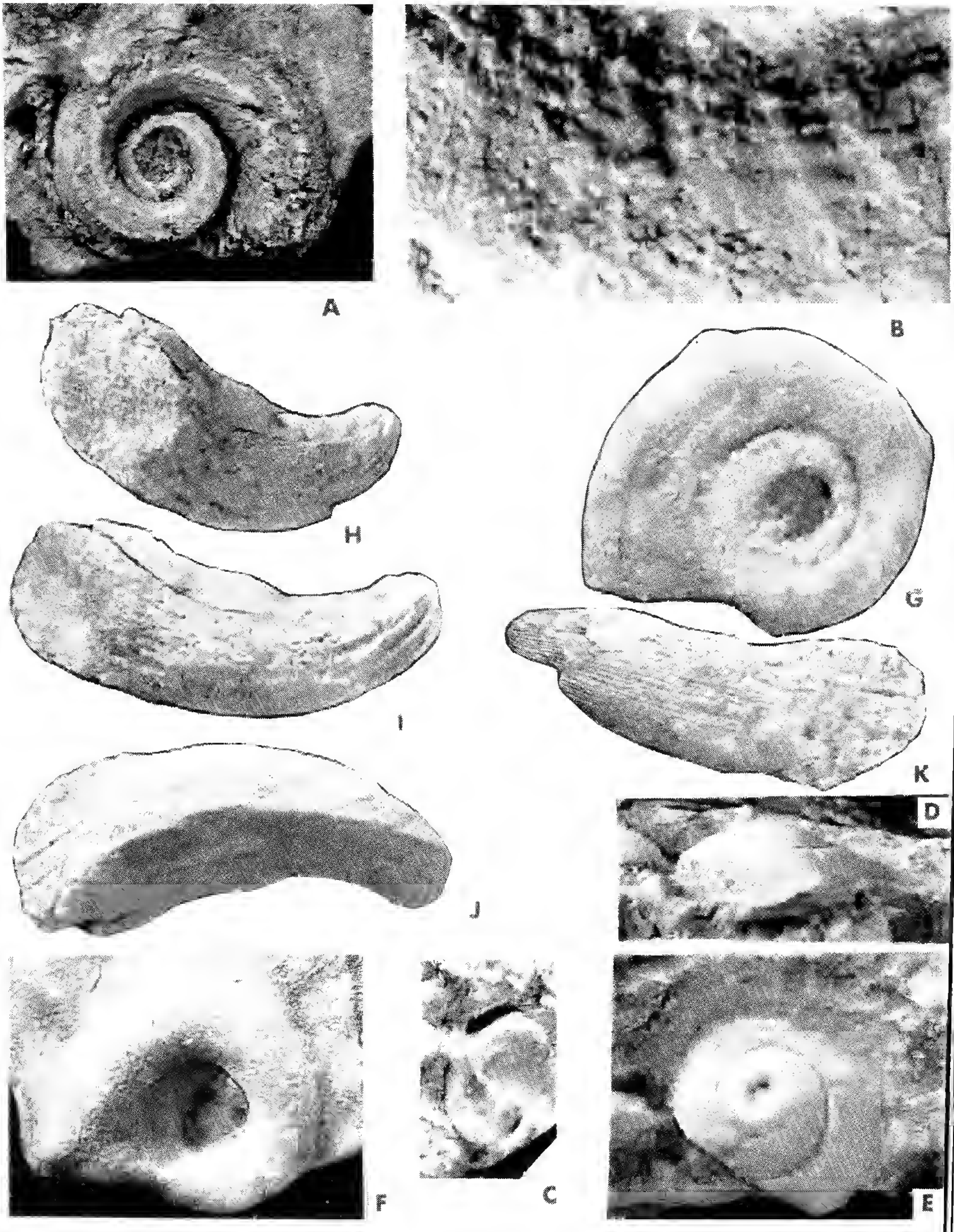
Diagnosis

Shell uniformly coiled. Whorls three to four in number with elongate elliptical sections. The dorsum gently flattened and bearing a relatively wide and concave selenizone. Umbilicus wide. Surface ornamented with lamellose growth lines.

Description

Shell of medium size, consisting of three to four whorls with elongate elliptical sections. The whorls increase regularly in size, the last whorl embracing the penultimate whorl just above periphery. The umbilicus is wide and shallow and the umbilical suture is rather impressed. The umbilical wall steeply inclined with a subangular umbilical edge, from where the surface ascends first with greatest convexity and then slopes toward the dorsum. The dorsum gently flattened, near the median selenizone, very gently concave. Selenizone rather wide and concave with distinct lunulae, and bounded by two spiral lirae. The surface of the shell is ornamented with lamellose growth lines and with fine growth lines intercalated between the lamellae. Aperture is not well-preserved, but the general form can be observed, which is subelliptical in shape.

◀ **Figure 3** **A-D**, *Peelerophon oehlerti* (Bergeron). **A-C**, WAM 92.286, Emanuel Formation, Emanuel Creek, West Kimberley, dorsal, lateral and apertural views, x 4. **D**, WAM 92.285, lateral, x 4. **E-G**, *Bucania* sp. WAM 92.289, Emanuel Formation, Emanuel Creek, West Kimberley, apertural, lateral and dorsal views, x6. **H-I**, *Oriostoma? canningense* sp. nov. WAM 92.312, paratype, Gap Creek Formation, Emanuel Creek, West Kimberley, apical and apertural views, x 1.5.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Dimensions (in mm)

	LENGTH	WIDTH	THICKNESS
WAM 92.285	13.04		10.06
WAM 92.286	11.30	6.46	10.44
WAM 92.287	10.49		8.86
WAM 92.288	11.06	5.00 approx.	10.58

Remarks

These specimens figured agree in general features with those described by the previous authors, except that the growth lines are finer.

Stratigraphic range (Australia)

Emanuel Formation. Tremadocian - lower Arenigian.

Genus *Bucania* Hall, 1847

Bucania sp.

(Figures 3 E-G)

Material

Only a small, imperfectly preserved specimen of this species was gathered (WAM 92.289). Collected by B.F. Glenister in 1957 from the Emanuel Formation at Emanuel Creek, West Kimberley.

Description

Shell of small size, compressed-subglobose, nearly as high as wide, consisting of a few whorls with semi-circular cross-section. The last whorl increases rapidly in size, embracing about one-half of the preceding one. The dorsal side is broadly rounded, the selenizone is narrow and very obscure. Umbilicus is rather wide and deep, about one-half of the diameter of the shell. Umbilical wall high and steeply inclined, with a subangular umbilical edge and exposing the inner whorls. The aperture is slightly expanded, more or less reniform, wider than high; inner lip thin, outer and lateral lips not well-preserved. The ornamentation of the shell is very poorly preserved.

◀**Figure 4** **A-B**, *Oriostoma? canningense*, sp. nov. WAM 92.311, holotype, Gap Creek Formation, Emanuel Creek, West Kimberley. **A**, apical view, x 1.5. **B**, enlargement of sculpture on the inner side of whorl, x 10. **C**, *Ecculiomphalus* cf. *abendanoni* (Frech), WAM 92.299, Emanuel Formaiton, Emanuel Creek, West Kimberley, apical view, x1. **D-F**, *Pararaphistoma (Pararaphistoma) qualteriatum* (Schlotheim). **D-E**, WAM 92.319, Emanuel Formation, Emanuel Creek, West Kimberley, lateral and apical views, x 1.5. **F**, WAM 92.320, basal view, x 1.5. **G-K**, *Teiichispira kobayashi* Yochelson and Jones. **G**, WAM 92.291, Gap Greek Formation, Emanuel Creek, West Kimberley, basal view, x2. **H-K**, WAM 92.294, oblique attachment surface, basal surface, upper surface and convex outer surface, x 2.

Dimensions (in mm)

	LENGTH	WIDTH	THICKNESS
WAM 92.289	8.57	8.96	7.48

Remarks

A definite specific name cannot at present be given to this specimen. The wide aperture and large umbilicus, suggest that it resembles some species of *Bucania*, particularly *B. sulcatina* (Emmons) from the Middle Ordovician of New York, U.S.A. but it can be distinguished by its wider aperture and more angulate umbilical edge. In some respects, this species is similar to *Bucania sublata* Ulrich and Scofield (1897, p. 888. pl. LXVI, figs 16-19), differing in the proportion between the length and width of the shell and in the cross-section, which is more or less reniform. It is also allied to *Bucania gravada* Reed (1920, p. 31, pl. VI, figs 9, 9a) from the Lower Ordovician of England, but differs from the latter in the wider dorsal surface and smaller umbilicus.

Stratigraphic range

Emanuel Formation. Tremadocian - lower Arenigian.

Suborder Macluritina Cox and Knight, 1960

Superfamily Macluritacea Fischer, 1885

Family Macluritidae Fischer, 1885

Genus *Teiichispira* Yochelson and Jones, 1968

Teiichispira kobayashi Yochelson and Jones, 1968

(Figures 4 G-K)

Teiichispira kobayashi Yochelson and Jones, 1968: 138, p. 1, figs 2-8; Kobayashi, 1984: 195; Yochelson, 1992: 1340.

Teiichispira cornucopiae Gilbert-Tomlinson, in Hill, Playford and Woods, 1969: pl. O I, figs 12, 13; Gilbert-Tomlinson, 1973: 79, pls 29-32, pl. 33, figs 1-4, 6-9, pl. 34, text-figs 2, 5, 6; Yochelson, 1992: 1340.

Material

The species is represented by four incomplete shells and four opercula (WAM 92.290, 92.291, 92.292, 92.293, 92.294, 92.295, 92.296 and 92.297). Collected by W.S. Johnson in 1987 from the Gap Creek Formation at Emanuel Creek, West Kimberley.

Diagnosis

Shell discoidal, hyperstrophic, apical cavity deep and narrow; outer whorl moderately high; operculum slightly twisted and curved, upper edge sharply angulated, consisting of many elongate tubes, each tube with a polygonal cross-section.

Description

Shell of medium size, hyperstrophic, discoidal, with broadly rounded base and deep apical cavity. It consists of about three to four rapidly increasing whorls. Apical cavity wall steep and separated by moderately shallow sutures. Outer whorl surface gently convex and gradually sloping to the basal edge. Basal edge roundly angulated. Outer part of basal whorl surface slightly rounded and then sloping to the suture. Suture well impressed. The ornamentation of the shell is very poorly preserved.

Operculum elongated, slightly twisted and curved, consisting of many elongate tubes, each tube with a polygonal cross-section. Upper edge sharply angulated. Outer surface broadly rounded and slightly curved. Juncture of outer surface and basal surface well rounded. Basal surface gently rounded. Inner surface curving upward and outward to near the midline. Attachment surface poorly preserved.

Remarks

In the round basal surface of the whorls, in the strongly curved and weakly twisted operculum, in the sharply angulated upper edge and in the roughly teardrop cross-section, this form is very closely related to *Teiichispira kobayashi* Yochelson and Jones from the Lower Ordovician Setul Formation of Malaysia, but differs from the latter in the broader size.

From the outline of the shell, the regularly increasing whorls, the arched basal surface and the general characters of the operculum, *Teiichispira cornucopiae* Gilbert-Tomlinson is possibly conspecific with the present species.

Stratigraphic range (Australia)

Gap Creek Formation. upper Arenigian.

Superfamily Euomphalacea de Koninck, 1881

Family Euomphalidae de Koninck, 1881

Genus *Ecculiomphalus* Portlock, 1843

Ecculiomphalus cf. *abendanoni* (Frech, 1911)

(Figures 4C, 5 G-H)

Raphistoma (Eccyliopterus) abendanoni Frech, 1911: 12, pl. III, figs 1 a-d.

Eccyliopterus abendanoni (Frech): Yabe and Hayasaka, 1920: 47, pl. 19, figs 7a-b.

Ecculiomphalus abendanoni (Frech): Yu, Wang and Li, 1963: 72, pl. 17, figs 1-4.

Material

Of this species there are nine internal moulds in the collection (WAM 92.298, 92.299, 92.300, 92.301, 92.302, 92.303, 92.304, 92.305 and 92.306). Collected by J. Pas in 1991 from the Lower Ordovician Emanuel Formation at Emanuel Creek, West Kimberley.

Diagnosis

Shell discoidal and openly coiled. Whorls four in number, increasing slowly in early whorls, rapidly in last one. Whorl profile subtriangular with sharp crest at upper-outer edge. Basal side widely rounded.

Description

Shell of medium size, discoidal and openly coiled. Whorls three to four in number, early whorls increasing slowly and regularly, while last one abruptly increasing in size and with a sharp angulation at upper-outer edge. The inside of the last whorl below upper angulation is slightly curved inward and inclined downward; the outer whorl surface gently convex. The basal whorl surface widely rounded, curved to join the outer whorl surface at a rounded angulation. The surface markings are not well preserved, but the faint lines of growth can be observed on the inside of the last whorl. The aperture is more or less subtriangular in shape, the outer lip is not well preserved.

Dimensions (in mm)

	WIDTH	HEIGHT
WAM 92.298	16.26	2.60 approx.
WAM 92.299	21.20	4.50
WAM 92.300	20.41	3.60 approx.
WAM 92.301	24.00	4.20
WAM 92.302	19.00	
WAM 92.303	26.84	5.60 approx.
WAM 92.304	37.40	8.32
WAM 92.305	39.71	
WAM 92.306	13.00	

Remarks

In apical view, the Australian specimens appear to be closely related to *Ecculiomphalus abendanoni* (Frech) from the Lower Ordovician Dawan Formation of Hubei, China, except that the Australian shell is smaller in size.

Ecculiomphalus, one of the openly coiled gastropods, is known to occur from the Lower Ordovician to the Silurian in North America, Europe and China. In China, eleven Ordovician species and varieties have been attributed to this genus. After making a comparison with the generic diagnosis of *Ecculiomphalus*, the species *Ecculiomphalus abendanoni* (Frech), *E. tangshanensis* (Grabau), *E. magniumbilicatus* (Endo) and *E. robustus* (Koken) may be included in this genus. The other species, such as *Ecculiomphalus sinensis* (Frech) from the Lower Ordovician Dawan Formation of Jiangsu, Hubei and Guizhou and the Lower Ordovician Quilitagh Formation of southern Xinjiang; *E. kushanensis* (Grabau), *E. solitarius* (Endo) and *E. louderbacki* (Endo) from the Lower Ordovician Machiakou Formation of North China; *E. kepintaghensis* Yu and *E. kepintaghensis* var. *similis* Yu from the Lower Ordovician Saergan Formation from southern Xinjiang and *E. dainelli* (Gortani) from the Middle Ordovician of Karakorum Mountains are characterized as having tightly coiled or advolute whorls. They are very different from *Ecculiomphalus*. For this reason, they are better placed in the genus *Lesueurilla* Koken than in *Ecculiomphalus*.

Stratigraphic range (Australia)

Emanuel Formation. Tremadocian to lower Arenigian.

Suborder Pleurotomariina Cox and Knight, 1960
Superfamily Pleurotomariacea Swainson, 1840
Family Raphistomatidae Koken, 1896
Genus *Pararaphistoma* Vostokova, 1955
Subgenus *Pararaphistoma* Vostokova, 1955

Pararaphistoma (Pararaphistoma) qualteriatum (Schlotheim, 1820)
(Figures 4 D-F)

Helicites qualteriatus Schlotheim, 1820: 103.

Pleurotomaria qualteriata Schlotheim: Lindström, 1884: 108, pl. 13, figs 15, 16.

Raphistoma qualteriatum Schlotheim: Koken, 1897: 163, fig. 19; Koken and Perner, 1925: 75-76, pl. 5, figs 1-3, 11-12.

Pararaphistoma (Pararaphistoma) qualteriatum (Schlotheim): Vostokova, 1955: 85, pl. 1, fig. 1; Yochelson, 1962: 243, pl. 1, figs 1-4.

Pararaphistoma cf. *qualteriatum* (Schlotheim): Yu, 1961: 369, pl. III, figs 8-11; Yu, Wang and Li, 1963: 66, pl. 14, figs 12-15.

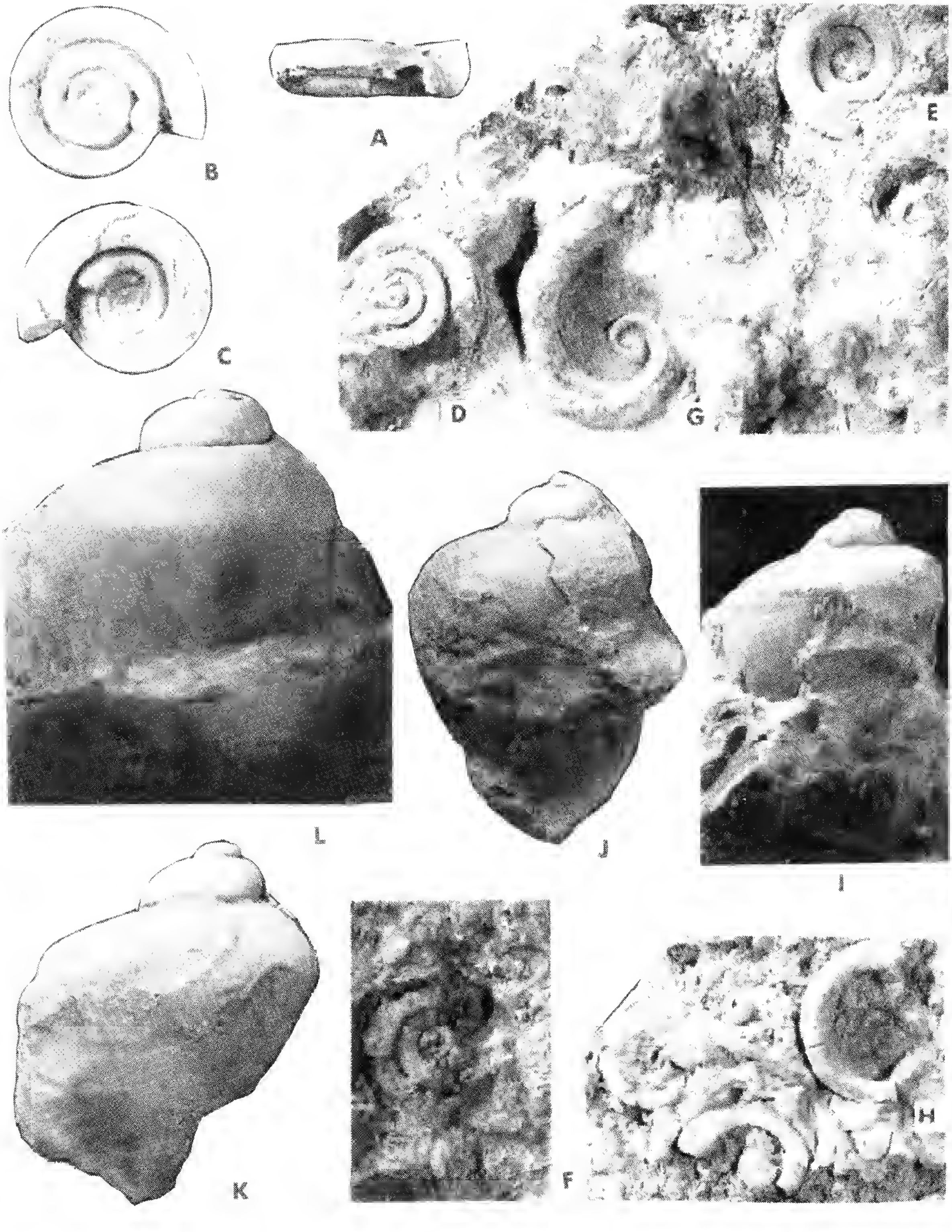
Material
This species is represented by three internal moulds. WAM 92.319 and 92.320, collected by B.F. Glenister in 1957 from the Emanuel Formation at the Emanuel Creek, West Kimberley. WAM 92.318 was collected by D. Merrilees in 1960 from the same locality and horizon.

Diagnosis
Lenticular, spire depressed-conical, early whorls increasing slowly, last one rapidly and embracing below the periphery. Upper whorl surface broadly flattened; periphery sharp; basal surface convex. Umbilicus deep and wide.

Description
Shell of medium size, lenticular, spire depressed-conical. Whorls four in number, early whorls increasing slowly and regularly, the last one enlarging rapidly and embracing the penultimate whorl below the periphery. Upper whorl surface of inner whorl is almost flat, the last one is slightly rounded, gently sloping from the suture to periphery. Periphery sharp. Suture rather deep. Lower side is convex and sloping to the umbilicus. Umbilicus deep and wide, more than one-half of the diameter of the shell. The aperture is more or less subtriangular in shape, the outer lip is rather thick but not very well-preserved. The ornamentation of the shell is very poorly preserved.

Dimensions (in mm)

	HEIGHT	WIDTH
WAM 92.318	13.41	32.71
WAM 92.319	11.32	22.50
WAM 92.320		27.60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Remarks

This form closely resembles *Pararaphistoma (Pararaphistoma) qualteriatum* (Schlotheim) from the Lower Ordovician of Western Europe and South Xinjiang, China in the general shape of the shell, particularly in the flattened upper whorl surface, except that this material is smaller.

Stratigraphic range (Australia)

Emanuel Formation. Tremadocian to lower Arenigian.

Subgenus *Pararaphistoma (Climacoraphistoma)* Vostokova, 1955

Pararaphistoma (Climacoraphistoma) vaginati (Koken and Perner, 1925)

(Figures 5 A-F)

Raphistoma vaginati Koken and Perner, 1925: 85, pl. 12, fig. 7.

Pararaphistoma (Climacoraphistoma) vaginati (Koken and Perner): Vostokova, 1955: 87, pl. 1, fig. 6; Yochelson, 1982: 58, pl. 13, figs 5-7, 10.

Material

This species is represented by five specimens (WAM 92.313, 92.314, 92.315, 92.316 and 92.317). Collected by D. Merrilees in 1960 from the Emanuel Formation at Emanuel Creek, West Kimberley.

Diagnosis

Discoidal, whorls increasing regularly and embracing at the periphery. Upper surface of all the whorls rising to the same height and with a rounded rim at the upper-outer edge. Outer surface nearly vertical. Basal surface rounded. Umbilicus wide and concave.

Description

Shell of medium size, discoidal, consisting of four whorls. Whorls increase slowly and regularly, and embracing at the periphery. The upper whorl surface of all whorls rising to the same height. Suture moderately deep. The upper side gently inclined and sloping inward towards the suture and with a rounded rim at the upper-outer edge. Outer whorl surface broadly flattened, nearly vertical. Basal surface broadly rounded. The umbilicus wide and concave, being two-thirds the diameter of the shell. Umbilical wall flattened. The inner side of the whorls in the umbilicus is flattened and separated by the deep umbilical sutures. The ornamentation of the shell is very poorly preserved.

◀ **Figure 5** A-F, *Pararaphistoma (Climacoraphistoma) vaginati* (Koken and Perner). **A-C**, WAM 92.313, Emanuel Formation, Emanuel Creek, West Kimberley, apertural, apical and basal views, x 2. **D**, WAM 92.317, apical view, x 2. **E**, WAM 92.316, Basal view, x 2. **F**, WAM 92.315, basal view, x 2. **G-H**, *Ecculiomphalus* cf. *abendanoni* (Frech). **G**, WAM 92.298, Emanuel Formation, Emanuel Creek, West Kimberley, apical view, x 2. **H**, WAM 92.301, apical view, x 1. **I-L**, *Seelya emanuelensis* sp. nov. **I**, WAM 92.307, holotype, Emanuel Formation, Emanuel Creek, West Kimberley, dorsal view, x 1.5. **J-K**, WAM 92.309, paratype, apertural and dorsal views, x 1.5. **L**, WAM 92.310, paratype, dorsal view, x 1.5.

Dimensions (in mm)

	WIDTH	HEIGHT
WAM 92.313	14.51	4.36
WAM 92.314	10.90	3.10
WAM 92.315	10.32	
WAM 92.316	10.50	2.35
WAM 92.317	10.86	3.10

Remarks

These specimens differ from *Lesueurilla* Koken, 1898, which has a hyperstrophic shell and a rounded base. In the upper surface of all whorls rising to the same height, the nearly vertical outer side and the deep and wide umbilicus, the Australian specimens appear to be closely related to *Pararaphistoma (Climacoraphistoma) vaginati* (Koken and Perner) from the Lower Ordovician of the Baltic Region and southwestern France, except that the shell lacks ornamentation.

Stratigraphic range (Australia)

Emanuel Formation. Tremadocian to lower Arenigian.

Suborder Trochina Cox and Knight, 1960

Superfamily Oriostomatacea Wenz, 1938

Family Oriostomatidae Wenz, 1938

Genus *Oriostoma* Munier-Chalmas, 1876

Oriostoma? canningense sp. nov.

(Figures 3 H-I, 4 A-B)

Material

This species is represented by two specimens (Holotype WAM 92.311 and paratype 92.312). Collected by D. Merrilees in 1960 from the Gap Creek Formation at the Emanuel Creek, West Kimberley.

Diagnosis

Discoidal, depressed-spired, phaneromphalous, whorls subcircular. Whorl surface with two spiral carinae, basal carina not well marked. Suture impressed. Covered with cancellate sculpture.

Description

Shell of medium size, discoidal, phanerompholus, composed of four to five whorls, subcircular in cross-section. The early whorls slightly depressed and increasing regularly, while the last one rapidly increasing in size. The upper whorl surface is marked by two spiral carinae, one close to the suture, the other at the whorl crest. Interspace between them is slightly concave. The inner surface is steep with about ten spiral threads and inclined to the suture. Suture is rather impressed. The outer surface is gently convex with several spiral threads and gradually sloping to the base. The basal carina is not well marked. The growth lines are steeply prosocline, crossed by spiral threads to form cancellate sculpture, especially on the inner surface (Figure 4B). The aperture is not well-preserved, but the general form can be observed, which is subcircular in shape.

Dimension (in mm)

	HEIGHT	WIDTH
WAM 92.311 (Holotype)	9.50 approx.	30.20
WAM 92.312 (Paratype)	8.71	17.67

Remarks

In apical view, this species is somewhat similar to *Oriostoma?* cf. *angulatum* (Wahlenberg) (Rohr and Blodgett 1985, p. 672, figs 2.11-2.12) from the Upper Ordovician of Alaska. This species is distinguished from the American species in the more depressed early whorls, the fewer of carinae and presence of sprial threads. In some respects, the new species also resembles *Oriostoma bromidensis* Rohr and Johns (1990, p. 733, figs 2.1-2.6) from the Middle Ordovician Bromide Formation of Oklahoma, but differs from the latter in the more depressed spire, the cancellate sculpture and in the absence of crenulate growth lines.

Etymology

The specific name is derived from that of the Canning Basin in Western Australia.

Stratigraphic range

Gap Creek Formation. upper Arenigian.

Suborder Murchisoniina Cox and Knight, 1960
Superfamily Murchisoniacea Koken, 1896
Family Plethospiridae Wenz, 1938
Subfamily Plethospirinae Wenz, 1938
Genus *Seelya* Ulrich in Ulrich and Scofield, 1897

Seelya emanuelensis sp. nov.

(Figures 5 I-L)

Material

This form is represented by four specimens. Holotype WAM 92.307 and Paratype 92.308 was collected by B. F. Glenister in 1957 from the Emanuel Formation at the Emanuel Creek, West Kimberley. Paratype, WAM 92.309, 92.310 was collected by D. Merrilees in 1960 from the same locality and horizon.

Diagnosis

Turbiniform, selenizone convex, located on periphery, bounded by two lines. Last whorl ventricose, upper whorl surface broadly rounded, slightly concave near the selenizone, lower whorl surface convexly rounded and gradually sloping to the base. Surface covered with growth lines and low spiral cords. Differs from *S. ventricosa* Ulrich *in* Ulrich and Scofield in its more convex peripheral selenizone and the shorter penultimate whorl.

Description

Shell of medium size, moderately high-spired, nucleus and early whorls are usually damaged with only the three last whorls retained. First two whorls increasing slowly and regularly, the last one increasing very rapidly and becoming ventricose especially near the aperture, and embracing the penultimate whorl below the periphery. Suture slightly impressed. Adapical whorl surface broadly rounded, gently inclined near the suture then sloping to the peripheral selenizone, but slightly concave near the selenizone. Selenizone convex, bounded by two obscure lines and located on the periphery; below the peripheral selenizone the whorl surface is slightly concave, then gradually sloping to the base. The surface of the shell is ornamented with growth lines and spiral cords. The growth lines are strong and prosocline above the selenizone and opisthocline below it. The spiral cords are not very clear but can be seen on the last whorl which is strong and low (this feature is shown in Figure 51). The aperture is not well-preserved, the outer lip is broken, the inner lip slightly curved.

Dimensions (in mm)

	WIDTH	HEIGHT
WAM 92.307 (Holotype)	24.68	26.00 approx.
WAM 92.308 (Paratype)	25.10	
WAM 92.309 (Paratype)	31.00	37.70
WAM 92.310 (Paratype)	31.20	

Remarks

In the general form of the shell, in the convex selenizone and in the ornamentation, this species is similar to the type species of the genus, *Seelya ventricosa* Ulrich (Ulrich and Scofield, 1897, p. 1009, fig. 7 C-D; Knight, 1941 p. 313 pl. 25 fig. 5; Knight et al. (in Moore, 1960, p. I295, figs 192-8) from the Lower Ordovician of Vermont, but differs in the more convex peripheral selenizone, the more flattened adapical whorl surface and the shorter penultimate whorl.

Etymology

Specific name after the Emanuel Creek where the species is found.

Stratigraphic range (Australia)

Emanuel Formation. Tremadocian - lower Arenigian.

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VARIICHTHYS, A REPLACEMENT NAME FOR THE TERAPONTID FISH GENUS *VARIA* AND FIRST RECORD OF *V. LACUSTRIS* FROM AUSTRALIA

Gerald R. Allen*

Vari (1978) revised the family Terapontidae (spelled Theraponidae or Teraponidae by some authors). These perch-like fishes inhabit the Indo-West Pacific region with 33 of 45 known species being confined to fresh waters of Australia and New Guinea. Vari provisionally assigned *Therapon jamoerensis* Mees (1971) from southern New Guinea to the genus "*Terapon*". He stated that it belonged to a new genus, but failed to describe it because of its uncertain relationships. Although he did not examine specimens of *Therapon lacustris* Mees and Kailola (1977), Vari mentioned in the addendum of his 1978 work that it was possibly the sister species of *T. jamoerensis*.

Allen (1991) eventually placed the two species in a new genus *Varia*. However, Carl J. Ferraris, Jr. of the Department of Ichthyology at the American Museum of Natural History (New York) recently informed the author that this generic name is preoccupied. Walker (1867) described *Varia* as a new genus of moths (Lepidoptera). Therefore, its use for terapontid fishes is invalid. The replacement name *Variichthys* is proposed herein.

A brief diagnosis of this genus is presented below and the first record of its presence in Australia is noted.

Variichthys, nom. nov.

Varia Allen, 1991: 128 (preoccupied by *Varia* Walker 1867, a genus of Lepidoptera).

Type species

Therapon jamoerensis Mees, 1971: 214.

Diagnosis

A genus of terapontid fishes characterised by the following combination of features: posttemporal bone covered externally with skin and scales, not expanded posteriorly, and not having a serrate posterior margin; two fin spines arising from the first proximal dorsal pterygiophore; lateral-line scale count 55-66; each jaw with a band of fixed (non-depressible), conical teeth, the outer row somewhat enlarged; dorsal rays XII to XIV, 10 or 11; anal rays III, 8 or 9; pectoral rays 14 or 15; gill rakers on first arch 5 or 6+1+10 or 11; vertebrate 11+14.

Remarks

The genus contains two species: *V. jamoerensis* (Mees), **comb. nov.** known only from Lake

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Jamur (sometimes spelled Jamoer or Yamur) in Irian Jaya (approximately 3°39'S, 134°58'E) and *V. lacustris* (Mees and Kailola), **comb. nov.** formerly thought to be confined to the Fly River Delta region of Papua New Guinea (see comments below).

FIRST RECORD OF *V. LACUSTRIS* FROM AUSTRALIA

A specimen of *V. lacustris* was recently presented to the author by Gordon Stables of Cairns, Queensland. A number of individuals were caught (all released except one) with a seine net by Mr. Stables in Twelve-Mile Lagoon, Mitchell River Drainage, Cape York Peninsula, Queensland (approximately 16°24'S, 143°09'E) in September 1992. This specimen is now deposited in the collection of the Western Australian Museum (reg. no. WAM P.30652-001). The species was previously known only from the Fly River Delta of Papua New Guinea, including the Balimo area, Morehead River, Lake Murray, and the lower Fly River (Allen, 1991). It is apparently common in Twelve Mile Lagoon in the Mitchell River system and future collecting will probably reveal a broader distribution on Cape York Peninsula.

Counts and measurements for the specimen (164.2 mm SL) from Twelve-Mile Lagoon are as follows: dorsal rays XIII,10; anal rays III,8; pectoral rays 14; tubed lateral-line scales 63; scales in horizontal row just above lateral line 73; gill rakers on first arch 6+1+10; maximum body depth 66 mm; maximum body width 28.5 mm; head length 46.0 mm; snout length 13.2 mm; upper jaw length 13.8 mm; eye diametre 11.1 mm; predorsal length 64.6 mm; prepelvic length 62.3 mm; preanal length 111.1 mm; least depth of caudal peduncle 20.8; length of caudal peduncle 32.3 mm; length of dorsal fin base 92.4 mm; longest (fourth) dorsal spine 30.2 mm; longest (first) soft dorsal ray 23.8 mm; length of anal fin base 29.5 mm; longest (second) anal spine 26.9 mm SL; longest (first) soft anal ray 26.5 mm; length of caudal fin 43.0 mm.

ACKNOWLEDGEMENTS

I thank Gordon Stables for donating the specimen of *V. lacustris* to the WAM fish collection. Special thanks are also due Carl Ferraris, Jr. for his discovery of the preoccupied status of *Varia*.

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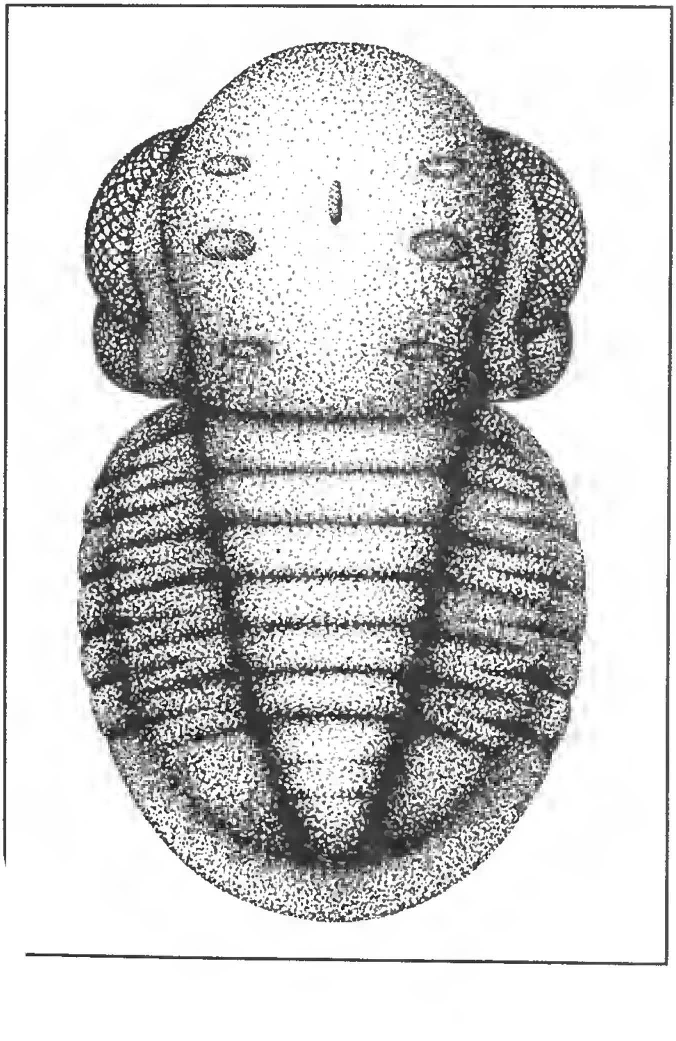

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Cover: Reconstruction of the Early Ordovician cyclopygid trilobite *Prospectatrix exquisita* from northwest China, x 5.

Illustration by Jill Ruse.

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RELATIVE ABUNDANCE AND SEASONAL CHANGES IN THE MACROZOOPLANKTON OF THE LOWER SWAN ESTUARY IN SOUTH-WESTERN AUSTRALIA

Daniel J. Gaughan* and Ian C. Potter*

ABSTRACT

Macrozooplankton, *i.e.* plankton collected with a 500 µm mesh net (Kennish 1990), was sampled in twelve consecutive months at three sites, located 0.3 (site A), 2.5 (site B) and 7.2 km (site C) from the mouth of the 7.5 km long entrance channel of the Swan Estuary. The macrozooplankton community underwent marked seasonal changes in abundance, with concentrations at particularly sites A and B increasing markedly between November and January, as water temperatures rose towards their annual maxima. Concentrations then fell precipitously at each site in February, before rising sharply again at the two downstream sites (A and B) in April. These trends reflected to a large extent those exhibited by the cladoceran *Penilia avirostris*, which contributed 80.7% to the total number of individuals collected during the study. The other main contributors were *Acartia (Acartiura)* sp. (3.4%), leucosiid (brachyuran) zoea (2.0%), the larvacean *Oikopleura dioica* (1.3%), anomuran crab zoea (1.2%), the penaeid *Lucifer hanseni* (1.1%) and the zoea of the brachyuran *Halicarcinus ovatus* (1.1%). Crustaceans contributed about three quarters of the approximately 100 species collected, with the copepods, most of which were calanoids, contributing 21 of those species. The majority of the species were marine, which accounts for the progressive decline in the concentrations of the macrozooplankton in an upstream direction, with the numbers at sites A, B and C contributing 58.0, 34.0 and 8.0%, respectively, to the total number obtained from all sites.

INTRODUCTION

The composition of the zooplankton, and occasionally also the seasonal changes in that composition, have been studied in some estuaries in eastern Australia (Kott 1955; Bayly 1965; Arnott and Hussainy 1972; Neale and Bayly 1974; Nyan Taw and Ritz 1978; Griffiths 1983). The only comparable investigations that have been carried out on the zooplankton of the estuarine waters of south-western Australia is work on the broad taxonomic groups and main species in the Peel-Harvey Estuary (Lukatelich 1987), and the various studies on the main copepod species in the Swan Estuary (Bhuiyan 1966; Hodgkin and Rippingale 1971; Rippingale and Hodgkin 1974; Rippingale 1987). Moreover, apart from limited data in two reports (Environmental Resources of Australia 1971, 1973), there is no information on the composition and seasonality of zooplankton in the inshore, coastal marine waters of this region.

Information on the composition and seasonality of zooplankton in the estuarine and marine environments in south-western Australia is crucial for constructing detailed food webs for the

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waters in this region. In this context, it is noteworthy that three of the commercially important fish species in south-western Australia, namely the anchovy *Engraulis australis*, the sandy sprat *Hyperlophus vittatus* and the Western Australian pilchard *Sardinops neopilchardus*, are zooplanktivores (Gaughan, unpublished data), and that these species are common in the estuarine as well as marine waters of this region (Loneragan *et al.* 1989; Potter *et al.* 1990).

The zooplankton has been separated into a number of categories, according to the mesh size used for collecting the samples (Kennish 1990). The zooplankton retained by 502 µm mesh are referred to as macrozooplankton. The 500 µm mesh that was used by Gaughan *et al.* (1990) to sample ichthyoplankton at three sites in the lower Swan Estuary over twelve consecutive months, yielded a large bycatch of the invertebrate components of the macrozooplankton. It should be recognized, however, that many individuals of the smaller taxa, such as *Acartia* species and the zoea of various crab species, would have tended to pass through the 500 µm mesh, and thus, in the context of the zooplankton as a whole, they would be under-represented in these samples. At the same time, however, the numbers of such taxa were still sufficiently large to provide data on the way in which their relative abundance varied seasonally and with different regions in the lower estuary.

This paper provides a semi-quantitative checklist of the taxa that were found in the macrozooplankton during twelve consecutive months of sampling in the lower Swan Estuary. It also describes the seasonal trends in abundance exhibited by both the macrozooplankton community and its major taxa, and their relationships to salinity and temperature.

MATERIALS AND METHODS

The lower region of the Swan Estuary comprises a narrow 7.5 km long channel, ranging from 200 to 600 m in width. Samples were collected monthly between May 1986 and April 1987 at sites A, B and C in the lower Swan Estuary, the mid-points of which were located 0.3, 2.5 and 7.2 km from the estuary mouth, respectively, and where the average water depth was 10 m. Full details of the location of these sampling sites and of the sampling regime are given in Gaughan *et al.* (1990).

In brief, sampling, which was carried out in the third quarter of each month, commenced 1-2 hours after sunset and was completed at all three sites within the next 1.5 hours. Samples were collected with a pair of conical nets towed behind a power boat and against the current. Each net was 2 m long and had a mouth diameter of 0.6 m. A stepwise oblique tow (Austin 1976) of 10 minutes duration was made upwards at each site from a depth of 8 m to just below the surface at a speed of *ca* 1 m s^{-1}. The volume of water filtered was measured with a flowmeter fitted in the mouth of one of the nets. The average volume of water sampled by each net was 85 m^3. The nets were washed at the end of each tow, and the samples fixed in 10% formalin and seawater. Surface and bottom salinities and temperatures were recorded at each site at the time of sampling.

Samples were sorted under a dissecting microscope and the taxa identified and counted. Due to the large numbers of organisms usually present, subsampling was carried out employing the method of Wooldridge (1977), whereby the sample was made up to a predetermined volume (500, 750 or 1000 ml) in a large beaker, through which a stream of air was passed to facilitate thorough mixing. A wide-mouthed pipette was used to extract up to five 25 ml subsamples in order to obtain at least 300 individuals of the dominant taxa in the macrozooplankton. The numbers of macrozooplankton taken by each net at each site were standardized by conversion to a concentration, *i.e.* numbers per m^3. The mean of the concentrations for the two nets at each site was then recorded. These concentrations were used to calculate the percentage contributions of the main taxa at each of the three sites to the respective total numbers of those taxa from all three sites and the contribution of all macrozooplankton taxa at each site to the total number of all those taxa.

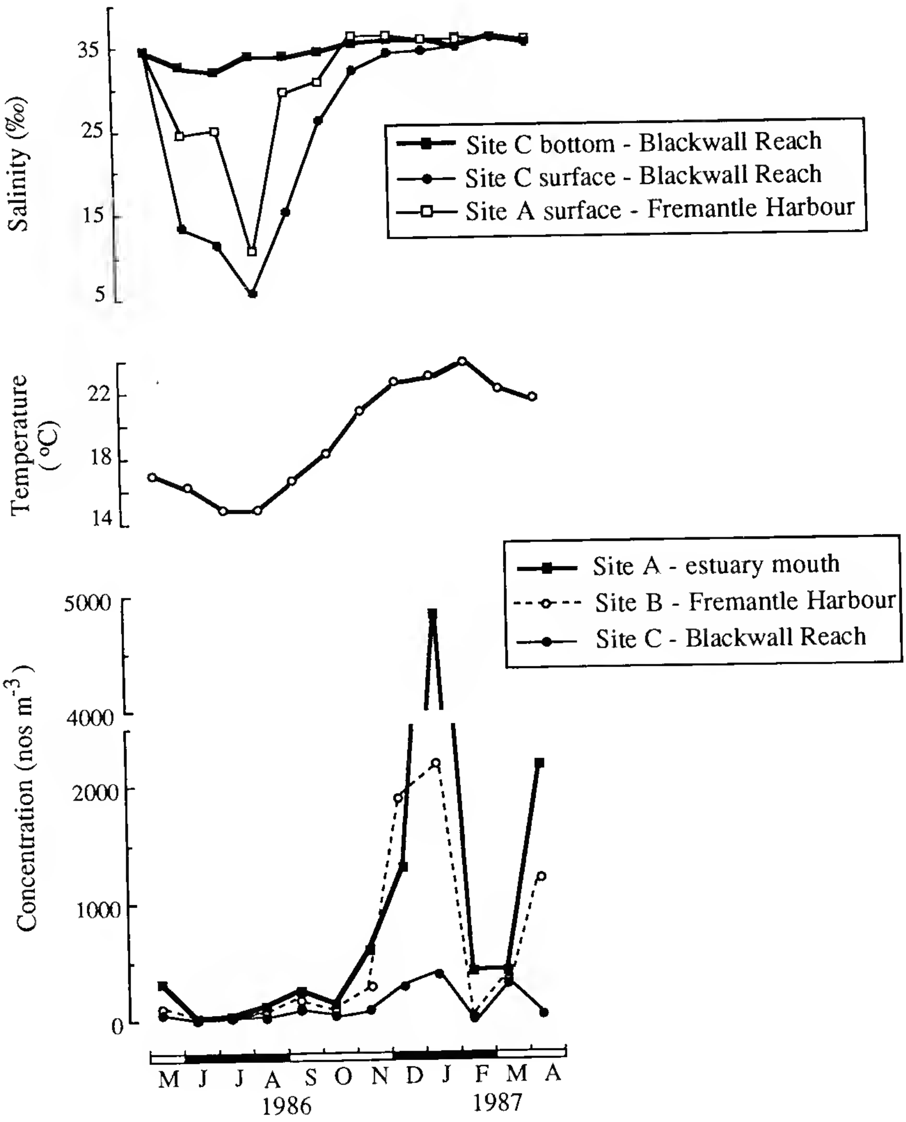

Figure 1 Salinities, water temperatures and concentrations of macrozooplankton in the lower Swan Estuary between May 1986 and April 1987. N.B. Surface salinity at site B was very similar to that at site A, and at both sites A and B the salinity at the bottom was close to 35‰ throughout the year.

RESULTS

Environmental conditions

The trends shown hy salinity and water temperatures in the lower Swan Estuary during this study are described in Gaughan *et al.* (1990). In brief, bottom salinities at each of the sites were always greater than 31‰, and were usually of full-strength seawater (35‰) at sites A and B towards the mouth of the estuary (Figure 1). During winter, *i.e.* the wet season, the surface salinity at each site, and particularly at site C, declined markedly. Thus, in August, surface salinity decreased to 10‰ at sites A and B and to as low as 5.4‰ at site C (Figure 1). At each site, the surface salinities increased during spring and by December approached 35‰.

Temperatures at the surface and the bottom of the water column at each of the three sites in any given month never differed hy more than 1°C. Mean temperatures in the lower estuary declined from 17.0°C in May 1986 to *ca* 15°C in July and August, before gradually rising to reach a peak of *ca* 24°C in February 1987 (Figure 1).

Macrozooplankton composition

Approximately 100 species were represented in the macrozooplankton of the lower Swan Estuary, of which 17 could be identified to a particular species and a further 19 to genus. The Crustacea contributed the majority (76%) of the macrozooplankton taxa in the lower Swan Estuary. Since the majority of the species could not be identified to species, they were grouped into broader groups, with the result that *ca* 60 "taxa" were enumerated in this study (Table 1).

Several of the taxa that could be identified to species or genus were recorded for the first time in south-western Australia. These included the mysids *Doxomysis* sp. and *Rhopalophthalmus* sp. Furthermore, some taxa, including *Acartia (Acartiura)* sp. and *Haplostylus* spp., were represented by undescribed species or at least by species that were new for Australia (D. McKinnon, T. Wooldridge, pers. comm.).

The most diverse group within the zooplankton in the lower Swan Estuary was the Copepoda, which comprised at least 21 species, the majority of which were holoplanktonic, *i.e.* species which spend their entire life in the plankton, and most of which were calanoids (Table 1). The Cladocera, the other main group of holoplanktonic species, contributed a further five species, of which four were marine and the fifth, a species of *Daphnia*, was derived from freshwater inflow in winter. The zoeal stages of crabs were also well represented in the macrozooplankton, with at least seven species, belonging to the Anomura and the Brachyura, being found.

Relative contributions of the dominant taxa

Seven taxa each contributed at least 1.0% to the total numbers of the macrozooplankton, which was about 1.6 million individuals, and these collectively contributed 90.8% to that total. *Penilia avirostris* was by far the dominant member of the macrozooplankton, contributing 80.7% to the total numbers. The other abundant taxa and their relative contributions to the total were *Acartia (Acartiura) sp.* (3.4%), leucosiid (brachyuran) zoea (2.0%), *Oikopleura dioica* (1.3%), anomuran crab zoea (1.2%), *Lucifer hanseni* (1.1%) and *Halicarcinus ovatus* zoea (1.1%). It should be recognised, however, that *Acartia* (*Acartiura*) sp. and leucosid, anomuran and *H. ovatus* zoea do not reach a large size and would thus not have been sampled efficiently by our 500 μm net. Thus, the above percentage contributions refer to the situation in the macrozooplankton and not to that in the water column.

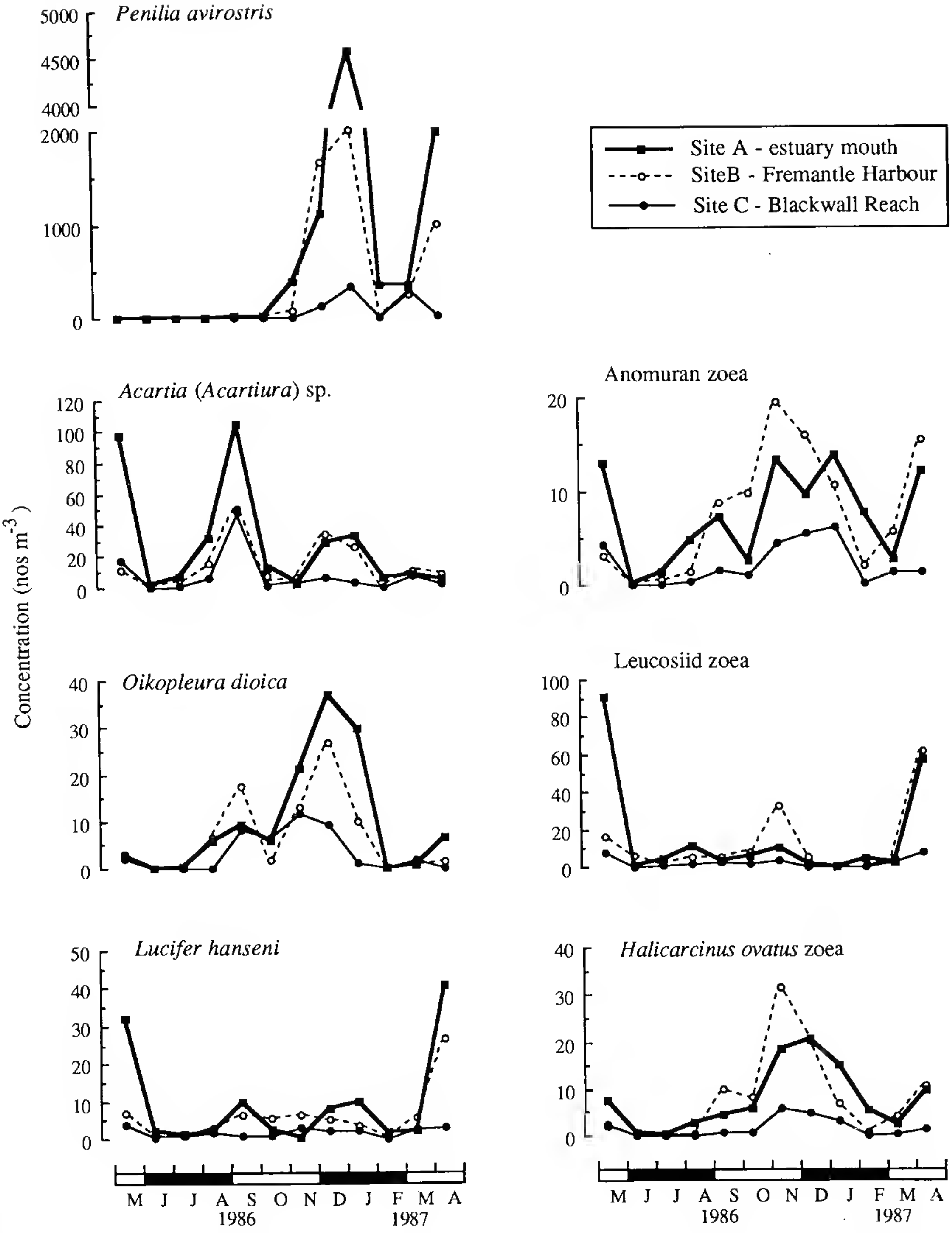

Figure 2 Monthly concentrations of the seven most abundant taxa in the macrozooplankton in the lower Swan Estuary between May 1986 and April 1987.

Table 1 Relative mean monthly concentrations of macrozooplankton in the lower Swan Estuary between May 1986 and April 1987. Concentrations (nos m^{-3}) are given as +, < 1.0; 1, 1 -19; 2, 20-99; 3, 100-999; and 4, > 1 000.

	M	J	J	A	S	O	N	D	J	F	M	A
Platyhelminthes												
Turbellaria	+		+									
Coelenterata												
Hydromedusae	1		+	1	1	+	1	1	1	1	1	1
Cubomedusae											+	
ephyra	+	+	+	+	+	+		+			+	+
Annelida												
Polychaetes												
larvae	2	+	1	1	1	1	1	1	+	1	+	+
adults	+	+	+	+	+	+	+	+		+		
Mollusca												
Gastropoda	1	+	+	1	1	1	+	+	1	1	+	1
Bivalvia		+	+	+		+			+	+	+	+
Chelicerata												
Pycnogonida	+		+	+	+	+	+	+	+	+	+	+
Crustacea												
Branchiopoda												
Cladocera												
Penilia avirostris	1		1	+	2	1	3	4	4	3	3	4
Pseudevadne tergestina	+		+	+	2	2	2	2	2	1	1	1
Evadne nordmanni							+	+				
Podon intermedius	1		1	+	2	1	2	1	1		+	1
Daphnia sp.				+								
Ostracoda	1	+	+	1	1	1	1	1	1	+	+	+
Copepoda												
Calanoida												
Acartia (*Acartiura*) sp.	2	1	1	2	3	1	1	2	2	1	2	1
Acartia sp.	1		+	1	1	1	1	1	+		1	+
Bestiola similis	+						+	1	+	+		1
Centropages australiensis	+		+	+		1	1	2	+	+	1	1
Centropages orsini												
Eucalanus sp.	+		+	+			+					+
Gladioferens imparipes	+	+	+	+	+							
Labidocera cervi	+	+	+	1	+	+	1	1	+	+	+	1
Paracalanus indicus	+	+	+	+	1	+	+		+	+	+	+
Pontellopsis sp.					+	+		+			+	+
Sulcanus conflictus	+	+	1	1				+				
Temora turbinata	1	+	1	2	2	+						
Temora discaudata	+										+	+
Tortanus spp.	1		+	+	+	+	+	+	1	+	+	1
Cyclopoida												
Oithona spp.	1		+	+	1	+	+	1	+		+	+
Corycaeus sp.	+	+	+	+	+	+	+	+	+			1
others			+	+		+	+		+		+	+

Table 1 (cont.)

	M	J	J	A	S	O	N	D	J	F	M	A
Harpacticoida												
Peltidium sp.	+	+	+	+	+	+	+					
others		+			+	+	+	+			+	
Cirrepedia												
nauplii	1		+	1	1	2	2	2	1	+	+	1
Malacostraca												
Leptostraca												
Nebalia sp.	+					+	+	+	+	+		+
Stomatopoda												
Squilla sp. antizoea						+	+	+	+		+	+
Decapoda												
Penaeidea and Caridea												
Sergestidae												
Lucifer hanseni	2	1	1	1	2	1	1	2	2	1	1	2
larvae (mysis stage)	2	1	1	2	2	2	2	3	3	1	2	2
Panulira												
phyllosoma							+	+				
Anomura												
Porcellanid zoea	+		+		+	1	1	1	1	1	1	1
other zoea	2	+	1	1	2	1	2	2	2	1	1	2
megalopae	1	+	+	1	1	+	+	1	1	+	1	1
Brachuyra												
Leucosiid zoea	3	1	1	2	1	1	2	1		1	1	3
Halicarcinus ovatus zoea	1	+	+	1	1	1	2	2	2	1	1	2
Portunus pelagicus zoea					+	+	1	1	2	2	1	+
unidentified zoea				+	1	1	2	2	2	1	1	1
Mysidacea												
Doxomysis sp.	+	+	+	+	+	+	+	+	+	+	+	+
Haplostylus spp.	+	+	+	+	+	+	+	+	+	+	+	+
Rhopalophthalmus sp.	+	+	+	+		+			+	+	1	+
juveniles	+	+	+	+	+	+	+	+	+	+	+	+
Cumacea	+	+	+	1	1	1	1	+	+	+		+
Tanaidacea	+	+	+	+	+	+	+	+	+	+	+	+
Isopoda	+	+	+	+	+	+	+	+	+	+	+	
Amphipoda												
Caprellidae	1	+	+	+	+	+	+	+	+	+	+	1
others	1	1	1	2	1	2	2	1	1	1	1	1
Echinodermata												
Ophiuroidea	+											+
Asteroidea	+											
unidentified larvae	+	+									+	+
Chaetognatha												
Sagitta spp.	1	+	+	+	+	+	1	1	+	+	+	1
Urochordata												
Ascidacea												
larvae	1	+	+	+	+	+						+
Thaliacea										+		+
Larvacea												
Oikopleura dioica	1	+	+	1	2	1	2	2	2	+	1	1

Distribution and seasonality of the macrozooplankton

It was originally intended to use the concentrations of the macrozooplankton community and its main component taxa at sites A, B and C to provide overall mean concentrations for both the community and the most abundant species in the lower Swan Estuary. However, the data in Figures 1 and 2 show that, while the seasonal trends exhibited by the concentrations at each of the three sites were very consistent, the concentrations at each site differed markedly in magnitude in certain months. Since the concentrations at the three sites are considered to reflect the relative abundances of the macrozooplankton in the different regions of the lower estuary, they have been plotted separately.

The concentrations at each site rose from less than *ca* 11 individuals m^{-3} in June 1986 to form a small peak in September and then increased markedly after October to produce a far more prominent peak in December and January. Furthermore, the concentrations of 4,834, 2,116 and 398 individuals m^{-3} recorded in January at sites A, B and C, respectively, represented the maximum annual monthly concentrations at each of those sites (Figure 1). A precipitous decline in the concentration of macrozooplankton occurred at each site in February 1987, with only 420 individuals m^{-3} being recorded at site A and less than 15 individuals m^{-3} at sites B and C. Although the concentrations of macrozooplankton subsequently increased markedly to over 1,000 individuals m^{-3} at sites A and B in April, there was no such increase at site C.

The very high concentrations of macrozooplankton at the three sites in December and January accounts for the fact that the numbers collected in these two months contributed *ca* 60% to the total number of macrozooplankton collected from the lower Swan Estuary during the twelve months of this study. Since the numbers in April contributed a further 19%, 79% of the annual total number of macrozooplankton was recorded in just three months.

Macrozooplankton was most abundant at site A in the estuary mouth in every month except December. Moreover, the concentrations of macrozooplankton were lower at site C at the upstream end of the lower estuary than at sites A or B in every month. The abundance of macrozooplankton thus decreased in an upstream direction, with the differences between the upstream site (C) and the two downstream sites (A and B) being particularly pronounced in December, January and April. The relative contribution by the numbers at sites A, B and C to the total numbers of macrozooplankton were 58, 34 and 8%, respectively (Table 2).

Table 2. The relative proportions of the total macrozooplankton and of each the seven most abundant taxa obtained from each of the three sites in the lower Swan Estuary between May 1986 and April 1987.

Taxa	Percent at site A	Percent at site B	Percent at site C
Penilia avirostris	60.4	34.4	5.2
Acartia (Acartiura) sp.	56.3	27.8	15.9
Oikopleura dioica	49.6	33.5	16.9
Lucifer hanseni	55.2	34.3	10.5
Anomuran zoea	42.4	44.7	12.9
Leucosiid zoea	53.6	38.8	7.6
Halicarcinus ovatus zoea	44.8	45.6	9.6
Total macrozooplankton	58.0	34.0	8.0

Distribution and seasonality of the main taxa

The concentrations of *Penilia avirostris*, *Acartia (Acartiura)* sp., leucosiid zoea, *Oikopleura dioica* and *Lucifer hanseni* each declined in an upstream direction. Although the concentrations of the zoea of both *Halicarcinus ovatus* and anomurans were also lowest at site C, they did not show any consistent trend to be greater at site A than at site B (Table 2). The total numbers of each of these seven abundant taxa at site A near the estuary mouth each contributed at least 42% of the total numbers of these taxa from all the sites. In contrast, the numbers of none of these seven taxa at site C at the upstream end of the lower estuary contributed more than 17% to the overall numbers of their respective taxa (Table 2).

Penilia avirostris dominated the macrozooplankton of the lower Swan Estuary from November 1986 to April 1987 and was particularly abundant at the two downstream sites, *i.e.* A and B (Figure 2). This point is emphasised by the fact that the maximum monthly concentrations of 4,500 and 2,000 individuals m^{-3} at sites A and B, respectively, which were recorded in January, were far greater than the maximum monthly concentration of 340 individuals m^{-3} at site C.

Acartia (Acartiura) sp. was present at each site in the lower Swan Estuary throughout this study and was usually more abundant towards the estuary mouth (Figure 2). However, the differences between the sites were only pronounced at the times of peak abundance in May and September, at which times this species was the numerically dominant member of the macrozooplankton.

Oikopleura dioica was present throughout the lower estuary in all months except June, and was the most abundant of those species that were not crustaceans. It was particularly abundant between November and January and, in most months, was more abundant at sites A and B than at site C. The highest concentration of *O. dioica* recorded in the lower estuary was 36 individuals m^{-3} at site A in December 1986.

Lucifer hanseni was present at all three sites in the lower Swan Estuary throughout the sampling period and was the most abundant taxon in June 1986. This species peaked in abundance in autumn (May 1986 and April 1987), when concentrations exceeded 30 individuals m^{-3} at the estuary mouth (Figure 2). *Lucifer hanseni* was usually most abundant at the estuary mouth and the maximum concentration at site C never exceeded 3.5 individuals m^{-3}.

Anomuran crab zoea were present at each site in each month of sampling, with the concentrations typically being greatest at sites A and B (Figure 2). These zoea were most abundant from November to January and in May and April. The highest monthly concentration of anomuran zoea in the lower Swan estuary during this study was 20 individuals m^{-3} at site B in November.

Leucosiid zoea were found in the lower Swan Estuary in all months except January 1987 and were usually present at each site (Figure 2). Concentrations of leucosiid zoea peaked in April and May, *i.e.* autumn, at which time concentrations greater than 55 individuals m^{-3} were recorded at either or both of sites A and B. Concentrations of leucosiid zoea were usually least at site C, where the maximum monthly concentration was 8 individuals m^{-3}.

Halicarcinus ovatus zoea were present at each site in the lower estuary in all months except June, when they were found only at site A (Figure 2). They were particularly abundant between November and January and, in most months, were more abundant at sites A and B than at site C. The highest monthly concentration of *H. ovatus* zoea recorded in the lower estuary was 31 individuals m^{-3} at site B in November 1986.

As with the above seven most abundant taxa, many of the other taxa were also present in the lower Swan Estuary for much of the year, although generally only in small concentrations (Table 1). Most of these taxa were more abundant at sites A and B near the estuary mouth than at site C at the upstream end of the lower estuary.

DISCUSSION

Composition

It must be remembered that the quantitative values given in this paper for the concentrations of the different taxa, and thus their contributions to the zooplankton community, have been derived from data collected using a 500 µm mesh. While these concentrations are valid for the macrozooplankton *sensu stricto*, they do not fully reflect the concentrations of the smaller taxa in the zooplankton as a whole. However, it is worth reiterating that the abundant smaller taxa were still well represented and that five of these taxa ranked amongst the seven most abundant taxa caught. Indeed, the composition of the holoplankton in the lower Swan Estuary was similar to that recorded in zooplankton surveys carried out in estuarine and inshore waters elsewhere in Australia, despite the fact that the mesh sizes used in the present and those other studies ranged from 158 to 500 µm (Rochford 1951; Kott 1955; Bayly 1965; Arnott and Hussainy 1972; Neale and Bayly 1974; Griffiths 1983; Kimmerer *et al.* 1985; Kimmerer and McKinnon 1985). Thus, the copepods and cladocerans that were found in the lower Swan Estuary were often represented by either the same species or at least the same genera in eastern Australian estuaries (Bayly 1975). For example, the dominant copepods in Lake Macquarie in 1954 were *Acartia clausii (cf. Acartia (Acartiura)* sp.), *Paracalanus parvus* (now *P. indicus*) and *Temora turbinata*, with other major contributors including *Centropages* spp., *Tortanus barbatus*, and *Sulcanus conflictus* (Kott 1955). Furthermore, *Penilia avirostris* and species of *Podon* and *Evadne* were also present in Lake Macquarie.

Penilia avirostris was by far the most abundant taxa in the macrozooplankton of the lower Swan Estuary, which in part reflects the fact that it is larger (Smirnov and Timms 1983) than many of the copepods. Concentrations of similar magnitude to those of *P. avirostris* in the present study were recorded in the early 1970s in Cockburn Sound, a large marine embayment 25 km to the south of the Swan Estuary (Environmental Resources of Australia 1971, 1973). Examination of samples collected with 500 µm-mesh on the southern coast of Western Australia demonstrated that *P. avirostris* was often the dominant component of the macrozooplankton in the waters of this region (Fletcher and Gaughan, unpublished data). *Penilia avirostris* was also a numerically important component of the zooplankton in Lake Macquarie and Port Hacking in eastern Australia (Kott 1955; Griffiths 1983) and has been recorded in marine embayments in Australia as far north as Shark Bay on the west coast and Moreton Bay in Queensland on the east coast (Kimmerer *et al.* 1985; Davie 1990). This cladoceran is thus widely distributed in Australia and is seasonally abundant in the nearshore waters of southern Australia. It has also been recorded in inshore marine waters of north-eastern North America and Japan (Maurer *et al.* 1978; Madhupratap and Onbé 1986).

The larval stages of benthic or bentho-pelagic crustaceans were well represented in the macrozooplankton of the lower Swan Estuary. The zoeal stages of anomuran and brachyuran crabs and the mysis-stage larvae of other decapods were relatively abundant in the plankton. Likewise, large numbers of crab zoea have previously been recorded from estuaries in Victoria, New South Wales and North America (Rochford 1951; Kott 1955; Arnott and Hussainy 1972; Maurer *et al.* 1978). The relatively small number of mysids recorded in the lower Swan Estuary contrasts with the situation in the Peel-Harvey Estuary (Lukatelich, 1987) and in many southern African estuaries, where they are one of the most abundant taxa in the zooplankton (Grindley 1981).

The most abundant species in the macrozooplankton of the lower Swan Estuary represented marine taxa. The ichthyoplankton of the lower Swan Estuary also largely consists of marine species, with the larvae of only two of the eleven most abundant species belonging to teleosts which spawn within the estuary (*cf.* Loneragan *et al.* 1989; Gaughan *et al.* 1990; Neira *et al.* 1992). This situation contrasts with the zooplankton found in the basins of the Swan and Peel-Harvey Estuaries, where the estuarine copepods *Sulcanus conflictus* and *Gladioferens imparipes* are abundant (Bhuiyan 1966; Rippingale 1987; Lukatelich 1987). This contrast emphasises that, apart from during the winter and early spring, the lower reaches of the lower estuary remain at full strength sea water throughout each tidal cycle and can thus be regarded as essentially a marine embayment.

Distribution and seasonality

The data presented in this paper clearly demonstrate that, during the present study of the lower Swan Estuary, the abundance of macrozooplankton peaked in mid-summer, and decreased upstream from the estuary mouth. Furthermore, the abundance of each of the seven most abundant taxa within the macrozooplankton also decreased in an upstream direction, which implies that these taxa originated from surrounding marine waters or within Fremantle Harbour. This conclusion is consistent with the fact that all of the major macrozooplankton species were marine.

Although the tidal amplitude in the lower Swan Estuary is small (Spencer 1956), the amount of water movement would still be sufficient to transport some planktonic organisms backwards and forwards within this part of the system. The marked decrease in abundance of the macrozooplankton in an upstream direction in the Swan Estuary presumably reflects the progressive and rapid dilution of marine water as it mixes with estuarine water after being drawn into the river by tidal action, a situation paralleling that observed for the larvae of marine teleosts in the lower Swan Estuary (Gaughan *et al.* 1990). The upstream dispersal of marine zooplankton has been recorded in estuaries elsewhere in the world (*e.g.* Ketchum 1954; Barlow 1955) and, as in the lower Swan Estuary, the intrusion of marine plankton into at least some eastern Australian estuaries is limited (Kott 1955; Nyan Taw and Ritz 1978). Bayly (1975) has also noted that, although many inshore marine and marine euryhaline species have been recorded from estuaries in eastern Australia, they are usually not numerically important within these systems.

Besides tidal transport, it is also important to recognise that, during the spring and early summer, there is an overall net upstream movement of marine water through the lower estuary as the rate of freshwater discharge declines. This movement accounts for the marked rise in salinity that occurred at particularly the most upstream site (C) during the present study. This in turn almost certainly helps account for the increase that occurred in the abundance of the predominantly marine macrozooplankton at site C during that period.

Although the trend towards an increasing abundance of macrozooplankton during the spring and early summer at the two downstream sites is paralleled by that at the upstream site, but not of course to the same degree, the same parallel was not found in April, when marked increases in the macrozooplankton at sites A and B were not recorded at site C. It is thus relevant that, by April, the salinities throughout the lower estuary had stabilised at full strength sea water (Figure 1) and there is thus no longer a net upstream movement of marine water (see also Spencer 1956).

The progressive increase that occurred in the abundance of macrozooplankton at all three sites in the lower Swan Estuary between October and January paralleled the trends in both water temperatures and surface salinities, as these variables rose towards their annual maxima over this period. The ichthyoplankton, which is likewise dominated by marine taxa, also increased in abundance over this period (Gaughan *et al.* 1990).

The marked decline in the abundance of macrozooplankton in February may have been in part related to an unusually large discharge of water from the estuary on the day of sampling, and which occurred as a result of a marked increase in barometric pressure following several days when it had been relatively low. However, since the abundance of macrozooplankton recovered only slightly in the following month, and then only at sites B and C, the relatively low concentrations in February and March are more likely to reflect a late summer decline in the abundance of macrozooplankton in the marine waters outside the estuary. The marked rise in the abundance of macrozooplankton at sites A and B in April could thus represent the type of autumnal peak in zooplankton production that occurs in temperate marine waters of the Northern Hemisphere (Heinrich 1962). The seasonal trends recorded at sites A and B contrast with those exhibited by the zooplankton in the basins of the Peel-Harvey Estuary, where the peaks occurred in winter/early spring when the density of phytoplankton was high (Lukatelich, 1987).

The limited intrusion of marine macrozooplankton through the length of the lower Swan Estuary was paralleled by the restricted intrusion of estuarine species downstream into this part of the estuary. Thus, estuarine species, such as the calanoid copepods *Gladioferens imparipes* and *Sulcanus conflictus*, which are usually restricted to waters with salinities of less than 25‰ and have been found in large numbers in the middle Swan Estuary (Rippingale and Hodgkin 1974), were recorded in the lower estuary only during winter and spring when salinities were greatly reduced. The small numbers that were present in the lower estuary at that time had presumably been transported downstream by seasonally high discharges of fresh water.

Macrozooplankton as a food source for clupeoid fishes

Sardinops neopilchardus, Engraulis australis and *Hyperlophus vittatus* are at least intermittent planktivores and each feeds on copepods and *P. avirostris*, presumably by filtering these crustaceans from the water. Certain morphological characteristics of the cladoceran *Penilia avirostris, e.g.* the large antennae which protrude forward from the body, would presumably make this species highly susceptible to capture by filtering mechanisms. The large concentrations of *P. avirostris* may therefore represent a major food source for the above clupeoids in south-western Australian waters during summer.

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AUSTRALITES FROM GINDALBIE AND MENANGINA PASTORAL STATIONS, WESTERN AUSTRALIA

W.H. Cleverly*

ABSTRACT

The Tonkin australite collection from Gindalbie and Menangina Pastoral Stations, Western Australia differs from other samples collected in the Eastern Goldfields region. Most differences can be ascribed to a small content (several percent) of australites from a small area where they had been protected from weathering and erosion during much of their terrestrial residence by shallow burial. Australites from that area (The Patch) are largely forms which consist partly or wholly of secondary glass (56.6%), lens-forms (33.3%) and cores (6.1%). The cores/lens-forms ratio is only 0.18. This material provides an insight into the likely constitution of the australite population immediately after arrival on the earth's surface.

INTRODUCTION

Gindalbie and the adjoining Menangina Pastoral Stations are centred about 30°S, 122°E, 100 km north-north-east of Kalgoorlie in the Eastern Goldfields of Western Australia. Access from Kalgoorlie is via Kanowna or Comet Vale (Figure 1).

The region has very low relief and the climate is semi-arid with mean rainfall about 210 mm/a. Drainage is internal to salt lakes. Lake Marmion, so-called "Boomerang" Lake on Menangina Station and Lake Rebecca are members of a chain of salt lakes occupying the partly choked and much modified, old age valley of a river system dating from more humid times, but now draining to south-east only after rare heavy rains.

Australites occur on the surface of the ground, especially where gravelly drifts have accumulated, in rain-wash gutters and on the margins of the salt lakes. A small area 10.5 km in direction 95° from Menangina homestead discovered by Mr R. McMeekin in 1970 is exceptional in that australites were thinly covered some time after fall by sand which became fixed by vegetation. They are now being released, a process hastened by grazing sheep. The australites from this small area, which will be designated by its colloquial name of "The Patch", include some fully flanged forms and others which are unusually small or frail for an area with such a harsh climate (Cleverly 1973).

The purpose of this paper is to describe the features of australites found on Gindalbie and Menangina Stations and to account for any peculiarities compared with other australites from the region. The largest sample available is the collection of Mr S.J. Tonkin, but as that collection is known to contain some australites from The Patch, it was desirable that further samples be examined from each of The Patch and from those parts of the stations outside it. The contributions of each to the Tonkin collection could thus be assessed. In the event, as explained in more detail below, it was not possible to obtain an acceptable sample for the country outside The Patch, and regional average figures were used instead.

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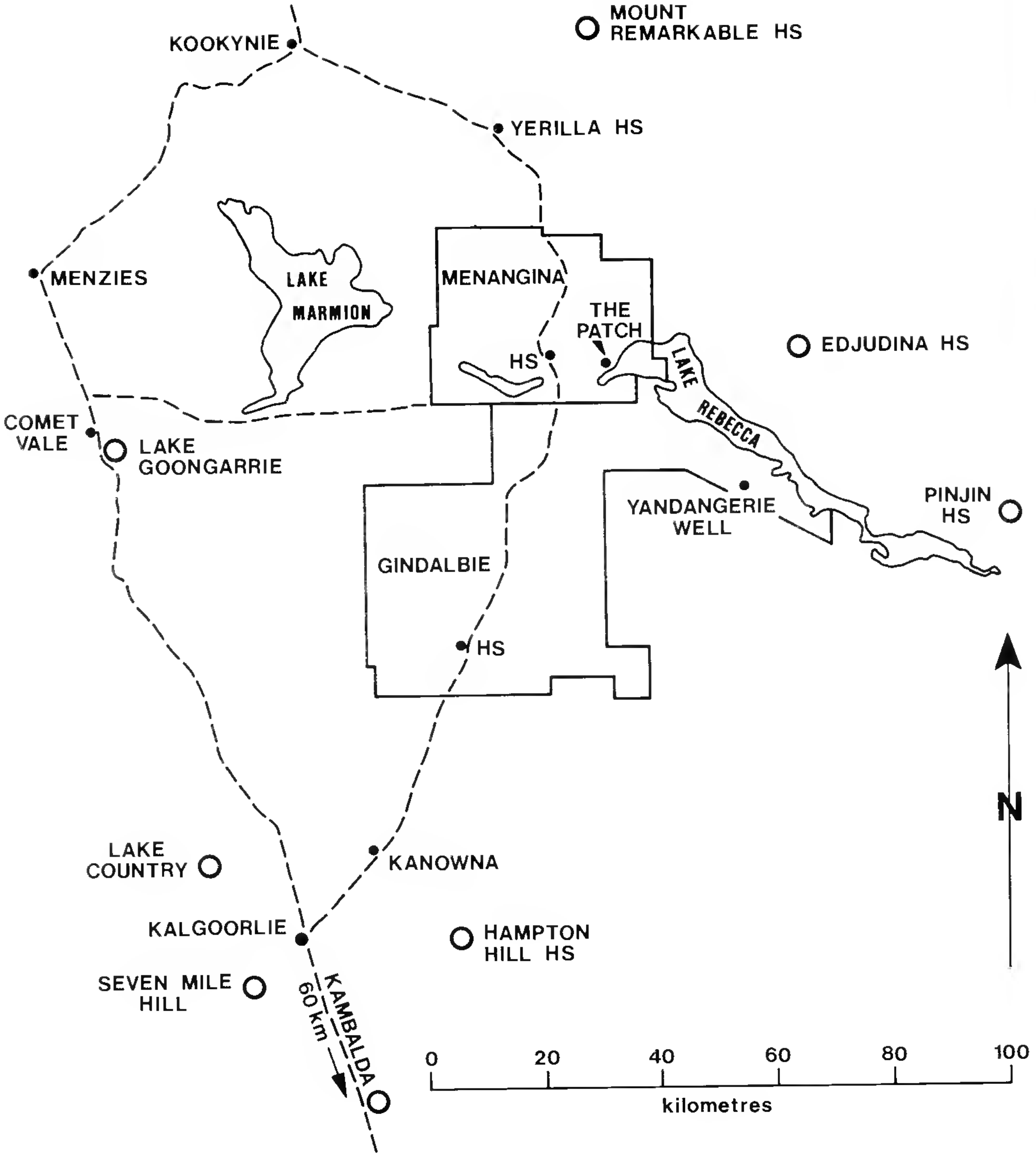

Figure 1 Map of Gindalbie and Menangina Pastoral Stations. Open circles are focal points of areas from which previous samples have been examined.

MATERIAL AND PROCEDURE

Sample 1 is the private collection of 1876 australites assembled by Mr S.J. Tonkin and family, formerly of Menangina Station. The Menangina component of the collection includes some specimens from The Patch. Many australites were collected from the fringe of Lake Rebecca north of Yandangerie Well on Gindalbie Station, and in recent years, Mr S.F. Tonkin and family have contributed further specimens from that station. Although small forms such as bowls in this sample were most likely found in The Patch, there is less certainty of attribution for larger forms such as cores. Thus the australites found in The Patch cannot be separated with confidence from those found outside it.

Sample 2 comprises 173 australites from The Patch in the Western Australian School of Mines collection. This sample is made up of the small numbers of australites released from the sand from time to time, especially after sporadic thunder-storms. It is the product of numerous close searches at intervals over more than 22 years, but is still numerically somewhat inadequate. The several hundred australites collected by the McMeekins following their discovery of The Patch are not available.

Samples 1 and 2 were classified morphologically and weighed. Extracts from the statements of morphology and weight are presented in Table 1. The system of classification and procedure are those of Cleverly (1986).

An additional 265 australites from Gindalbie and Menangina Stations dispersed in 8 collections other than the Tonkin collection were examined, but it was not possible to assemble a sufficiently large and representative sample for parts of the stations outside The Patch. The several reasons for rejection include insufficiently specified localities and unacceptably high numbers of australite flakes which are probably Aboriginal artifacts (34/59 specimens in one collection, 14/37 in another). Instead of a third sample, regional average figures were calculated (Table 1) from samples previously examined (Cleverly 1986, 1988a, 1990, 1991b, 1992). These samples were gathered from areas which encircle Gindalbie and Menangina Stations (Figure 1) and the average figures should therefore provide a norm by which Samples 1 and 2 may be judged.

The specific gravities were determined by loss of weight in pure toluene at measured temperature for 66 australites taken at random from 139 specimens from The Patch, *i.e.* from the 173 specimens of Sample 2 less the 34 specimens for which values had been determined previously (Cleverly 1973). Thus 100 values were available for australites from The Patch.

The specific gravities were determined also for 45 specifically located australites from Gindalbie Station taken at random from the 109 available in the Tillotson private collections. Together with 300 previous determinations (Cleverly 1988a, 1990, 1991b), 345 values were thus available for the country surrounding The Patch.

MORPHOLOGY OF AUSTRALITE SAMPLES

Most of the important differences between Sample 2 (The Patch) and regional average (Table 1, columns 2 and 3) can be ascribed to burial-preservation. The differences include:- the higher percentage of whole forms; the higher percentage of incomplete but classifiable forms, and thus the total of classifiable forms in Sample 2 (items 1, 2 and 3 of Table 1); the higher percentage of aberrant forms (item 13), for example the lens with anomalously transverse flow ridge would be unrecognisable as aberrant if abraded; the extremely high percentage of forms consisting wholly or partly of secondary glass (items 14 plus 15), as these

Table 1 Morphological features and mean weights of australites. Sample 1, Tonkin collection from Gindalbie and Menangina Stations. Sample 2, School of Mines collection from The Patch on Menangina Station. Regional mean and standard deviation for eight samples from the region from Cleverly (1986, 1988a, 1990, 1991b, 1992).

Item		Sample 1	Sample 2	Regional Mean	Regional S.D.
1	Whole forms or essentially so %	37.8	44.5	38.2	9.5
2	Incomplete but classifiable %	16.4	16.8	12.8	2.2
3	Total classifiable %	54.2	61.3	51.0	9.8
4	Fragments and indeterminate %	40.8	38.1	47.9	9.9
5	Flakes and flaked cores %	5.0	0.6	1.1	1.1
6	Round forms %	67.4	48.5	69.0	7.9
7	Broad oval forms %	7.7	24.2	8.2	3.5
8	Round plus broad oval forms %	75.1	72.7	77.2	4.6
9	Narrow oval forms %	7.4	7.1	7.6	2.0
10	Boat forms %	3.0	6.1	5.1	0.8
11	Dumbbell forms %	11.0	11.1	7.2	1.5
12	Teardrop forms %	3.4	3.0	3.0	1.7
13	Aberrant forms as % of classifiable	2.9	6.6	3.0	0.9
14	Flanged, disk and plate, bowl and canoe forms %	2.2	50.5	2.4	3.0
15	Indicators I %	5.0	6.1	1.7	1.4
16	Lens-forms %	57.1	33.3	60.4	11.1
17	Indicators II %	1.8	4.0	1.2	1.1
18	Cores including conical %	33.8	6.1	34.2	11.0
19	Cores/lens-forms ratio	0.59	0.18	0.61	0.27
20	Number of whole australites	709	77		
21	Mean weight of whole australites (g)	2.93	1.64	2.75	1.07
22	Total number of specimens	1876	173		
23	Mean weight of all specimens (g)	2.01	1.16	1.87	0.57
24	Number of shape types in sample	36	32		

forms are either frail or have weakly attached secondary features; the low percentage of lens-forms (item 16) and very low percentage of cores (item 18) as these are developed largely as a result of weathering (Cleverly 1986) and become eventually the predominant forms as at Goongarrie (Cleverly 1991b); the low cores/lens-forms ratio (item 19), since cores are the ultimate weathering product; the low mean weights (items 21 and 23), which follow from the abundances noted above *viz.* numerous small bowl and similar forms, fewer lens-forms than usual and even fewer cores.

One of the most distinctive features of Sample 2 is the high number (32) of shape types represented in a collection containing only 106 identifiable specimens (item 24). In general, the number of shape types in a sample from the semi-arid zone increases slowly with the numerical size of the sample (Figure 2). A perusal of published statements of morphology shows that in areas of severe erosion the odd specimen of some small or frail type will survive, possibly favoured by some special localized circumstance, and the chances of survival increase with the size of the sample. Even in the harsh conditions of Lake Yindarlgooda on Hampton Hill Station the high number of 35 shape types was represented, but the sample was of 21 927 specimens (Cleverly 1986). Seven of the shape groups in that sample were

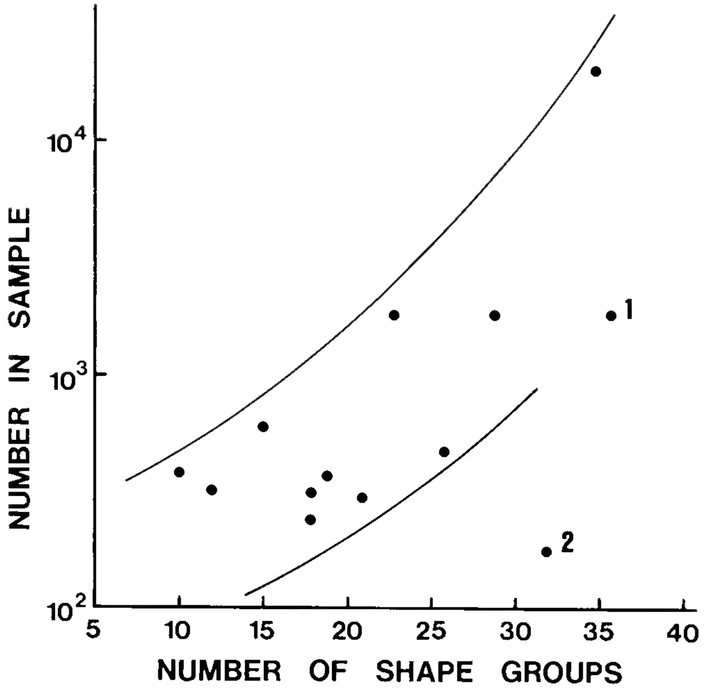

Figure 2 Scatter diagram illustrating general slow increase in number of shape groups represented with numerical size of australite samples from the semi-arid region (data from Cleverly 1986, 1988a, 1990, 1991a, 1991b, 1992). Numerals 1 and 2 indicate Samples 1 and 2 of this paper.

represented by single specimens *i.e.*, each of those groups comprised less than 0.01% of the 10 913 classified australites. Samples from the country surrounding Gindalbie and Menangina Stations plot within the general trend zone (Figure 2), but Sample 2 is uniquely isolated outside it.

The unusual australite morphology in The Patch influences Sample 1 (compare columns 1 and 3, Table 1). These influences include:- the higher percentage of classifiable forms in Sample 1 (item 3); the abundance of dumbbell forms; the lower total percentage of lens-forms (item 16) and cores (item 18), total 90.9% compared with 94.6% for the region (the inclusion of 7% of specimens from The Patch could account for this low figure); the very high number of 36 shape groups which thus plots marginally to the general trend (Figure 2). Sample 2 contains 11 shape groups which are not represented in Sample 1. The inclusion of a quantity equal to Sample 2 (173 specimens or 9%) in Sample 1 would probably have been adequate to account for the high number of shape groups present.

Some minor differences, between Sample 1 and regional average cannot be attributed to inclusion of australites from The Patch. The abundance of flakes and flaked cores (item 5) is a feature of the general area which includes Aboriginal occupation sites such as McAuliffe Soak, Carr Boyd Rocks and Cane Grass Waterhole (Cleverly and Cleverly 1985). The mean weights (items 21 and 23) are a little higher than regional average despite the presence of australites from The Patch. High mean weights are probably also a feature of the general area as they are yet higher in the Mount Remarkable area to the immediate north (Cleverly 1988a).

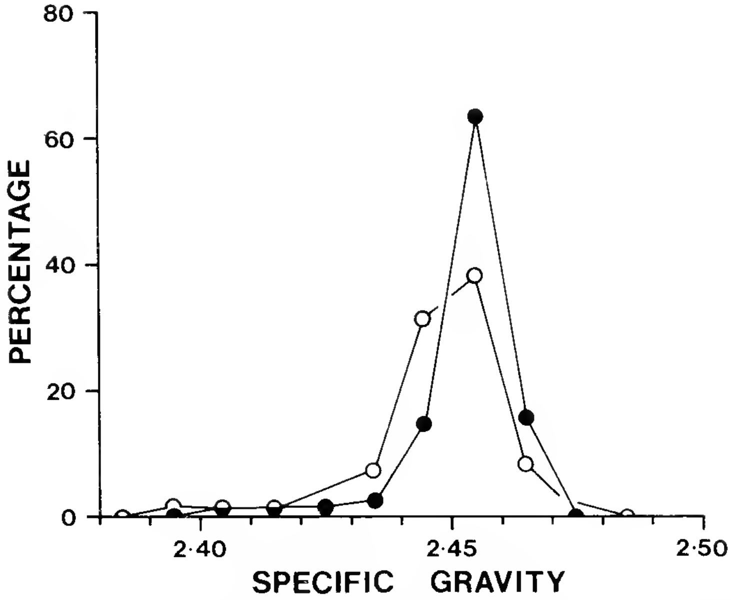

Figure 3 Frequency polygons of specific gravity for australites. Open circles: sample of 100 australites from The Patch on Menangina Station. Filled circles: composite sample of 345 australites from country surrounding Gindalbie and Menangina Stations. Simplified slightly for specific gravity values less than 2.43.

SPECIFIC GRAVITY

Numerous australites in Samples 1 and 2 show breached bubble cavities in the range 1-10 mm diameter. A few fragments suggest rare larger cavities. When a population of australites containing randomly distributed bubble cavities is reduced in size by weathering and erosion, one result is the greater spread of specific gravity values (Cleverly 1988b). The situation at Menangina is rather the reverse. Small and frail australites have survived in The Patch but most of them have been eliminated from the surrounding country. Thus the outside population tends increasingly to larger specimens which are more representative samples of a heterogeneous material and closer to average. The specific gravity frequency diagram therefore shows a larger modal percentage and smaller spread of values than for Sample 2 from The Patch (Figure 3).

The weighted mean specific gravity for 100 specimens from The Patch is 2.451 and for 100 from outside it is 2.452. The closeness of those means is taken to confirm the opinion (Cleverly 1973) that Sample 1 derives from the same regional population, now seen after different conditions of preservation.

NOTES ON SOME INDIVIDUAL SPECIMENS

Some larger australites from Gindalbie and Menangina Stations are illustrated in Figure 4. For some small forms, see Cleverly (1973).

The flanged oval (Figure 4D-F) has faintly etched, radial, secondary schlieren on the anterior surface which are just visible in oblique illumination. These schlieren are much less evident than on the "well preserved" buttons from Victoria figured by Baker (1967). Thus the oval is less severely weathered than the buttons.

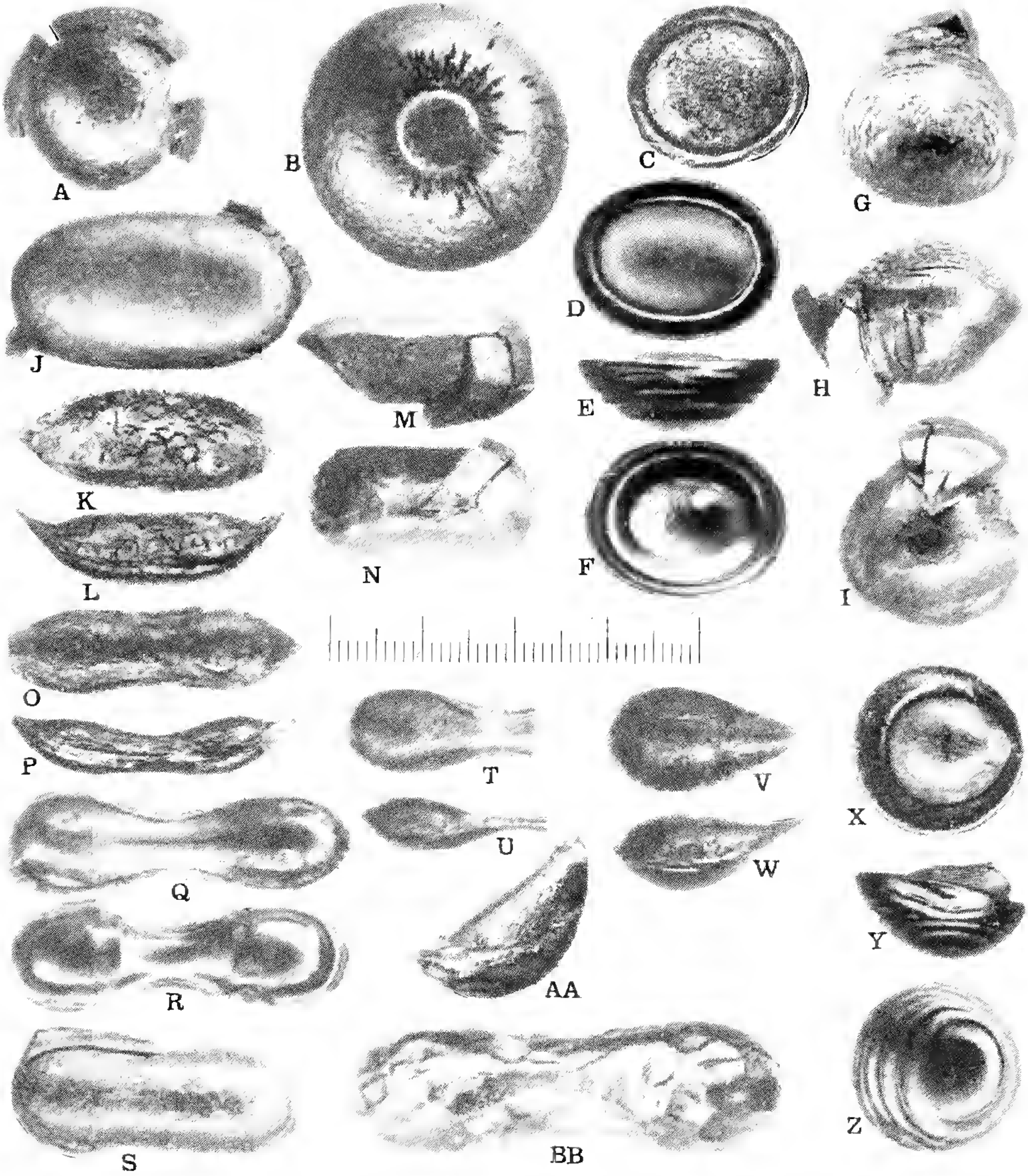

Figure 4 Australites from Gindalbie and Menangina Stations (except X, Y and Z). PS indicates posterior surface of flight, SE side elevation, AS anterior surface. SM - the W.A. School of Mines collection, T - the Tonkin private collection. Scale: centimetres and millimetres. A: PS of round indicator II, T. B: PS of round core with central bubble crater and radiating v-grooves with divided ends, T. C: PS of flanged broad oval, elongation 1.13, T. D, E and F: PS, SE and AS of flanged broad oval, elongation 1.27, private collection of W.R. Moriarty. G, H and I: PS, end elevation and AS of broad oval indicator II, SM. J: PS of narrow oval indicator I, T. K and L: PS and SE of boat-canoe, SM. M and N: SE and AS of boat-indicator II with emergent wedged core, SM. O and P: PS and SE of dumbbell - canoe, SM. Q and R: PS and AS of dumbbell-indicator I, T. S: PS of dumbbell - indicator I, SM. T and U: PS and SE of broken dumbbell-lens ex canoe, waist centre 0.8 mm thick, SM. V and W: PS and SE of flanged teardrop, SM. X, Y and Z: PS, SE and AS of flanged teardrop, Motpena, S.A., Univ. Adelaide collection. AA: SE of flanged teardrop, SM. BB: Aberrant dumbbell, orientation indeterminate, T.

One cause of variability in teardrop forms is the degree of tapering of the primary apioid, which influences the angle of inclination of the apioid axis to the line of flight during ablation stripping. An australite formed from a gently tapering apioid (Figure 4V,W) has narrow flange, too undeveloped to be backwardly rolled, and typical teardrop shape. Another example formed from a bluntly tapered apioid was oriented more steeply with a circular section normal to the line of flight. It resembles a button, but with a remnant of the apioid within the circular, backwardly curled flange instead of a remnant of sphere or oblate spheroid. A South Australian example has been illustrated (Figure 4X-Z) instead of the incomplete one from The Patch. A third variant of the flanged teardrop is shown in Figure 4AA.

The dumbbell-shaped aberrant form (Figure 4BB) resembles certain dumbbells from south-east Asia in having no defined zone of ablation or stress shell loss, and hence no evident flight orientation. There is an overall coverage of dimpled flow ridges.

CONCLUSIONS

The important differences between the Tonkin australite collection from Gindalbie and Menangina Stations and samples from the surrounding Eastern Goldfields region are accountable to a small content of australites from an area where they had been protected from destructive processes by shallow burial.

A sample of australites from that small area and a consideration of the changes which have occurred to australites in the region outside it provide an insight into the likely constitution of the australite population immediately following arrival on the earth's surface. The australites were probably predominately forms consisting of secondary glass (such as certain bowls) or having attached secondary glass (such as flanged forms). Lens forms would be poorly represented compared with present populations, being principally those small ones formed by loss of flange late in ablation flight. Cores would be even more poorly represented, being formed only from the few secondary bodies large enough to lose the stress shell spontaneously while cooling. Impact may have resulted in minor contributions to indicators I and lens-forms by damage to or loss of flanges, and contributions to indicators II and cores by fracturing of stress shells. The cores/lens-forms ratio was very low. Aberrant forms were more numerous and varied than they are now. The mean weight of complete forms was probably not much more than one gram.

Subsequently, weathering and the slow changes summed up by Cleverly (1986, Figure 3) have reduced the proportion of forms with secondary glass, sometimes to vanishing point, and increased lens-forms and ultimately cores to become the predominant forms (total 86.5% to 100% in Eastern Goldfields samples). Thus australite samples from the region are very poor representations of the original population.

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MORPHOLOGICAL VARIATION IN MALUKU POPULATIONS OF *SYCONYCTERIS AUSTRALIS* (PETERS, 1867) (CHIROPTERA : PTEROPODIDAE)

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ABSTRACT

The skull, dentary, dental and external morphology of populations of *Syconycteris australis* from Ambon, Seram, Kai, Aru, and New Guinea Islands were compared using univariate and multivariate statistics. The Ambon and Seram populations are distinct and recognised as *S. a. major* Andersen, 1911, although it may warrant recognition as a separate species. The Kai Island population is morphologically distinct from those of New Guinea but are conjoined by the Aru Island population. The taxonomic status of the Kai Island population is indeterminate.

INTRODUCTION

Andersen (1912) recognised three species of *Syconycteris*: *S. crassa* (Thomas, 1895) (Maluku islands; New Guinea and associated eastern islands, except Woodlark Island); *S. australis* (Peters, 1867) (Queensland) and *S. naias* (Andersen, 1911) (Woodlark Island). More recently *S. hobbit* Ziegler, 1982 was described from Papua New Guinea and *S. carolinae* Rozendaal, 1984 from NW Halmahera Island.

Tate (1942) reported both *S. crassa* and *S. australis* from New Guinea. However, Lidicker and Ziegler (1968), McKean (1972), Hill (in Greig-Smith 1975), Koopman (1979, 1982) and Ziegler (1982) could find no consistency with diagnostic characters used to separate these species (elongation of PM4 and M1 and presence of M^2 and M_3). Consequently *Syconycteris crassa* is currently considered a subspecies of *S. australis*. The subspecies of *S. australis* recognised by Hill (1983) are as follows (type locality in bold):

S. a. australis (Peters, 1867) - **Queensland**, Australia.

S. a. papuana (Matschie, 1899) - New Guinea; **Andai, NW New Guinea**, Aru I.

S. a. crassa (Thomas, 1895) - SE New Guinea Is; (Tobriand Is; D'Entrecasteaux Is, **Fergusson** I.).

S. a. keyensis Andersen, 1911 - **Kai** Is.

S. a. major Andersen, 1911 - **Ambon** I. and Seram I.

S. a. finschi (Matschie, 1899) - **Bismark Archipelago.**

Hill (1983: 139) considered that the subspecies of *S. australis* "seem only slightly differentiated". This observation explains why McKean (1972) synonymised *keyensis* and *finschi* with *papuana* and regarded *naias* as synonymous with *S. a. australis*. Koopman

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(1982), however, considered *finschi* a subspecies. Hill (1983: 139) suggested that *naias* from Woodlark I. is possibly synonymous with *australis* but "may prove to be another weakly separable subspecies".

There has been no study of the morphology and taxonomic status of the Maluku populations of *S. australis* since Andersen (1912). This paper reports on a univariate and multivariate analysis of the morphology of *S. australis* populations from Seram, Ambon, Kai and Aru islands, Maluku (Figure 1), and makes comparison with populations from Papua New Guinea and Irian Jaya.

MATERIALS AND METHODS

A total of 133 adult specimens (listed in specimens examined section) was examined. These were from Ambon (15), Seram (26), Dullah I. / Kai Kecil (2), Kai Besar I. (37) Wokam I. / Aru islands (13), Irian Jaya (3) and Papua New Guinea (37). The locality of these specimens is shown in Figure 1. All specimens are currently lodged in the Western Australian Museum. The specimens from Indonesia were collected during 1987-1993 by staff from the Western Australian Museum and Museum Zoologicum Bogoriense.

Seventeen measurements of skull, dentary and dental characters and 10 of external characters (all in mm) were recorded from adult specimens.

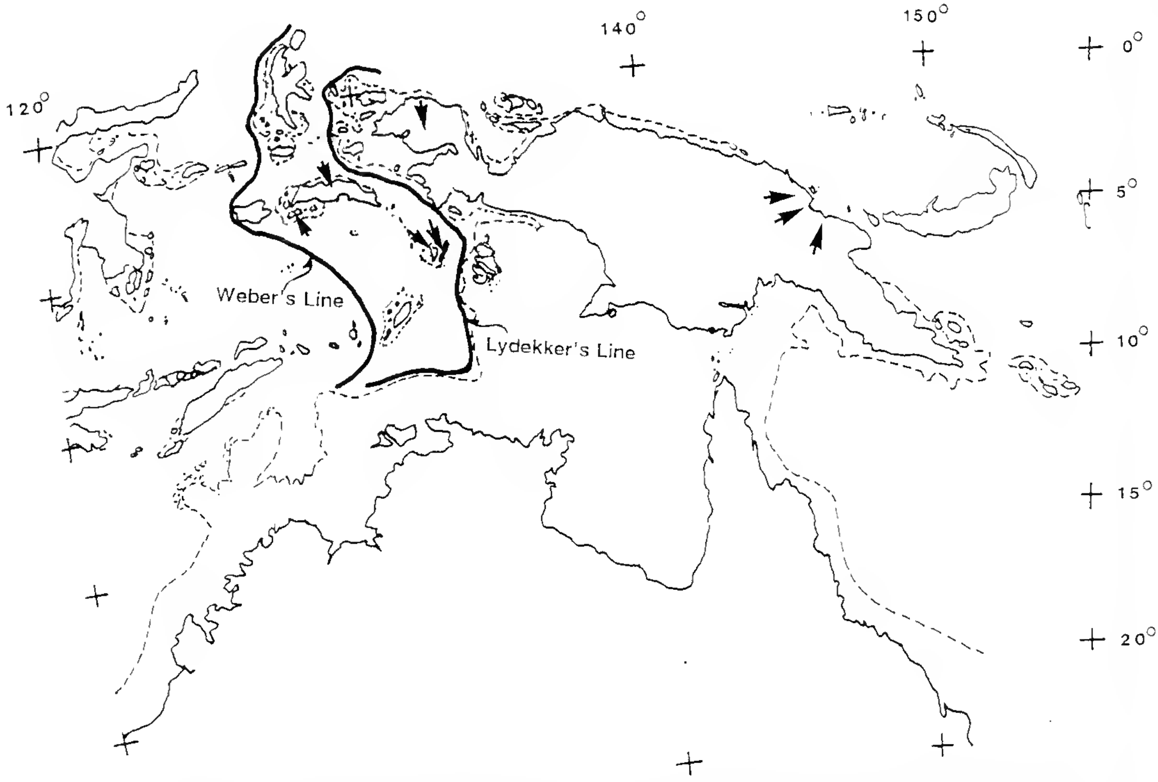

Figure 1 Localities of *Syconycteris australis* specimens used in this study. Also shown are the boundaries of the Sahul Shelf (dotted) and both Weber's and Lydekker's biogeographic lines (broad lines).

The measurements recorded follow those in Kitchener *et al.* (1993). They were (all measurement involving teeth are to alveoli): GSL, greatest skull length; CBL, condylobasal length, PIF, minimum length from posterior margin of incisive foramen to margin of posterior palate; RL, rostrum length, from anteriormost internal margin of orbit to nares; RH, rostrum height, from upper canine alveoli to level of dorsal surface of nasals; BB, braincase breadth above zygoma; ZW, zygomatic width; M^1M^1 and C^1C^1, width across M^1M^1 and C^1C^1 respectively, from the labial side; C^1M^1 and C_1M_2 upper and lower canine to last molar length; IOB, minimum interorbital breadth; POB, minimum postorbital breadth; MFW, mesopterygoid fossa width, at the widest point of the palatal flange; P^4P^4, palatal width between the lingual aspect of P^4P^4; ML, mandible length, from condyle to anteriormost point of dentary; CH, dentary coronoid height; SV, tip of rhinarium to anus length; EAR, basal notch to apex length; FA, forearm length; MC3-5, metacarpal 3,4 and 5 length. D3P1-3, digit 3 phalanx 1, 2 and 3 length and TIB, tibia length.

The skull, dentary and dental characters were measured to 0.01, while the external characters were measured to 0.1. Terminology used in the description of skull, dentary, dental and external characters follows Hill and Smith (1984).

Adults were diagnosed as those specimens with the following sutures fused: basioccipital - basisphenoid, basisphenoid - presphenoid and palatine - maxillary.

The effect of sex and island for all characters was examined by standard multiple regressions (where all effects were assessed simultaneously) for the five islands: Ambon, Seram, Kai (Kecil and Besar combined), Aru, and Papua New Guinea. Irian Jaya was excluded because of the small sample size. Examination of the residuals from regression analyses gave no indication of heteroscedasticity.

Because of the large number of interactions being tested the level of significance is taken at $P<0.01$.

A discriminant function analysis was run for skull, dentary and dental characters and external characters using all characters and a reduced set of these characters. This reduced set of characters was selected because they provided values that minimise Wilk's Lambda.

RESULTS

Univariate statistics

The sample size, mean, standard deviation, maximum and minimum values for skull, dentary, dental and external characters of the Ambon, Seram, Kai, Aru, Papua New Guinea and Irian Jaya populations are presented in Table 1a,b (males and females combined). These descriptive statistics show that the Ambon and Seram populations average larger in all skull and external measurements from the other populations, but particularly in the following:

Greatest skull length 28.83 (27.85-29.90) *v.* 25.55 (24.13-27.02), minimum length from incisive foramen posterior margin to posterior palate margin 11.74 (11.03-12.60) *v.* 10.21 (9.46-10.97); mandible length 21.55 (20.69-22.65) *v.* 18.69 (17.37-20.59); C_1M_1 length 9.50 (8.89-10.36) *v.* 8.09 (7.09-8.90), forearm length 48.2 (45.6-50.3) *v.* 42.6 (39.6-46.8) and tibia length 19.3 (17.9-20.9) *v.* 16.9 (15.0-18.3).

The multiple regression analysis of the main effects of sex and islands and the interaction between sex and island showed that the dominant effects were due to differences between the islands (Table 2). All characters were significant at $p<0.001$ between islands, except digit 3 phalanx 3 length ($F_{5,80} = 1.311$, $p=0.273$, NS) and postorbital breadth ($F_{4,80} = 4.314$, $p=0.003$).

Table 1 Measurements, in mm, for (a) skull, dentary, dental and (b) external characters (see Materials and Methods for explanation of character codes) of adult *Syconycteris australis* from Ambon Island, Seram Island, Kai Islands, Aru Islands, Papua New Guinea and Irian Jaya. N, sample size; SD, standard deviation; min., minimum; max., maximum.

Table 1a Skull, dental and dentary

LOCALITY		GSL	CBL	PIF	RL	RH	BB
AMBON	N	11	11	11	11	11	11
	MEAN	28.71	27.29	11.57	8.80	3.55	11.67
	STD	0.42	0.55	0.27	0.30	0.08	0.20
	MIN	27.97	26.49	11.03	8.40	3.46	11.44
	MAX	29.36	28.38	11.97	9.31	3.73	12.03
SERAM	N	26	25	26	26	26	26
	MEAN	28.88	27.44	11.81	9.06	3.61	11.72
	STD	0.51	0.56	0.33	0.35	0.13	0.27
	MIN	27.85	26.27	11.21	8.32	3.34	11.30
	MAX	29.90	28.60	12.60	9.80	3.87	12.29
SERAM/ AMBON	N	37	36	37	37	37	37
	MEAN	28.83	27.39	11.74	8.98	3.59	11.70
	STD	0.48	0.55	0.33	0.35	0.12	0.25
	MIN	27.85	26.27	11.03	8.32	3.34	11.30
	MAX	29.90	28.60	12.60	9.80	3.87	12.29
ARU	N	11	11	11	11	11	11
	MEAN	25.44	24.12	10.25	7.34	3.13	11.16
	STD	0.61	0.51	0.28	0.31	0.12	0.32
	MIN	24.44	23.17	9.98	6.84	2.83	10.62
	MAX	26.49	25.06	10.82	7.85	3.29	11.66
KAI	N	31	30	32	31	31	32
	MEAN	25.48	24.17	10.13	7.51	3.11	10.94
	STD	0.45	0.48	0.29	0.29	0.14	0.32
	MIN	24.45	23.17	9.49	6.78	2.82	10.39
	MAX	26.25	25.09	10.90	8.14	3.41	11.68
IRIAN JAYA	N	3	3	3	3	3	3
	MEAN	24.52	23.16	9.74	7.14	2.91	10.56
	STD	0.35	0.32	0.25	0.16	0.08	0.11
	MIN	24.13	22.81	9.58	7.00	2.82	10.46
	MAX	24.80	23.44	10.03	7.32	2.98	10.68
PAPUA NEW GUINEA	N	33	32	37	37	37	37
	MEAN	25.74	24.37	10.30	7.63	3.25	10.88
	STD	0.74	0.70	0.39	0.44	0.26	0.34
	MIN	24.14	23.03	9.46	6.71	2.75	10.04
	MAX	27.02	25.85	10.97	8.58	3.59	11.58
PAPUA NEW GUINEA/KAI/ ARU/IRIAN JAYA	N	78	76	83	82	82	83
	MEAN	25.55	24.21	10.21	7.53	3.17	10.93
	STD	0.65	0.62	0.35	0.38	0.21	0.34
	MIN	24.13	22.81	9.46	6.71	2.75	10.04
	MAX	27.02	25.85	10.97	8.58	3.59	11.68

Table 1a (cont.)

ZW	M^1M^1	C^1C^1	C^1M^1	IOB	POB	MFW	P^4P^4	ML	CH	C_1M_1
11	11	11	11	11	11	10	11	11	11	11
17.36	6.97	5.87	7.58	6.31	7.17	3.54	5.02	21.35	8.54	9.14
0.69	0.27	0.26	0.28	0.17	0.39	0.13	0.24	0.41	0.52	0.23
16.50	6.58	5.44	7.11	5.98	6.61	3.38	4.65	20.69	7.69	9.09
18.40	7.44	6.13	8.09	6.53	7.77	3.85	5.48	22.13	9.42	9.91
26	25	26	26	26	26	25	25	26	24	26
17.16	6.91	5.70	7.63	6.03	7.00	3.56	5.07	21.63	8.57	9.54
0.64	0.27	0.23	0.28	0.34	0.45	0.14	0.32	0.48	0.44	0.34
15.97	6.49	5.22	7.17	5.42	6.16	3.35	4.39	20.71	7.86	8.89
18.25	7.49	6.21	8.20	6.53	7.91	3.86	5.63	22.65	9.50	10.36
37	36	37	37	37	37	35	36	37	35	37
17.22	6.93	5.75	7.62	6.11	7.05	3.56	5.05	21.55	8.56	9.50
0.65	0.27	0.25	0.27	0.32	0.43	0.14	0.29	0.47	0.46	0.31
15.97	6.49	5.22	7.11	5.42	6.16	3.35	4.39	20.69	7.69	8.89
18.40	7.49	6.21	8.20	6.53	7.91	3.86	5.63	22.65	9.50	10.36
11	11	11	11	11	11	11	11	11	11	11
15.34	6.24	4.98	6.68	5.20	6.69	3.27	4.54	18.86	7.11	8.24
0.43	0.20	0.23	0.27	0.24	0.28	0.17	0.19	0.41	0.33	0.23
14.40	5.94	4.78	6.20	4.91	6.28	3.04	4.19	18.08	6.67	7.85
16.05	6.60	5.36	7.09	5.57	7.24	3.59	4.79	19.52	7.67	8.62
30	32	32	32	31	31	28	32	32	32	30
15.21	6.06	4.96	6.63	5.55	6.76	3.24	4.45	18.59	7.20	8.03
0.53	0.23	0.22	0.24	0.27	0.38	0.11	0.21	0.43	0.36	0.23
14.10	5.56	4.49	5.90	4.95	5.89	2.98	4.06	17.50	6.55	7.55
16.11	6.48	5.36	6.99	5.94	7.44	3.52	4.97	19.43	8.16	8.40
3	3	3	3	3	3	3	3	3	2	3
13.44	5.53	4.44	5.95	4.61	6.55	3.15	4.06	17.57	5.57	7.43
0.19	0.12	0.10	0.16	0.17	0.39	0.11	0.11	0.29	0.25	0.33
13.31	5.40	4.36	5.80	4.44	6.12	3.06	4.00	17.37	5.39	7.09
13.66	5.62	4.56	6.12	4.78	6.88	3.27	4.19	17.90	5.75	7.74
37	36	37	37	37	37	37	37	36	36	36
14.72	6.21	4.94	6.68	5.13	6.70	3.41	4.49	18.81	6.81	8.16
0.83	0.41	0.35	0.50	0.45	0.39	0.20	0.29	0.77	0.44	0.52
13.06	5.19	4.16	5.80	4.34	5.80	2.92	3.89	17.52	6.14	7.11
16.13	6.87	5.52	7.53	5.93	7.79	3.89	5.03	20.59	7.74	8.90
81	82	83	83	82	82	79	83	82	81	80
14.94	6.13	4.94	6.53	5.28	6.72	3.32	4.47	18.69	6.97	8.09
0.77	0.35	0.30	0.42	0.43	0.37	0.19	0.26	0.64	0.48	0.42
13.06	5.19	4.16	5.80	4.34	5.80	2.92	3.89	17.37	5.39	7.09
16.13	6.87	5.52	7.53	5.94	7.79	3.89	5.03	20.59	8.16	8.90

Table 1b Externals

LOCALITY		SV	EAR	FA	MC3	D3P1	D3P2	D3P3	MC4	MC5	TIB
AMBON	N	11	11	11	11	11	11	11	11	11	11
	MEAN	61.8	16.5	47.8	38.1	27.0	30.3	0.6	37.7	38.0	19.5
	STD	2.6	0.6	1.7	1.3	1.2	1.3	0.2	1.5	1.5	1.0
	MIN	57.2	15.3	45.6	36.1	25.8	28.3	0.3	35.1	35.8	17.9
	MAX	65.4	17.3	50.3	40.3	29.1	31.9	1.1	40.2	40.6	20.9
SERAM	N	23	23	23	23	23	23	23	23	23	23
	MEAN	63.3	16.9	48.5	38.4	27.2	30.8	0.7	38.1	38.9	19.2
	STD	3.7	0.6	1.0	0.9	0.8	1.0	0.2	0.6	0.9	0.5
	MIN	55.3	16.0	46.7	36.7	25.9	28.3	0.2	37.0	37.2	18.2
	MAX	70.0	17.8	50.0	40.0	28.5	32.6	1.0	39.4	40.7	20.1
AMBON/ SERAM	N	30	30	30	30	30	30	30	30	30	30
	MEAN	62.8	16.8	48.2	38.3	27.2	30.6	0.7	38.0	38.6	19.3
	STD	3.4	0.6	1.3	1.1	0.9	1.1	0.2	1.0	1.2	0.7
	MIN	55.3	15.3	45.6	36.1	25.8	28.3	0.2	35.1	35.8	17.9
	MAX	70.0	17.8	50.3	40.3	29.1	32.6	1.1	40.2	40.7	20.9
ARU	N	11	11	11	11	11	11	11	11	11	11
	MEAN	53.1	15.4	42.6	33.0	23.4	26.6	0.6	32.8	33.6	16.5
	STD	4.2	0.7	1.3	1.0	0.8	1.1	0.1	1.1	1.0	0.7
	MIN	48.4	14.1	41.3	31.7	22.5	25.4	0.5	31.5	31.8	15.6
	MAX	62.3	16.2	44.7	34.5	25.0	28.8	0.9	34.9	35.4	17.6
KAI	N	30	30	30	30	30	30	30	30	30	30
	MEAN	54.5	15.3	42.0	33.1	23.7	27.1	0.6	32.6	32.7	16.6
	STD	2.9	1.0	1.0	0.9	0.9	1.2	0.2	0.9	1.2	0.6
	MIN	48.8	14.0	39.6	31.6	21.9	24.3	0.2	34.6	30.7	15.0
	MAX	60.8	17.8	43.9	35.1	26.1	29.7	1.1	34.5	35.6	17.6
IRIAN JAYA	N	3	3	3	3	3	3	3	3	3	3
	MEAN	49.8	15.4	41.5	32.2	23.9	25.2	0.7	31.5	31.4	17.4
	STD	5.2	0.1	0.9	0.1	0.6	0.9	0.2	0.3	0.4	0.6
	MIN	45.5	15.3	40.6	32.2	23.2	24.3	0.5	31.2	31.0	16.8
	MAX	55.6	15.5	42.3	32.3	24.4	26.0	0.8	31.8	31.8	18.0
PAPUA NEW GUINEA	N	36	36	36	36	36	36	36	36	36	36
	MEAN	52.1	16.5	43.2	33.6	24.1	26.9	0.6	33.0	33.2	17.2
	STD	3.5	0.7	1.4	1.2	0.8	1.4	0.2	1.4	1.8	0.7
	MIN	45.4	15.2	40.3	30.9	22.3	24.4	0.2	29.8	27.6	15.5
	MAX	63.6	18.0	46.8	36.1	25.6	29.5	1.0	35.5	36.4	18.3
ARU/KAI/ IRIAN JAYA/ PAPUA NEW GUINEA	N	80	80	80	80	80	80	80	80	80	80
	MEAN	53.0	15.8	42.6	33.3	23.9	26.9	0.6	32.8	33.0	16.9
	STD	3.6	1.0	1.4	1.1	0.9	1.3	0.2	1.2	1.5	0.7
	MIN	45.4	14.0	39.6	30.9	21.9	24.3	0.2	29.8	27.6	15.0
	MAX	63.6	18.0	46.8	36.1	26.1	29.7	1.1	35.5	36.4	18.3

The only characters that differed significantly ($p<0.01$) between the sexes were braincase breadth ($F_{1,80} = 10.871$, $p=0.001$), distance outside the upper canines ($F_{1,80} = 12.984$, $p=0.001$) and tibia length ($F_{1,80} = 10.255$, $p=0.002$). There were no significant interactions between sex and island.

Canonical variate (discriminant) analysis

Both sexes were combined for these analyses after excluding the characters that were shown above to be sexually dimorphic (BB, C^1C^1 and TIB).

The analysis was carried out separately for skull (plus dentary and dental) and external characters on the remaining 14 skull and 9 external characters, using the islands (Ambon, Seram, Kai, Aru and Papua New Guinea) as the *a priori* groupings; Irian Jaya was unallocated because of its small sample size (N=2). The association between these islands in discriminant function space was very similar for both skull and external characters.

The analysis was run for the 23 skull and external characters using the island groupings above (Irian Jaya unallocated) and again for a reduced set of seven characters (greatest skull length, GSL; rostrum height, RH; interorbital breadth, IOB; cranial height, CH; upper canine to M^1 length, C^1M^1; ear length, EAR and digit 3 phalanx 1 length) that were selected to minimise the values of Wilk's lambda. The reduced set of seven characters gave a very similar

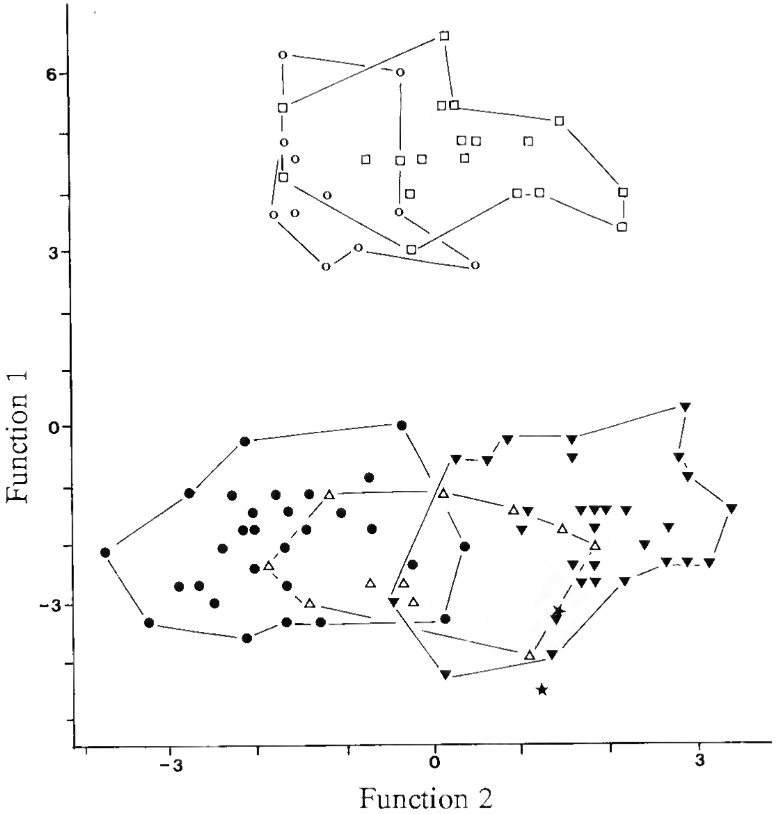

Figure 2 Canonical variate (discriminant) plots of functions 1 and 2 for male and female adult *Syconycteris australis* grouped by locality: Ambon Island (○), Seram Island (□), Kai Island (●), Aru Island (Δ), Papua New Guinea (▼) and Irian Jaya (★).

Table 2 Multiple regressions on sex and localities of *Syconycteris australis* (Ambon Island, Seram Island, Kai Islands, Aru Islands, Papua New Guinea) for skull, dentary, dental and external characters. F values are presented for the main effects and their interaction. For explanation of character codes see Materials and Methods section. Significance levels are *, $0.05>p>0.01$; **, $0.01>p>0.001$; ***, $p<0.001$.

	Main Effect		**Interaction**
Character	**sex**	**island**	**sex. island**
GSL	0.006	144.465***	1.056
CBL	0.091	130.384***	0.818
PIF	2.076	93.448***	0.326
RL	0.244	78.306***	1.169
RH	1.418	24.982***	0.082
BB	10.871**	30.616***	0.481
ZW	4.396*	9.322***	0.192
M^1M^1	0.005	28.750***	0.164
C^1C^1	12.984**	43.431***	0.824
C^1M^1	0.179	42.885***	0.099
IOB	0.034	25.693***	0.248
POB	0.418	4.314**	0.473
MFW	6.439*	14.505***	0.929
P^4P^4	0.218	22.875***	0.118
ML	1.158	111.063***	0.643
CH	4.828*	52.122***	1.463
C_1M_1	0.933	61.032***	0.181
SVL	0.800	37.461***	0.257
EAR	0.317	15.819***	0.434
FA	1.108	92.887***	2.718*
MC3	0.203	108.445***	2.747*
D3P1	1.691	68.632***	2.249
D3P2	0.008	38.256***	1.165
D3P3	5.520*	1.311	1.418
MC4	1.342	102.280***	2.260
MC5	0.433	68.099***	1.269
TIB	10.255**	66.793***	2.933
Degrees of freedom	1,80	4,80	4,80

pattern of association between these islands in discriminant function space. Because the total number of characters (23) greatly exceeds the sample size in these island groupings (e.g. Aru, N=11 - Irian Jaya is unallocated), the DFA presented and discussed below is that for skull and external characters using the reduced set of seven characters.

The DFA produced three significant functions, with function 1 explaining 80.2% of the variation; function 2, 17.9% and function 3, 1.5%.

The plot of functions 1 and 2 (Figure 2) shows two distinct groupings: first, Ambon and Seram and secondly, Kai, Aru and Papua New Guinea - with the unallocated Irian Jaya clustering close to Papua New Guinea. There are no misclassifications of individuals between these two broad groupings. These two broad groupings separate on function 1. The only character with DF coefficients loading heavily (>0.5) on function 1 is greatest skull length (Table 3), suggesting that it is overall skull size that differentiates these two broad groups. There appears also to be subtle shape differences in the skull of the Ambon and Seram animals, compared to those of Kai, Aru, Papua New Guinea and Irian Jaya. For example, both their condylobasal length is greater relative to C^1M^1 length (Figure 3) and greatest skull length is greater relative to mesopterygoid fossa width (Figure 4). Within these broad groups the clusters for Ambon and Seram broadly overlap (Figure 2), with a total of 22% of individuals misclassified between Ambon and Seram.

Within the second group (Kai, Aru and Papua New Guinea) the Kai population is separate in DFA space from that of Papua New Guinea, with only 1 out of 60 (2%) of individuals misclassified between these two populations. The Aru population, however, overlaps both the Kai and Papua New Guinea populations. Of the 11 Aru individuals, one was misclassified to the Kai population and two to the Papua New Guinea population (a total of 27.3% misclassified). The separation between the Kai and Papua New Guinea populations was on function 2 (Figure 2). The characters with DF coefficients loading heavily (>0.5) on function 2 were interorbital breadth (0.99), rostrum height (0.85) and ear length (0.59) (Table 3), suggesting that subtle differences in skull shape and ear length partially differentiate these populations. This is confirmed by Figure 5 which indicates that the rostral height is greater relative to interorbital breadth for the Papua New Guinea (and Irian Jaya population) than it is for the Kai population; the Aru population is intermediate.

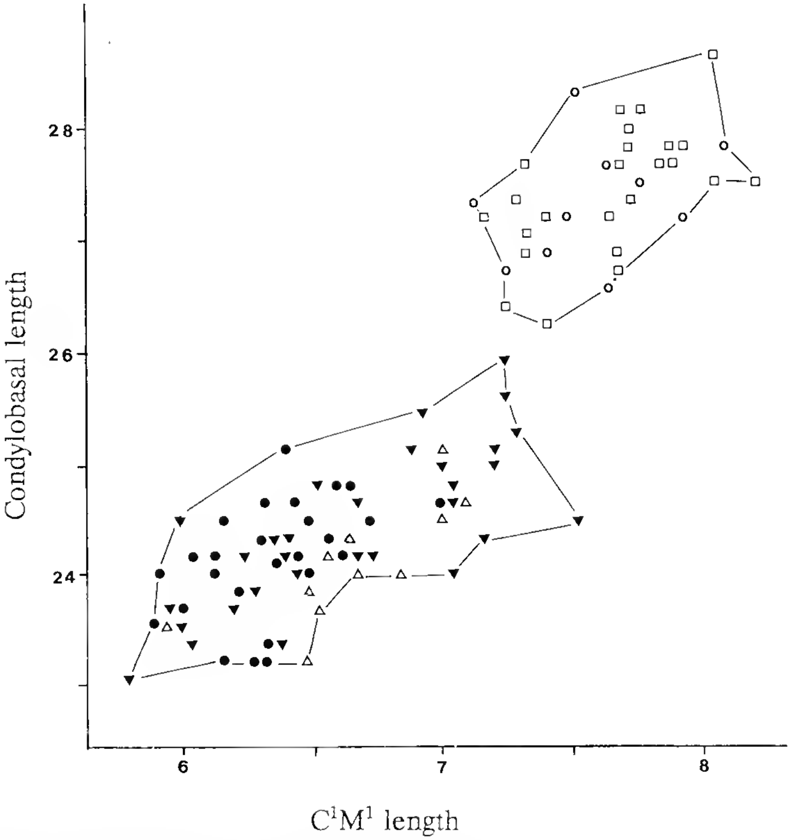

Figure 3 Plot of condylobasal length *versus* C^1M^1 length for *Syconycteris australis* from Maluku and New Guinea. Locality codes as for Figure 2, caption.

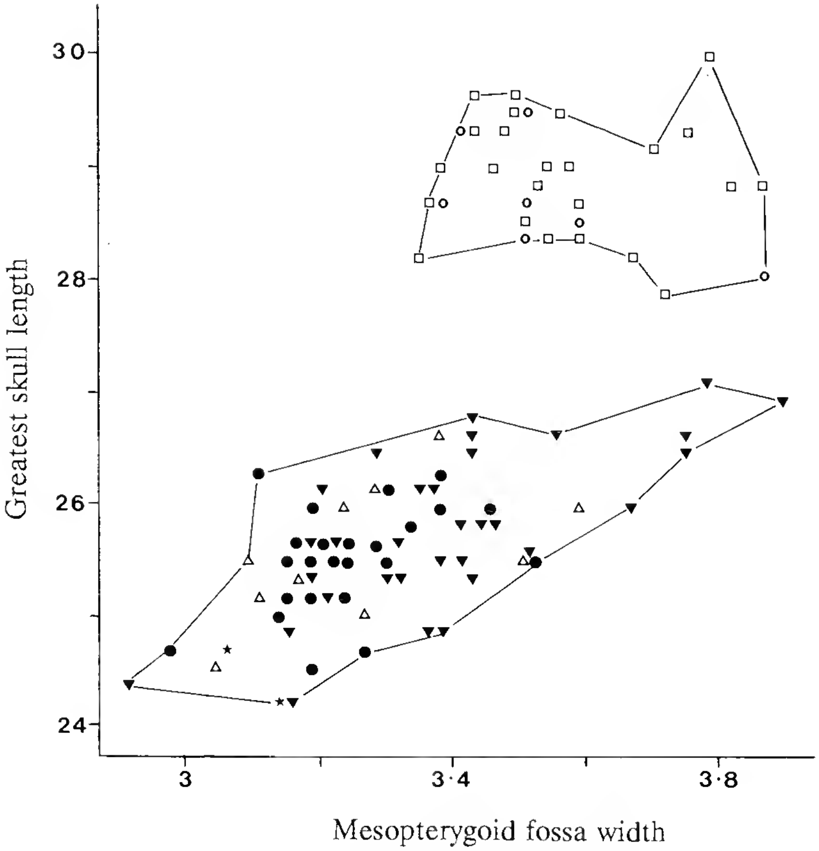

Figure 4 Plot of greatest skull length *versus* mesopterygoid fossa width for *Syconycteris australis* from Maluku and New Guinea. Locality codes as for Figure 2, caption.

Further, the Ambon and Seram population have a greater skull length relative to mesopterygoid fossa width than do the Kai Island, Aru Island and New Guinea populations (Figure 4).

DISCUSSION

Andersen (1912: 781) noted that the Ambon and Seram form (*major*) was the largest of the subspecies of *S. australis*. He stated that "in point of size there may be an absolute, though in any case small, difference between *major* and its nearest geographic neighbour, *papuana* (New Guinea); but *crassa* (Tobriand and D'Entrecasteaux islands) is intermediate".

The Kai Island form (*keyensis*) is almost separate in discriminant function space from *papuana* from Papua New Guinea. Further, it averages smaller in many measurements from the Papua New Guinea form (but not from the few specimens from Irian Jaya) and may be distinguished from the Papua New Guinea and Irian Jaya form by skull shape differences (Figure 5). Andersen (1912) considered the Kai form *keyensis* to be similar in every respect to *papuana*, except for the slightly shorter toothrows. There is no evidence from this study that

Table 3 Canonical variate function coefficients for *Syconycteris australis* from the following locality groups (Ambon Island, Seram Island, Kai Islands, Aru Islands and Papua New Guinea). Standardised values, followed by (in brackets) unstandardised values. For explanation of character codes see Materials and Methods section.

Character	Function 1	Function 2	Function 3
GSL	0.7284(1.2525)	-0.1540(-0.2648)	0.0238(0.0409)
IOB	-0.0169(-0.0480)	-0.9953(-2.8365)	0.6079(1.7325)
RH	0.0383(0.2121)	0.8489(4.6987)	0.2019(1.1178)
EAR	0.0923(0.1225)	0.5907(0.7838)	0.4170(0.5533)
CH	0.2885(0.6333)	-0.3592(-0.7885)	-0.4171(-0.9155)
C^1M^1	-0.1121(-0.3171)	0.4682(1.3250)	-0.8358(-2.3650)
D3P1	0.3592(0.4110)	0.0153(0.0175)	0.3713(0.4248)
Constant	-48.4798	-8.9695	-10.8148
Variation explained (%)	80.2	17.9	1.5

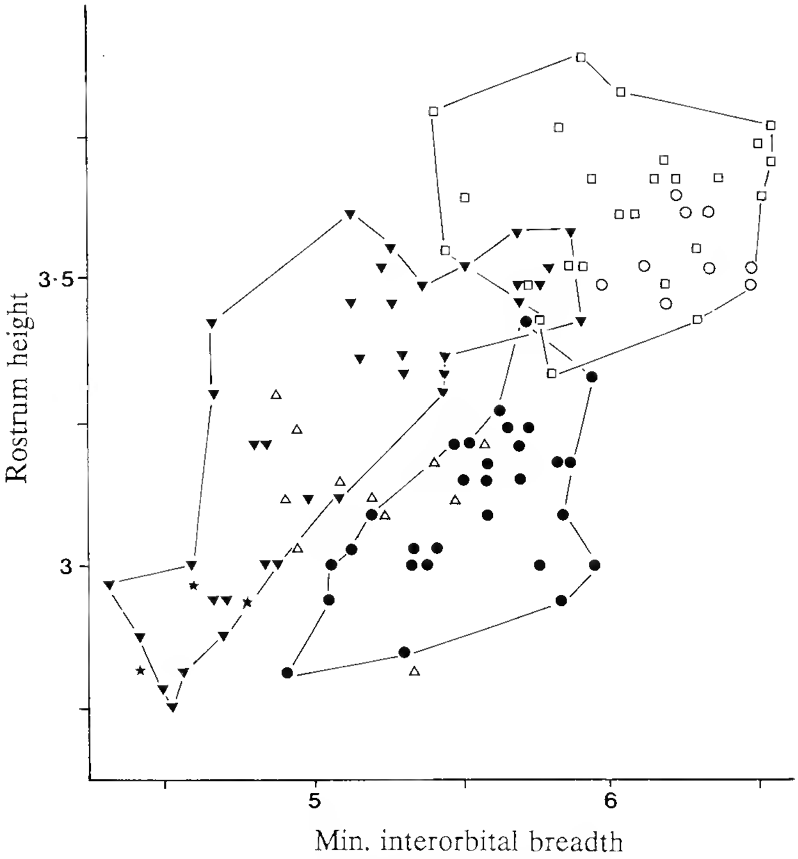

Figure 5 Plot of rostrum height *versus* interorbital breadth for *Syconycteris australis* from Maluku and New Guinea. Locality codes as for Figure 2, caption.

the toothrows of *keyensis* [6.63 ± 0.24 (N=32)] are significantly shorter than those of *papuana* from Papua New Guinea [6.68 ± 0.50 (N=37)] or Irian Jaya [5.95 ± 6.12 (N=3)] ($t_{67} = 0.54$, $p>0.5$ and $t_{33} = 0.19$, $p>0.5$, respectively).

The Aru Island specimens are considered to be *S. a. papuana* by Andersen (1912). This study shows them to be intermediate and to have measurements that overlap with both those of specimens from Kai and Papua New Guinea (Table 1).

This study shows that in the western part of its distribution *S. australis* has differentiated into a form on Ambon and Seram (*major*) that is quite distinct morphologically and which may in fact be specifically distinct from the forms on New Guinea, Aru and Kai Islands.

The population on Kai Island has been described as subspecifically distinct (*keyensis*) from the New Guinea form (*papuana*). This study confirms this distinction but records that the Aru Island population overlaps morphologically both the Kai Island and Papua New Guinea populations. This may be explained by several processes. First, the Kai population may have resulted from a filtered dispersion pattern from Papua New Guinea through Aru; as such the Kai form is the end point in a morphological cline and probably does not warrant subspecific recognition from the New Guinea population. Secondly, the Kai population is morphologically and taxonomically distinct from the New Guinea form and that both these forms exist on Aru; or thirdly, the Aru form is a hybrid between the Kai and New Guinea forms. Answers to these questions are difficult to obtain from a morphological approach such as this one, and will depend on future genetic studies.

Recently Kitchener *et al.* (1993) highlighted the importance of the zone between Lyddeker's and Weber's Line to an understanding of the processes that determine the interface between the southern parts of the Australian and the Oriental biogeographic regions. In an almost parallel study to this one on *Nyctimene albiventer*, Kitchener *et al.* (1993) noted that while the Aru Island population of *N. albiventer* was morphologically very similar to those of Papua New Guinea, those of Kai Island (and Banda Island) were clearly subspecifically distinct. This paper indicates again that Kai Island populations have differentiated morphologically somewhat from their conspecific populations on the Australian and New Guinea continental shelf.

SPECIMENS EXAMINED

Papua New Guinea

Maiwarva (4°55'S, 145°47'E), 2 unsexed, WAM M26281-2; *Nabanob* (5°09'30"S, 145°45'00"E), 6♂♂ 7♀♀, WAM M27492-3, M27497-8, M27501, M27503, M27556-7, M27560-1, M27564, M27572, M27574; *Nokopo* (5°57'S, 146°36'E), 2♂♂ 6♀♀, WAM M27509, M27542-6, M27549, M27554; *Duvi* (5°56'S, 146°37'E), 1♀, WAM M27514; *Duvi-Nokopo* (5°56'S, 146°36'E), 2♂♂ 3♀♀, WAM M27516-7, M27520, M27531, M27539; *Sempi* (5°00'40"S, 145°46'40"E), 1♀, WAM M27580; *Baumina* (5°29'S, 145°43'E), 1♀, WAM M27584; *Bundi* (5°45'S, 145°14'E), 1♂ ♀♀, WAM M27592, M27595, M28505; *Baiteta* (5°00'20"S, 145°44'40"E), 1♂, WAM M28519; *Usino* (5°33'50"S, 145°21'20"E), 1♀, WAM M28522; *Papua New Guinea* (5°30'S, 145°30'E), 1 unsexed, WAM M28529.

Irian Jaya

Porokma (4°00'S, 138°43'E), 1♂ 2♀♀, WAM M29092-4.

Seram Island

Kanikeh (3°00'S, 129°00'E), 11♂♂ 7♀♀, WAM M34167, M34173-5, M34181, M34184-5, M34191-2, M34193, M34205, M34208, M34210, M34214, M34216, M34219, M34227, M34259; *Solea* (2°53'S, 129°32'E), 5♂♂ 3♀♀, WAM M34228-9, M34231-2, M34235, M34238, M34247, M34252.

Ambon Island

Desa Amahusa (3°41'S, 128°10'E), 9♂♂ 6♀♀, WAM M38771, M38773-6, M38779, M38806, M38810, M38850-1, M38853-6, M42363.

Kai Besar Island

Tual and *Fakoi* (*ca.* 5°39'S, 132°59'E), 15♂♂ 21♀♀, WAM 42055-61, M42077, M42093-4, M42096-7, M42110, M42112-3, M42136-7, M42692-3, M42695-8, M42701, M42814-7, M42868-75.

Kai Kecil Island

Near Taman Anggrek, Pulau Dullah (5°38'S, 132°44'E), 1♂ 1♀, WAM M42647-8.

Aru Islands

Karangguli, Wokam Island (05°48'S, 134°15'E), 6♂♂ 7♀♀, WAM M42464, M42483, M42543, M42545-7, M42553-4, M42560, M42573, M42575, M42582-3.

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SALTICIDAE (ARACHNIDA: ARANEAE) OF ORIENTAL, AUSTRALIAN AND PACIFIC REGIONS, X. GENUS *SIMAETHA* THORELL

Marek Żabka*

ABSTRACT

The spider genus *Simaetha* is revised. Eleven species are diagnosed, described and figured. Six of these are new: *S. almadenensis*, *S. atypica*, *S. broomei*, *S. colemani*, *S. knowlesi* and *S. papuana*. *Dendryphantes laticeps* Strand is synonymised with *S. tenuior* (Keyserling). *Simaetha* seems to form a monophyletic group with the genera *Simaethula*, *Kinhia*, *Ligurra*, *Heratemis*, *Porius* and *Stertinius*. The distribution of the genus is considered endemic to Australia and some adjacent islands, with single species reaching, for example, Papua New Guinea and Aru Is. A key to the species is provided and distributional data are given.

INTRODUCTION

Since their original description only single species of *Simaetha* have been subjected to study. Diagnostic characters of the genus were given by Davies and Żabka (1989), the morphology of two species was illustrated by Prószyński (1983, 1984) and some behavioural aspects of *S. paetula* and *S. thoracica* were presented by Jackson (1985).

The genus was proposed by Thorell (1881) for *S. thoracica* Thorell. Four further species were described by Keyserling (1882) in the genus *Eulabes* – all of them transferred to *Simaetha* by Simon (1903). *S. chelicerata* described by Szombathy (1915) is a synonym of *S. tenuidens* (Keyserling). One species of *Simaetha*, classified as *Dendryphantes laticeps* Strand, 1911, now appears a synonym of *S. robustior* (Keyserling). Few other species listed by Bonnet (1958) in the genus *Simaetha* are not congeneric and have been excluded.

MATERIALS AND METHODS

The study is based on type specimens and on new material deposited in the museums listed below. The methods of specimen examination follow that used in my previous papers (e.g. Żabka, 1990). The details of terminology are presented in Figure 1 and the abbreviations are explained in the text. All measurements are in mm; the first figure refers to the type specimen, while those in brackets give the range for the specimens studied. The main diagnostic characters are marked with arrows.

Collections studied: Australian Museum, Sydney (AM); Museo Civico di Storia Naturale, Genova (MCSN); Queensland Museum, Brisbane (QM); Senckenberg-Museum, Frankfurt a.M. (SMF); Western Australian Museum, Perth (WAM); Zoologisches Institut und Zoologisches Museum, Universität Hamburg (ZMH).

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Abbreviations used: aat – additional anterior cheliceral tooth, AEW – anterior eyes width, ag – accessory gland, AL – abdominal length, apt – additional posterior cheliceral tooth, as – abdominal scutum, ca – cymbial apophysis, CL – cephalothorax length, co – copulatory opening, CW – cephalothorax width, dr – epigynal diagonal ridges, ds – distal spermatheca, e – embolus, EFL – eye field length, ep – epigynal pocket, f – fovea, fd – fertilization duct, fp – frontal cheliceral protrusion, ic – intermediate canal, id – insemination duct, PEW – posterior eyes width, ps – proximal spermatheca, rft – retromarginal fissidentate tooth, rut – retromarginal unidentate tooth, s – spermatheca, sp – sternal protuberance, sr – seminal reservoir, stg – subtegulum, ta – retrolateral tibial apophysis, tg – tegulum.

Genus *Simaetha* Thorell

Simaetha Thorell, 1881: 520.

Eulabes Keyserling, 1882: 1387.

Dendryphantes C. L. Koch, 1837: 31 (in part).

Type species

Simaetha thoracica Thorell, 1881, by subsequent designation.

Diagnosis

The genus differs from *Simaethula*, the only Australian relative, in the following characters: body dimensions larger, eye field relatively shorter, sternum with distinctive protuberance, epigyne with pocket and palpal tibia with retrolateral apophysis.

Description (Figure 1)

A robust spider, 3.80 – 8.70 mm in body length. Cephalothorax usually wide, compressed dorso-ventrally. Thoracic slope distinctive, cephalic slope gentle, fovea (f) located posteriorly. Posterior lateral eyes located at about the middle of the cephalothorax, much wider apart than anterior lateral eyes. In some species, the eye field has a small prominence. Abdomen egg-shaped, with distinctive apodemes (ap), in males usually with a scutum (as). Chelicerae more or less vertical, massive, with frontal protrusion (fp). Female chelicerae with fissidentate tooth, males with large retromarginal unident (rut) or fissident (rft) tooth. Chelicerae of some species with either an additional anterior (aat) tooth or a posterior (apt) tooth. Sternum with a distinctive protuberance (sp). First legs much heavier and longer than the remaining legs – especially in males. Spines of different length, sometimes very small. Leg formula I-II-IV-III (males) and I-IV-II-III (females). Cymbium with an apophysis (ca); retrolateral tibial apophysis (ta) single, varying in shape. Tegulum (tg) oval; seminal reservoir (sr) not meandering; in most species the subtegulum (stg) protrudes prolaterally from beneath the tegular margin. Embolus (e) straight or curved, never coiled. Palps of both sexes clothed in long hairs forming lateral fringes. Epigyne with a large central pocket (ep), in a few species with diagonal ridges (dr). Spermathecae consist of two thick-walled oval chambers; proximal chamber (ps) larger than distal one (ds). Intermediate canal (ic) more or less visible. Insemination ducts (id) usually very short – except for *S. paetula*. Accessory glands (ag) invisible or weakly indicated. The males are darker than the females, their abdominal apodemes are more distinctive and first legs much longer. The males with shiny metallic green, blue and red polish, whilst the females with lighter markings.

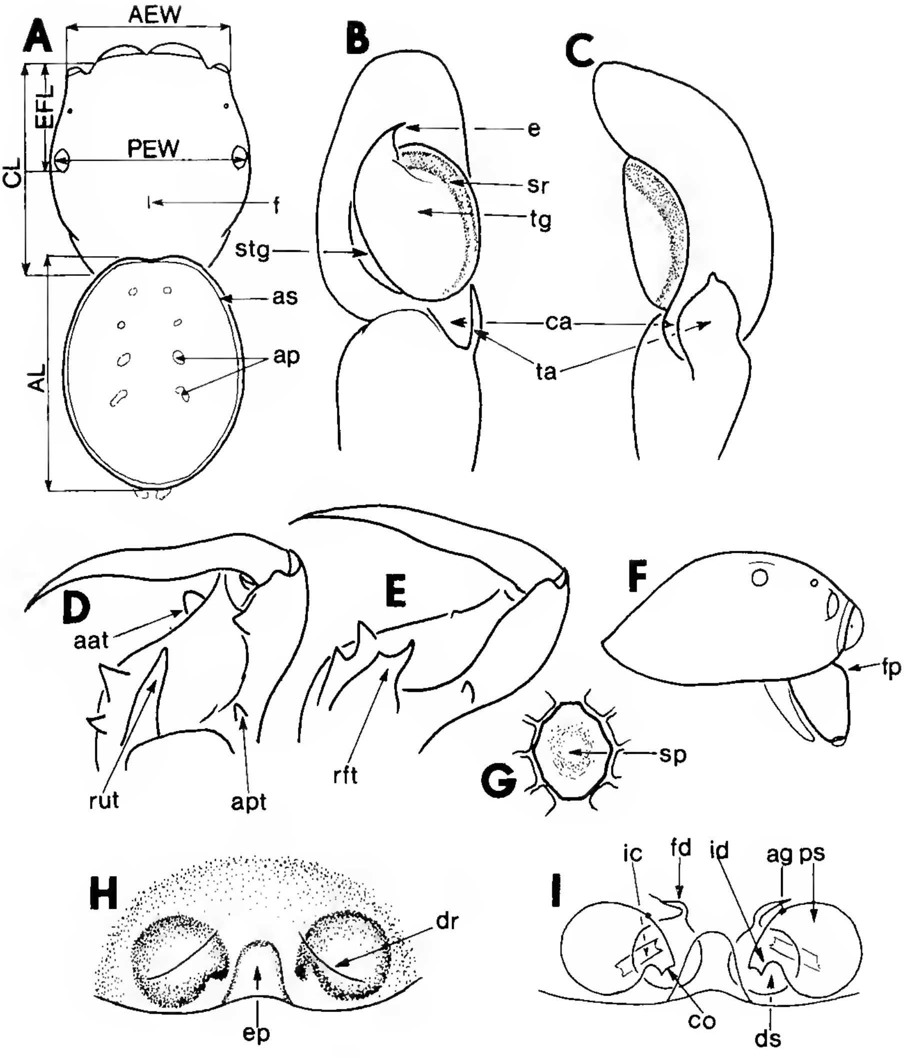


Figure 1 Diagnostic characters of *Simaetha* (abbreviations explained in the text). A – dorsal body and measurements taken. B – ventral aspect of male palpal organ. C – retrolateral aspect of male palpal organ. D – chelicera with unidentate tooth, E – chelicera with fissidentate tooth. F – lateral aspect of cephalothorax. G – sternum with its protrusion. H – epigyne. I – internal genitalia of female.

Remarks on relationships and distribution

Simon (1903) placed the genus *Simaetha* in Simaetheae – together with some other fissidentate genera. Of these *Simaetha*, *Simaethula*, *Ligurra*, *Heratemis*, *Stertinius* as well as *Porius* (until now in the Balleae) and the recently described *Kinhia* all have similar body form, genitalic structure and cheliceral dentition (Peng and Yin 1991; Prószyński 1983, 1984, 1987; Żabka, 1985) and seem to form a monophyletic group. All its representatives are characterized by the presence of a cymbial apophysis, an oval tegulum, a central epigynal pocket (except for *Simaethula*) and two-chambered spermathecae. A few other genera, particularly *Rhene*, *Dendryphantes*, *Irura*, *Homalattus* and *Bianor*, show some similarities in general appearance, while *Iona* shows similarities in the genitalia; all of these are phylogenetically distant.

The genera of Simaetheae have an Oriental and Australian distribution; *Simaetha* and *Simaethula* seem to be endemic to Australia and some adjacent islands (Aru, New Guinea). Other genera occur in southeast Asia but have not been recorded on Australia's mainland.

Of all the species, *S. tenuidens*, *S. paetula* and *S. tenuior* have the widest distribution, being mostly found in Queensland but also in Western Australia and Papua New Guinea; the latter species also occurs on offshore islands and in human habitations. *S. robustior* has been recorded from tropical Queensland, Aru Is. and Papua New Guinea and seems to have a northern (tropical) distribution. The remaining species are known from single localities in the Northern Territory, Queensland, New South Wales, Western Australia and Papua New Guinea.

Biology

The representatives of *Simaetha* are found on herbs, small trees and grass. Some specimens of *S. tenuior* and *S. tenuidens* have been collected in the nests of *Scelephron formosum* (Hymenoptera: Sphecidae), whilst others (*S. paetula* and *S. thoracica*) cohabit within colonies of *Badumna candida* (Araneae: Desidae) or (as in one case of juvenile *S. paetula*) with *Cyrtophora* sp. (Araneae: Araneidae), where they build their own nests within the nest of the host (Jackson 1985). Representatives of *Simaetha* build large prey-catching webs or display kleptoparasitic behaviour, gleaning insects from the nests of the other spiders with whom they cohabit. The occurrence of *S. tenuior* in human habitations suggests its synanthropic biology. Many other aspects of the biology of *Simaetha*, including courtship, mating behaviour and phylogenetic interpretation, are discussed by Jackson (1985).

Key to the species of *Simaetha*

Males

1. Cheliceral retromarginal tooth bifurcate (fissidentate) 2
   Cheliceral tooth pointed (unidentate) 3

2. Chelicerae with additional posterior tooth; subtegulum distinctive 4
   Additional tooth lacking 5

3. Chelicerae with additional posterior tooth; abdomen dark, with light anterior margin; tibial apophysis large, spatulate .... *S. tenuidens* (Keyserling)
   Additional tooth lacking, abdominal pattern variable; tibial apophysis not spatulate 6

4. Tibial apophysis short; abdominal scutum distinctive .... *S. thoracica* Thorell
   Tibial apophysis long; abdomen with three longitudinal, dorsal stripes, without scutum ... . *S. papuana* sp. nov.

5. Spinnerets rather long; scutum weakly indicated; subtegulum strongly protrusive, colour pattern distinctive; palpal tibia with long feather-like hairs on prolateral surface .... *S. atypica* sp. nov.

Spinnerets short; scutum distinctive; subtegulum weakly protrusive; body colour almost uniform .... *S. almadenensis* sp. nov.

6. Massive spider; abdomen with light contrasting stripe; subtegulum strongly protrusive; embolus curved .... *S. robustior* (Keyserling)

   Not as above 7

7. Tibial apophysis laterally bent; embolus straight 8

   Embolus curved; chelicerae with characteristic teeth .... *S. knowlesi* sp. nov.

8. Embolus relatively long; subtegulum invisible .... *S. paetula* (Keyserling)

   Embolus shorter; subtegulum visible .... *S. tenuior* (Keyserling)

Females

1. Epigynal pocket well marked, large, about the size of the proximal spermathecae 2

   Epigyne different 4

2. Large spider with a contrasting broad, light abdominal stripe, and a bell-shaped central epigynal pocket .... *S. robustior* (Keyserling)

   Contrasting stripe lacking or, if present, epigynal pocket located anteriorly 3

3. Spider dark; epigynal pocket located centrally, cone-shaped .... *S. knowlesi* sp. nov.

   Abdomen with light pattern; spinnerets relatively long; epigynal pocket located anteriorly .. .. *S. atypica* sp. nov.

4. Epigynal pocket distinctive but relatively small, close to the epigastric furrow; spinnerets short 5

   Epigynal pocket indistinct, more visible only after maceration 6

5. Proximal spermathecae more than three times larger than the distal ones; cephalothorax less robust than in the other species .... *S. broomei* sp. nov.

   Proximal spermathecae small; epigyne with more or less marked diagonal ridges .... *S. tenuior* (Keyserling)

6. Abdomen dark, with light frontal band; spermathecae widely spaced .... *S. tenuidens* (Keyserling)

   Abdomen with light pattern 7

7. Copulatory openings large, cup-like, insemination ducts long ...... *S. paetula* (Keyserling)

   Copulatory openings small, insemination ducts short 8

8. Insemination ducts very short; accessory glands weakly indicated but visible; intermediate canal distinctive ....*S. thoracica* Thorell

   Insemination ducts slightly longer; accessory glands invisible; intermediate canal very short ....*S. colemani* sp. nov.

TAXONOMIC SURVEY

Simaetha thoracica Thorell
Figures 2-4, Map 1

Simaetha thoracica Thorell, 1881: 521.

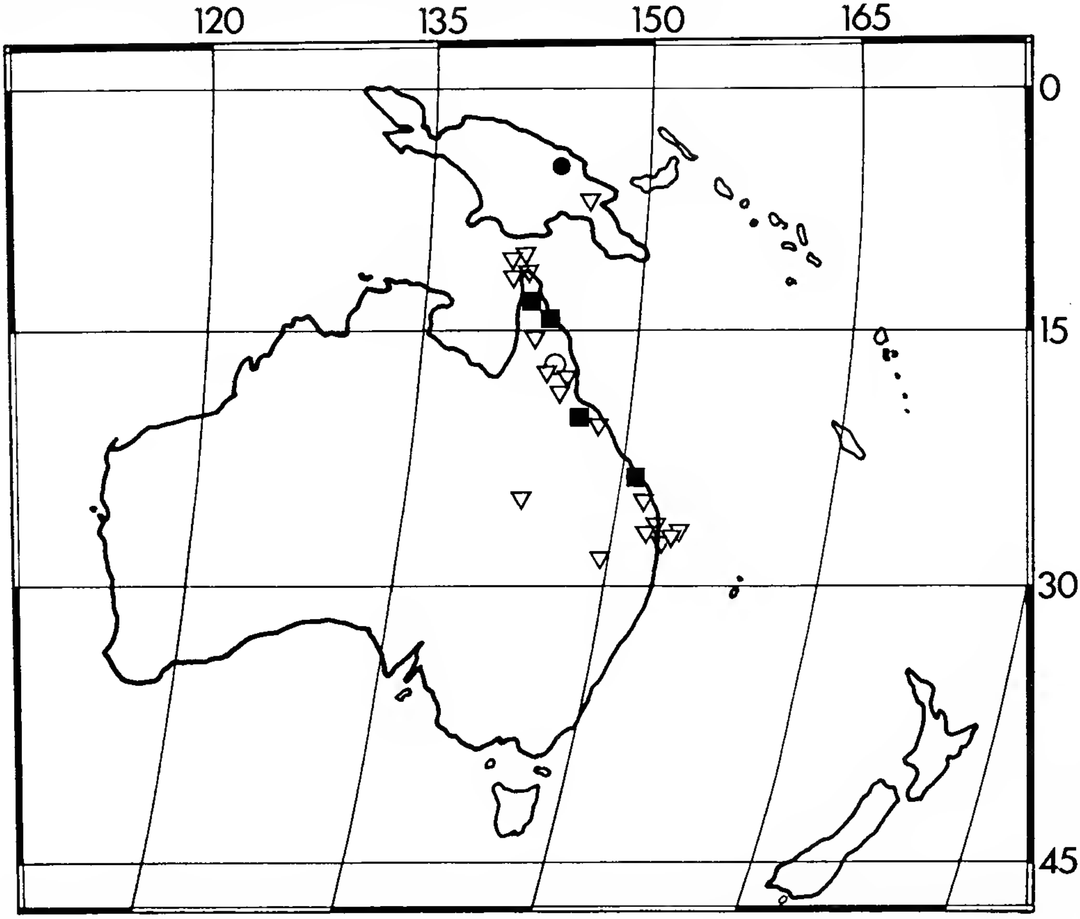
Eulabes fissidens Keyserling, 1882: 1391.

Holotype of *Simaetha thoracica*
♀, Cape York, Somerset, Queensland, Australia 1875, L.M. d'Albertis (MCSN).

Syntypes of *Eulabes fissidens*
1♂, 1♀, Rockhampton, Queensland, Australia (ZMH, Mus. Godeffroy Nr. 7689).

Other material examined

Australia: Queensland: 5♂, 3♀, 16 juv., Homevale, 1-7 April 1975, V. Davies, R. Raven (QM S4627). 1♂, Brandy Ck, camp site, 21-26 April 1975 (QM S4667). 1♂, 2♀, 4 juv., Rundle Ra, semi-evergreen vine thicket, 24-31 March 1975, V. Davies, R. Kohout (QM S4626). 1♀, from River 39 miles S Coen, 4 June 1973, V. Davies (QM S4664). **Western Australia:** 1♀, NW Australia, 1920 (AM KS22068).



Map 1 Distribution of four species of *Simaetha* – *S. thoracica* (■); *S. colemani* (○); *S. tenuidens* (▽); *S. papuana* (●).

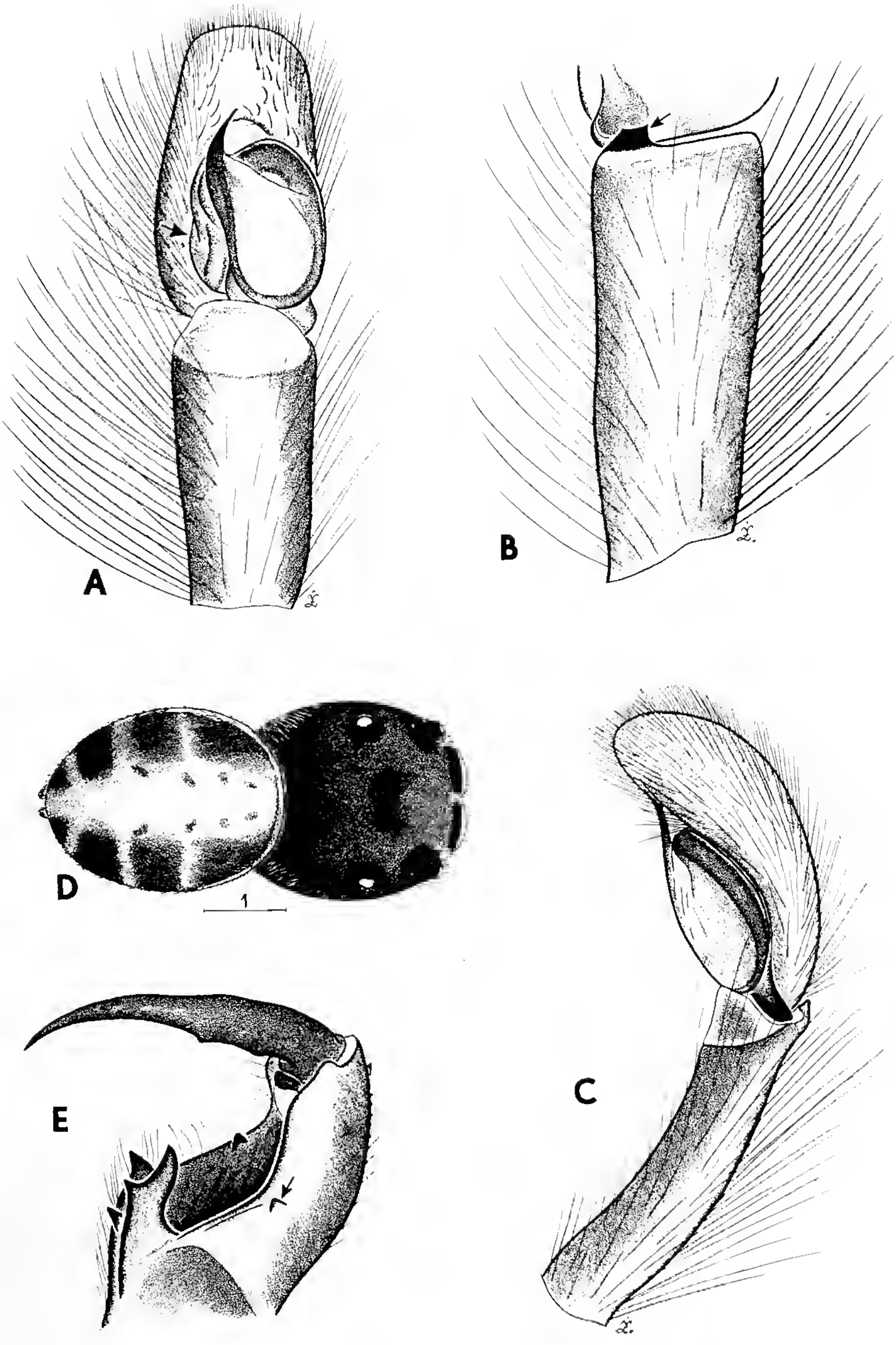


Figure 2 ♂ *Simaetha thoracica* Thorell, 1881. A–C – palpal organ: ventral, retrodorsal and retrolateral aspects. D – general appearance. E – chelicera.

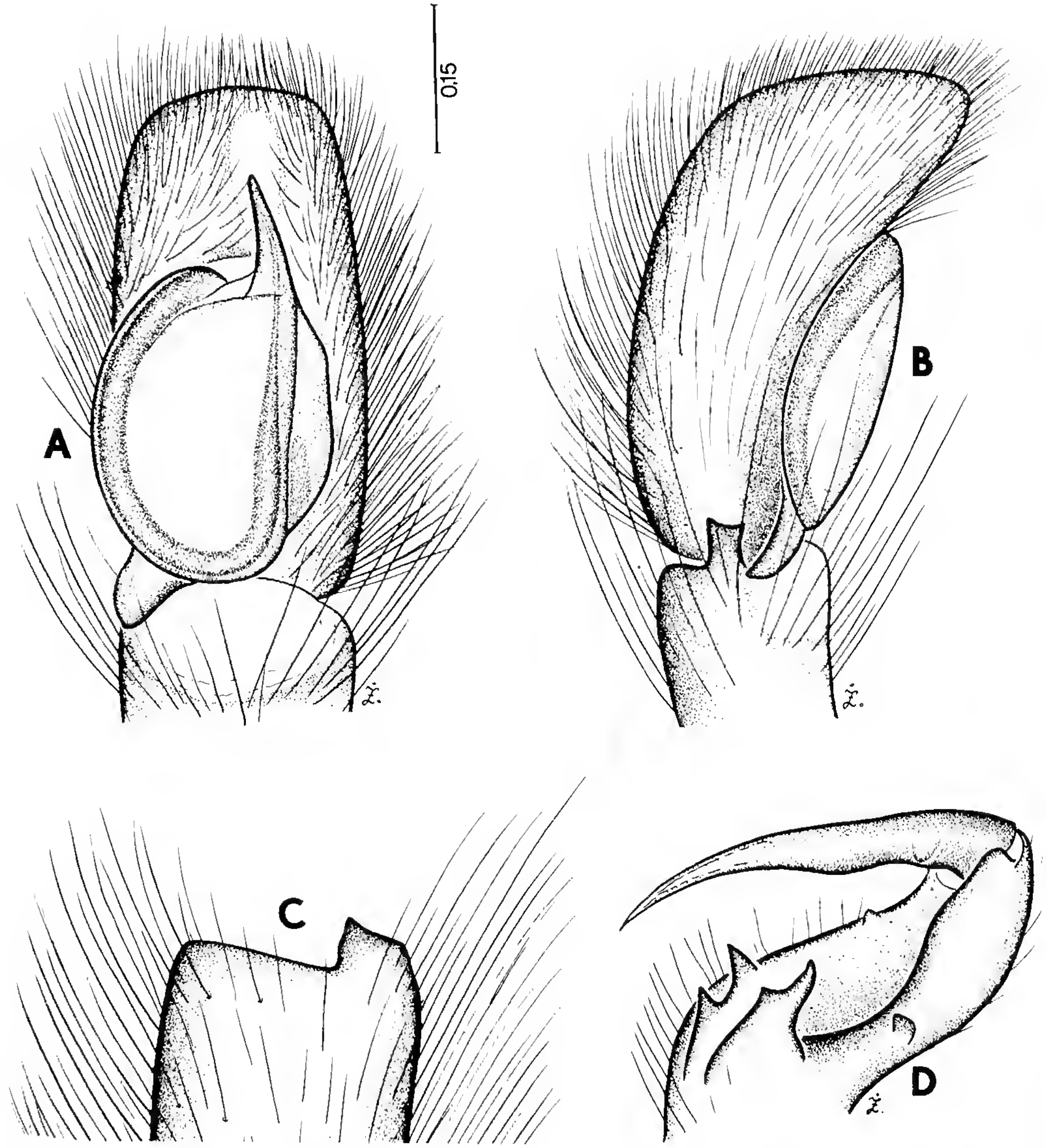


Figure 3 ♂ *Simaetha thoracica* Thorell, 1881. A–B – palpal organ: ventral and retrolateral aspects. C – palpal organ: retrodorsal tibia. D – chelicera. (Syntype from Rockhampton).

Diagnosis

Males similar to *S. atypica* but larger, abdominal pattern different, spinnerets shorter, subtegulum more protrusive, tibial apophysis smaller. Male chelicerae with a small posterior tooth. In comparison with *S. colemani* the insemination ducts are shorter, the intermediate canals are more distinct and the accessory glands are visible.

Description

Male (Figure 2D). Eye field orange to brown with two darker spots and with black eye surrounds. Anterior eyes fringed with short white hairs. Thorax brown, clothed in light scattered hairs, lower margins darker. Abdominal scutum orange to brown, darkening posteriorly, sides light-grey or dirty-grey, centrally a light longitudinal stripe and transverse stripes. Apodemes distinct, spinnerets dirty-brown. Clypeus brown with light-grey, yellowish and brownish hairs. Chelicerae (Figure 2E, 3D) brown, fissidentate tooth large, anterior and

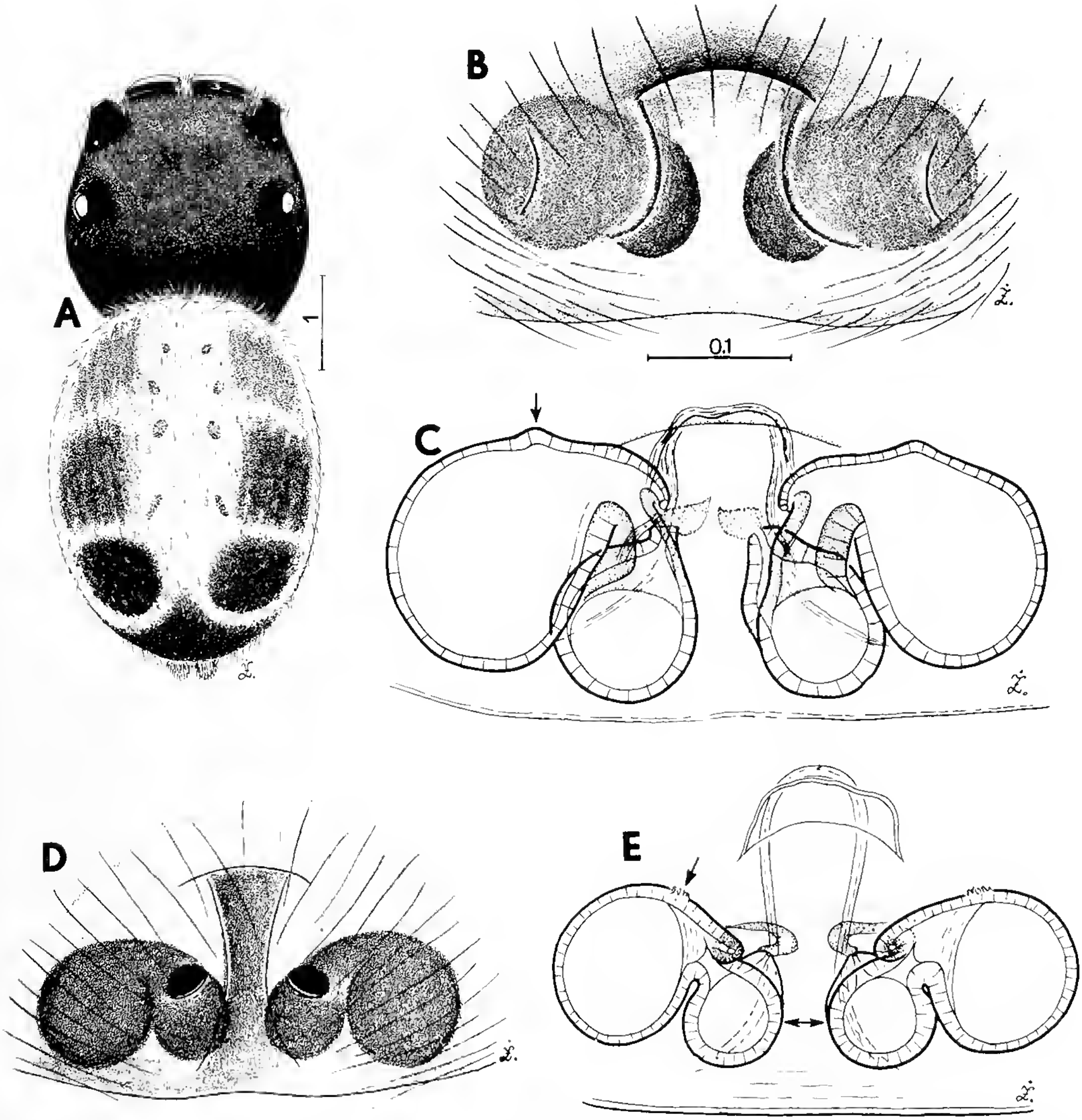


Figure 4 ♀ *Simaetha thoracica* Thorell, 1881. A – general appearance. B–E – epigyne and internal genitalia. (D–E – holotype).

posterior margins with smaller teeth. Maxillae and labium dark-brown with lighter scopular margins, sternum dark-brown, venter dirty-grey. Legs brown, prolateral sides darker – especially on femora I and II.

Palpal organ (Figure 2A-C, 3A-C): embolus relatively long, subtegulum and cymbial apophysis strongly developed, tibial apophysis short, truncate at the top.

Dimensions

CL 2.82 (2.50-3.30), EFL 1.20 (1.20-1.40), AEW 1.86 (1.70-1.95), PEW 2.22 (2.10-2.45), AL 3.36 (2.80-3.75).

Female (Figure 4A) similar to the male, abdominal stripe more distinctive, spinnerets orange to brown. Clypeus, chelicerae, maxillae, labium and sternum as in male, pedipalps brown, venter beige. Legs brown.

Epigyne (Figure 4B-E) with a longitudinal central depression leading to a large anterior pocket. Insemination ducts very short, intermediate canal distinctive.

Dimensions

CL 2.76 (2.20-2.85), EFL 1.26 (1.15-1.26), AEW 1.86 (1.65-1.90), PEW 2.34 (2.05-2.35), AL 3.36 (3.00-4.40).

Simaetha papuana sp. nov.

Figure 5, Map 1

Holotype

♂, p. Amanab, W. Sepik, Papua New Guinea, sugar cane shoot, 16 November 1985, W. Ismay (AM KS30813).

Diagnosis

In comparison with other species, the cephalothorax has a lateral fringe of white hairs, the abdomen lacks a scutum and has longitudinal stripes, the cheliceral fang is noticeably bent.

Description

Male (Figure 5A). Eye field brownish with darker eye surrounds. Thorax orange-brown. Sides of cephalothorax fringed with white hairs. Abdomen without a scutum, orange with three longitudinal dark stripes. Spinnerets yellowish, posterior ones with darker tips. Clypeus orange-brown with white hairs. Chelicerae (Figure 5B) orange with a fissidentate retromarginal tooth, fang long and noticeably bent. Maxillae, labium and sternum honey-orange with grey coating, maxillae long. Venter dark-grey with rows of light spots. Legs I very long, honey-orange, dorsally darker – especially on femora. Other legs short and delicate, yellowish with grey femoral bands and darker joint-areas. Leg formula I, IV, II, III.

Palpal organ as illustrated on Figure 5C-E.

Dimensions

CL 2.25, EFL 1.00, AEW 1.45, PEW 1.70, AL 3.30.

Remarks

The placement of this species in *Simaetha* is tentative. It possesses several atypical features, notably the leg formula, colour pattern and absence of a cymbial apophysis and abdominal scutum.

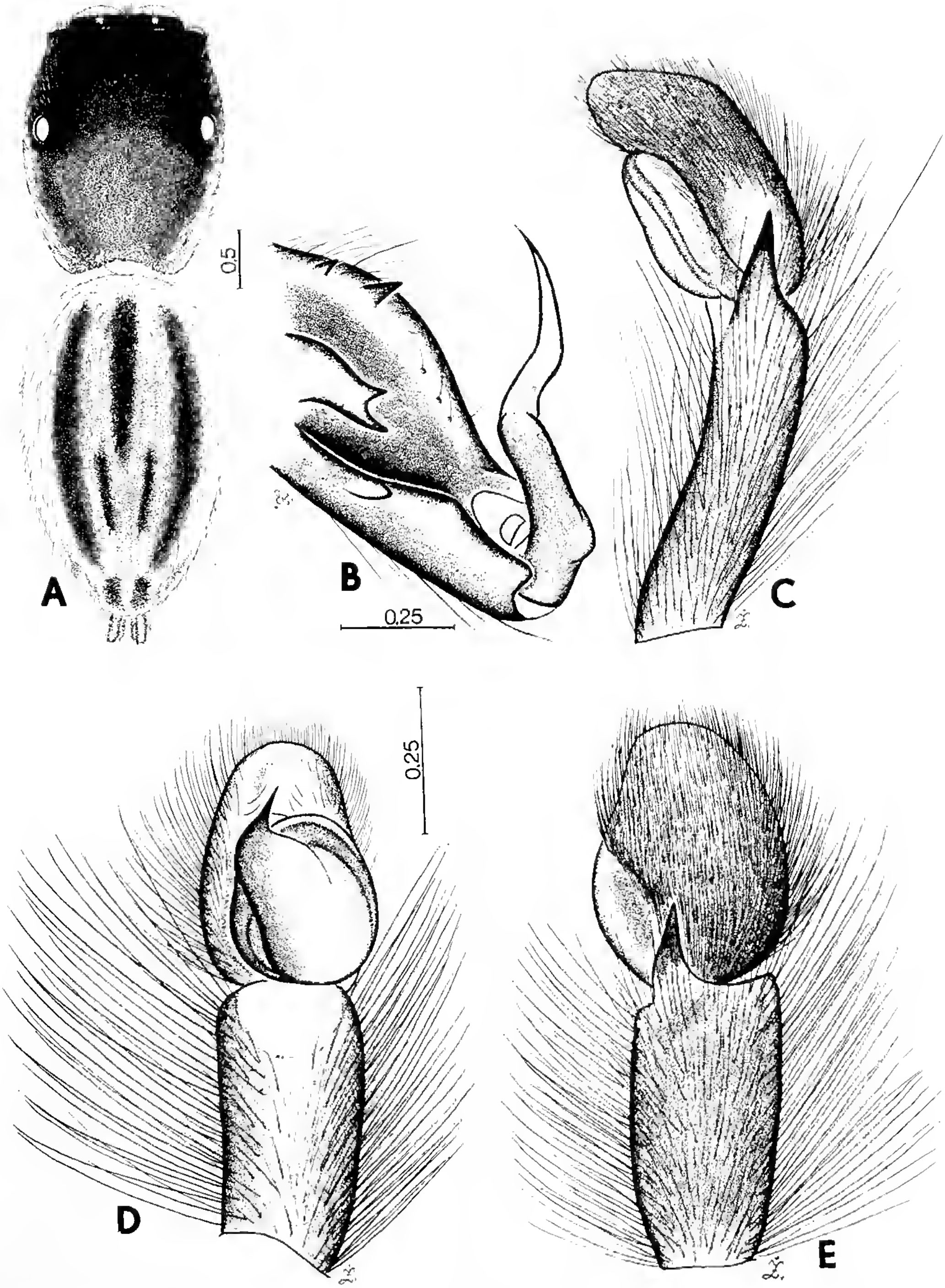


Figure 5 ♂ *Simaetha papuana* sp. nov. A – general appearance. B – chelicera. C–E – palpal organ: retrolateral, ventral and dorsolateral aspects.

Simaetha colemani sp. nov.
Figure 6, Map 1

Holotype
♀, Kuranda, Queensland, Australia, 25 March 1972, N. C. Coleman (QM S4654).

Diagnosis
In comparison with the similar *S. thoracica*, the insemination ducts are slightly longer, the intermediate canals are shorter, the accessory glands are not visible, the body size is much smaller and the abdominal pattern is different.

Description
Female (Figure 6A). Cephalothorax covered with white and dark-orange hairs. Eye field orange with two dark spots, eye surrounds darker. Thorax orange to brown. Abdomen brownish-grey with lighter central stripe. Spinnerets greyish. Clypeus and chelicerae orange. Pedipalps yellowish with brownish hairs. Maxillae and labium brown, chewing margins lighter, sternum dirty-orangish, venter light-beige. Legs I orange, remaining legs yellowish with grey joint-areas.

Epigyne (Figure 6B-C) similar to that of *S. thoracica* but epigynal pocket is weakly indicated, also the insemination ducts are slightly longer.

Dimensions
CL 2.40, EFL 1.25, AEW 1.90, PEW 2.30, AL 2.75.

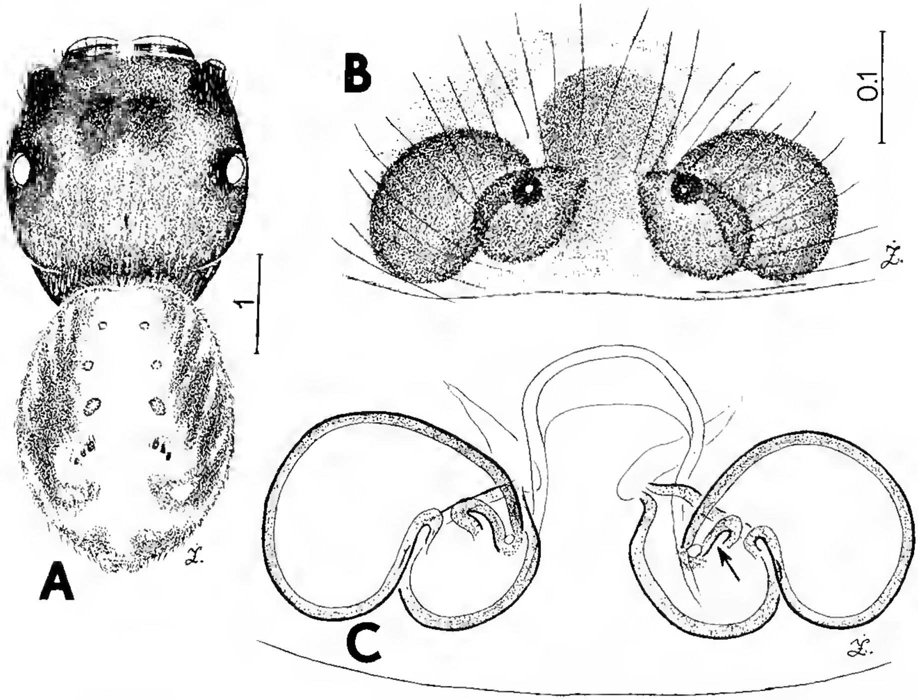


Figure 6 ♀ *Simaetha colemani* sp. nov. A – general appearance. B–C – epigyne and internal genitalia.

Etymology

The specific name is proposed in honour of N. C. Coleman, Australian naturalist and collector of the material studied.

Simaetha tenuidens (Keyserling)

Figures 7-8, Map 1

Eulabes tenuidens Keyserling, 1882: 1393.

Simaetha tenuidens: Simon, 1903: 833; Prószyński, 1987: 167.

Simaetha chelicerata Szombathy, 1915: 482; Prószyński, 1983: 296.

Syntypes of *Eulabes tenuidens*

1♂, 2♀, Gayndah, Peak Downs, Queensland, Australia (ZMH, Mus. Godeffroy Nr. 7690).

Other material examined

Australia: Queensland: 1♀, Acacia Ridge, mud wasp nest, 24 January 1971, E. C. Dahms (QM S4628). 1♂, 1♀, Cape York, Sanamere Swamp, N Jardine River, 3 September 1985, M. Bennie (QM S3608). 1♀, Cape York, Jardine River, 26 August 1985, M. Bennie (QM S3612). 1♀, Mareeba, 1 March 1970, N. C. Coleman (AM KS18968). 1♀, same locality, 22 July 1969 (AM KS22141). 3♂, 1 juv., Brisbane, Fig Tree Pocket, Roedean Street, in house, in wasps' nest, 11 February 1974, 28 April 1974, 25 July 1987, V. Davies (QM S4631, S4636, S4634). 1♀, Brisbane, Ferny Grove, 14 December 1982, R. R. Jackson (QM S4638). 3♂, 5♀, 3 juv., Brisbane, Rochedale State Forest, sweeping, 7 December 1979, 14-16 February 1980, 7 October 1980, V. Davies, R. Raven (QM S4646, S4642, S4643). 1♂, Brisbane, Mt Coot-tha, grass under open tree canopy, R. Monroe, July 1971 (QM S4681). 1♀, same locality, sweeping herbs, 2 August 1987. M. Żabka (AM KS30814). 1♂, Eureka Creek, 11 February 1972, N. C. Coleman (QM S4650). 1♂, 7 km NE Musgrave Station, 3 June 1973, V. Davies (QM S4675). 1♀, Lake Broadwater, bulloak, 26 December 1986, M. Bennie (QM S4632). 2♂, 5♀, Atherton Tableland, Mareeba, in webs, 21 January 1981, December 1982, R. R. Jackson (QM S4684, S4668). 1♂, 1♀, 2 juv., Torres Strait, NW side of Friday Is., in burnt low bushes behind dune, 7 December 1986, J. Gallon (QM S3626). 1♀, Torres Strait, Horn Is., beating, 2-8 December 1986, J. Gallon (QM S3618). 1♀, Altonvale Station, W Westmar, 10 January 1979, V. Davies, T. Adams, R. Raven (QM S4651). 1♀, Tinaroo, 15 November 1971, N. C. Coleman (QM S4662). 1♀, Bamaga, around motel, 8-11 December 1986, J. Gallon (QM S3619). 1♀, Brisbane, Fig Tree Pocket, 21 January 1973, V. Davies (QM S4688). 1♀, 2 juv., Mt Garnet, 24 July 1987, N. C. Coleman (QM S3614). 1♂, 5♀, Davies Ck., summer 1971-72, N. C. Coleman (QM S4676). 1♂, 1♀, Moreton Is., in leaves, 29 November 1978, T. Tabble, V. Davies (QM S4629). 1♀, Moreton Is., Blue Lagoon, 26 April 1981, G. Anderson (QM S4633). 3♀, Molloy Road, 18 February 1972, N. C. Coleman (QM S4678). 1♂, Belmont, 30 August 1966, R. Mascord (AM KS18974). **Papua New Guinea:** 1♀, Morobe Prov., Wau Ecology Institute, 6 July 1988, D. J. Court, M. Żabka (AM KS30815).

Diagnosis

Both sexes are dark. Palpal organ is similar to that of *S. robustior* but the tibial apophysis is larger, spatular instead of conical, the male chelicerae with large unidentate tooth and with additional posterior tooth. The central depression of the epigyne is much wider than in the other species, the spermathecae widely separated and the copulatory openings close to the epigastric furrow.

Description

Male (Figure 7E). Eye field orange to brown with two darker patches and some light pigmented spots, eye surrounds darker. Thorax orange-brown to dark-brown. Hairs sparse, anterior eyes surrounded with tufts of white hairs. Abdominal scutum orange to brown, darkening laterally, sides grey. Spinnerets brown. Clypeus orange-brown. Chelicerae (Figure

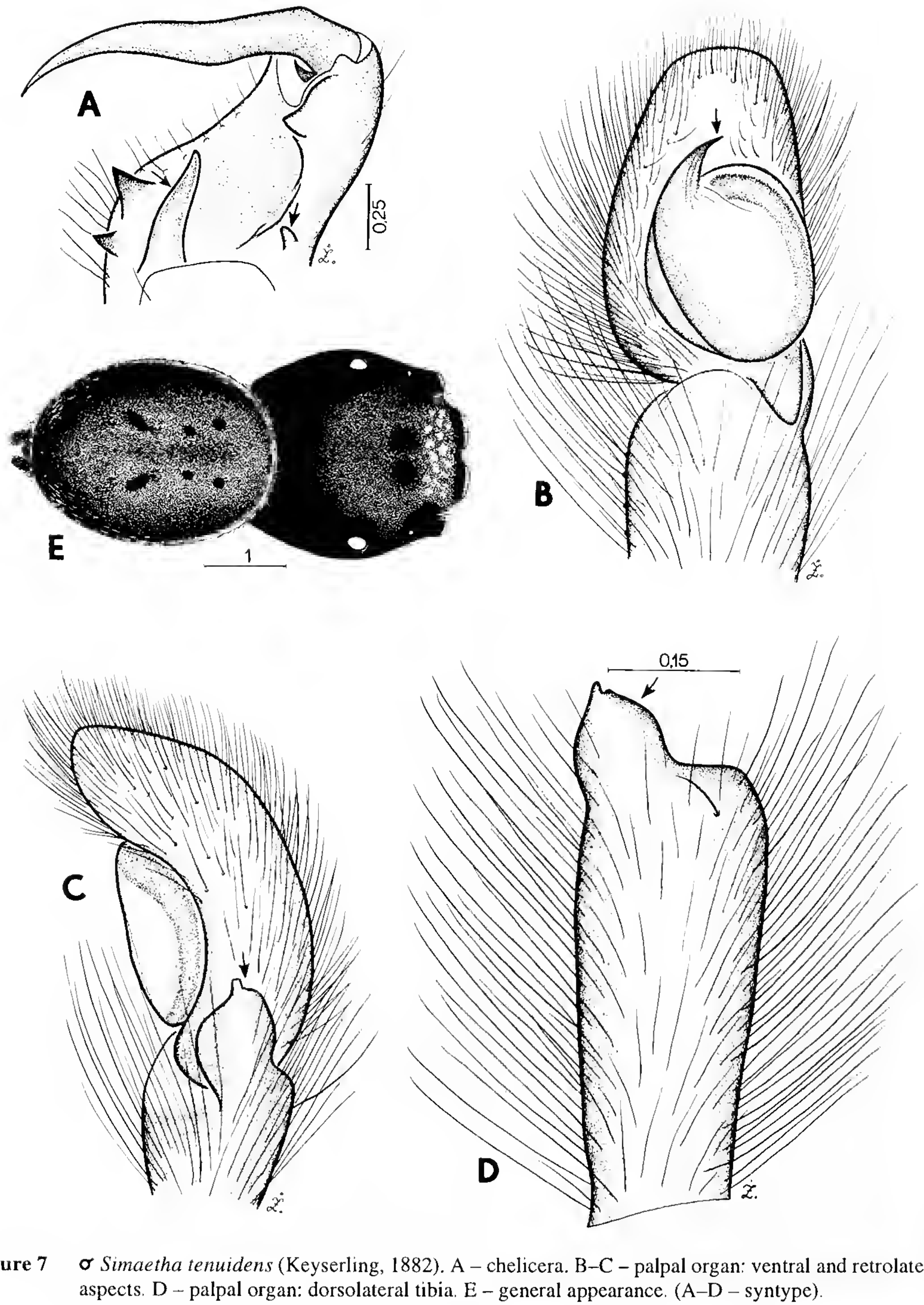


Figure 7 ♂ *Simaetha tenuidens* (Keyserling, 1882). A – chelicera. B–C – palpal organ: ventral and retrolateral aspects. D – palpal organ: dorsolateral tibia. E – general appearance. (A–D – syntype).

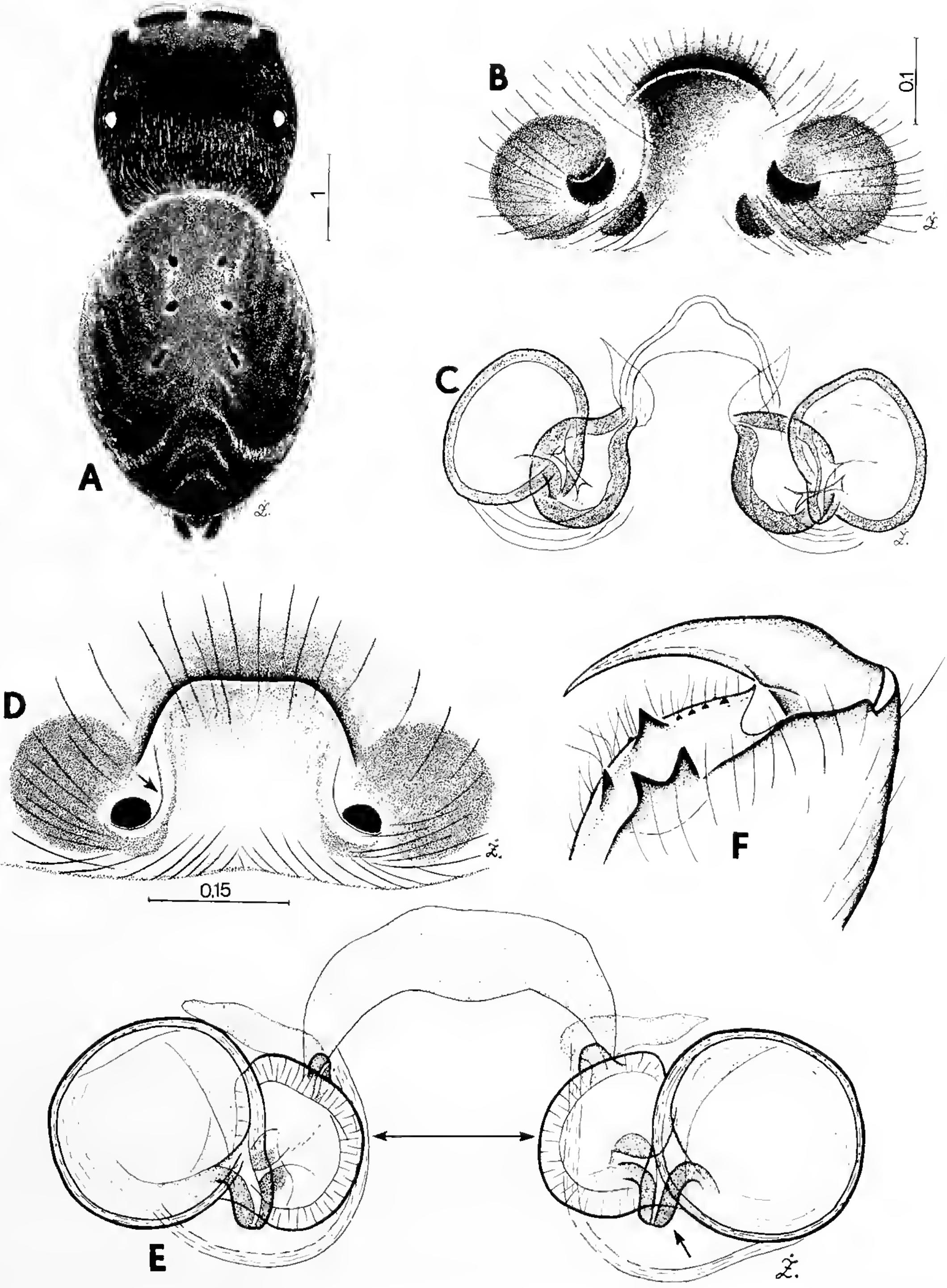


Figure 8 ♀ *Simaetha tenuidens* (Keyserling, 1882). A – general appearance. B–E – epigyne and internal genitalia. F – chelicera. (D–F – syntype).

7A) with long fang, retromargin with long unidentate tooth, posterior surface with additional small tooth. Maxillae and labium brown to dark-brown, scopular margins lighter. Sternum brown to dark-brown. Venter beige, darkening posteriorly and laterally. Legs I orange to dark-brown, darker prolaterally. Remaining legs gradually lighter, darker around the joints.

Palpal organ (Figure 7B-D). Tegulum oval, subtegulum rather small, embolus curved, cymbial and tibial apophyses large, the latter spatular.

Dimensions

CL 2.94 (2.25-3.40), EFL 1.26 (0.95-1.70), AEW 2.10 (1.65-2.40), PEW 2.40 (1.90-2.90), AL 3.24 (2.30-4.30).

Female (Figure 8A). Cephalothorax reddish- to black-brown, eye field with a darker spot, eye surrounds black with white and scattered brown hairs. Posterior and lateral cephalothorax clothed in numerous white hairs. Abdomen brown-grey to almost black, with a slightly lighter median and lateral pattern of whitish hairs and spots. Spinnerets grey-brown. Clypeus red-brown to dark-brown, densely clothed in white hairs. Chelicerae (Figure 8F), maxillae, labium, sternum and legs light- to black-brown, the last with scattered white and longer brown hairs. Pedipalps brown clothed in numerous white and brown hairs. Venter beige to greyish-brown, marginally darker.

Epigyne (Figure 8B-E) externally resembling the two previous species. Anterior epigynal pocket vast and shallow, spermathecae widely separated, insemination ducts distinctive.

Dimensions

CL 3.00 (2.30-3.20), EFL 1.44 (1.05-1.50), AEW 2.22 (1.70-2.30), PEW 2.64 (2.00-2.70), AL 4.20 (2.70-4.50).

Simaetha robustior (Keyserling)

Figures 9-10, Map 2

Eulabes robustior Keyserling, 1882: 1396.

Simaetha robustior: Simon, 1903: 838.

Dendryphantes laticeps Strand, 1911: 193, syn. n.

Holotype and paratype of *Eulabes robustior*

1♂, 1 juv., Port Mackay, Queensland (ZMH, Mus. Godeffroy Nr. 7688).

Holotype of *Dendryphantes laticeps*

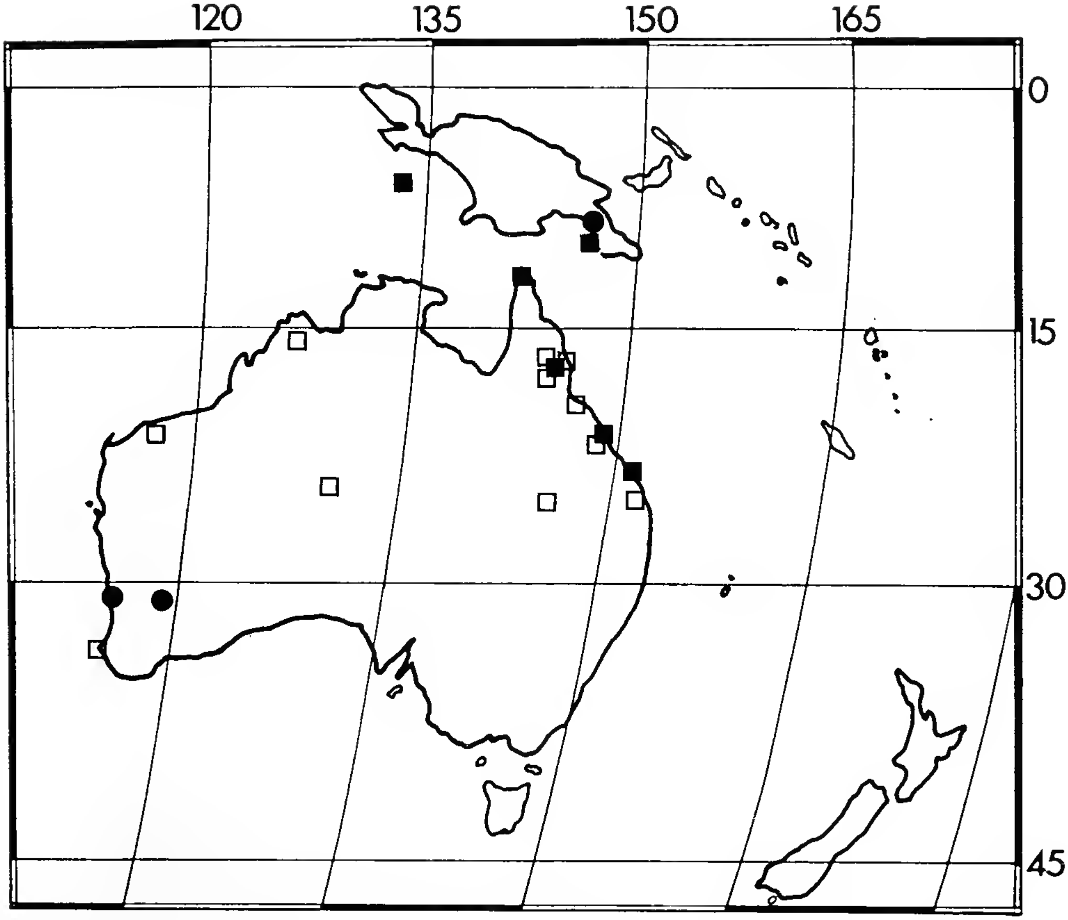
1♂, Popdjetur, Terangan, Aru Island, 10 February 1908 (SMF 2452).

Other material examined

Australia: Queensland: 1♀, 1 juv., Cape York, Lockerbie, general and beating, 9 December 1986, J. Gallon (QM S3625), 1♂, same data, 25-27 April 1974, G. B. Monteith (QM S3610). 2♂, 2♀, Mt Molloy, P. & F. Little, 1974 (QM S4655). 1♂, Rockhampton, 20 February 1974, G. May (QM S3611). 1♀, Spean Ck. near Mt Molloy, 3-10 November 1975 (QM S4653). 1♂, Mareeba, 15 February 1970, N. C. Coleman (AM KS22267). **Papua New Guinea:** 1♂, Boroko, National Capital District, garden vegetation, 20 October 1985, 1 March 1987, D. J. Court (AM KS30816). 1♀, same data (AM KS30817).

Diagnosis

Both sexes relatively large and robust, with a contrasting abdominal stripe. Embolus and tegulum similar to that of *S. tenuidens* but the tibial apophysis is of a different shape.



Map 2 Distribution of three species of *Simaetha* – *S. robustior* (■); *S. paetula* (□); *S. knowlesi* (●).

Cheliceral posterior tooth is lacking unlike *S. tenuidens*. Central epigynal pocket large, bell-shaped. Insemination ducts distinctive.

Description

Male. Eye field orange-brown to brown, centrally darker, thorax brown. Whole surface and especially the eye surrounds and the lower cephalothorax margin clothed in white, orange and brown hairs. Abdominal scutum less distinctive than in the other species, anterior part light, yellowish, posteriorly central light stripe edged by brown or grey-brown area, whole surface covered with white, grey and brown hairs. Spinnerets orange-grey-brown. Clypeus red-brown with scattered grey and brown hairs. Chelicerae (Figure 9C, F) robust, retromarginal tooth unident. Maxillae and labium brown to dark-brown, scopular margins lighter. Sternum brown, venter beige to grey. Legs I massive and long, brown, prolateral femora darker. Remaining legs shorter and lighter.

Palpal organ (Figure 9B, E) massive, clothed in numerous orange and brown hairs. Embolus relatively short and curved, tibial apophysis cone-shaped, cymbial apophysis large.

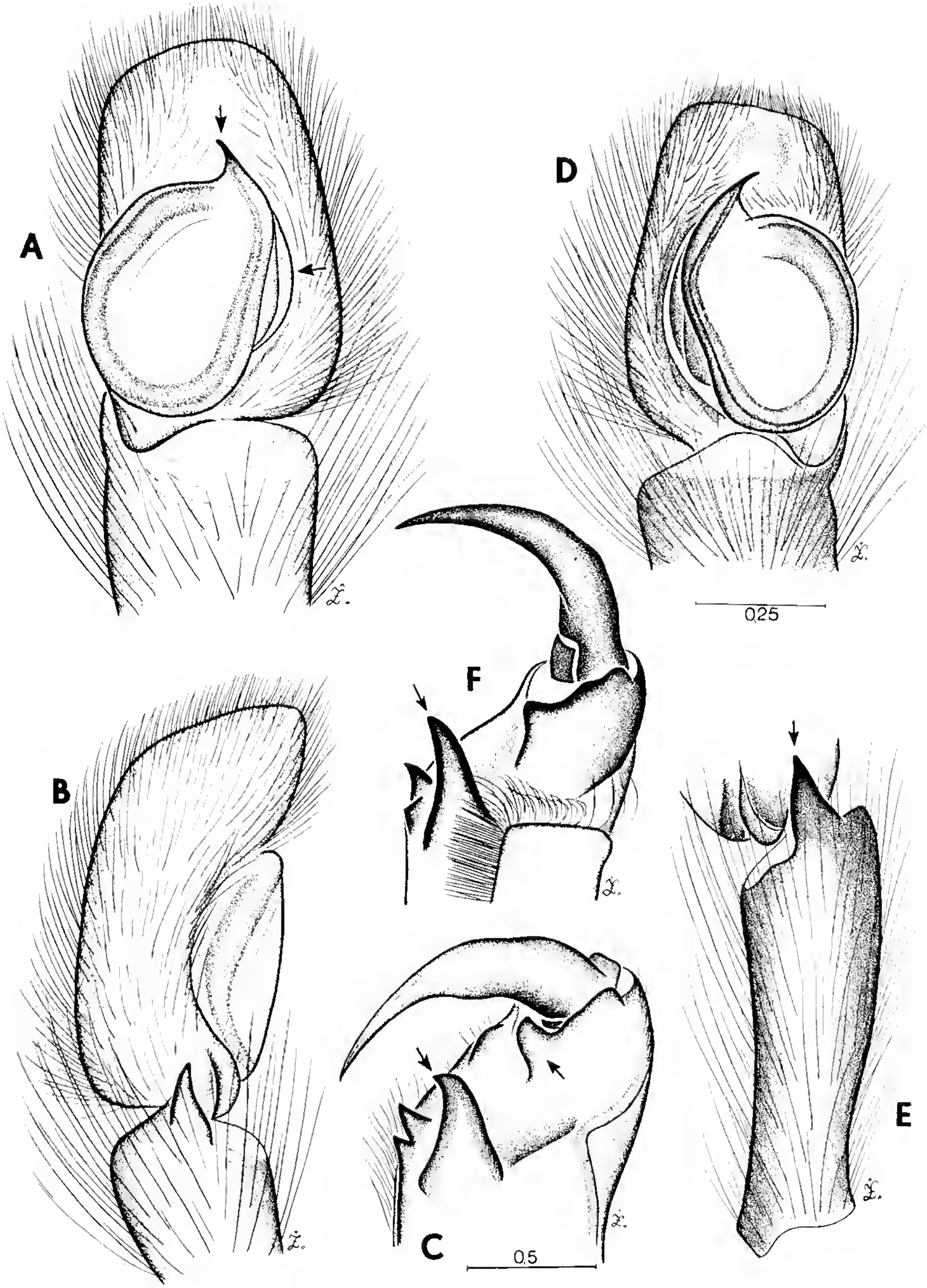


Figure 9 ♂ *Simaetha robustior* (Keyserling, 1882). A–B, D–E – palpal organ: ventral and retrolateral aspects. C, F – chelicerae. (A–C – holotype of *Eulabes robustior*, D–F – holotype of *Dendryphantes laticeps*).

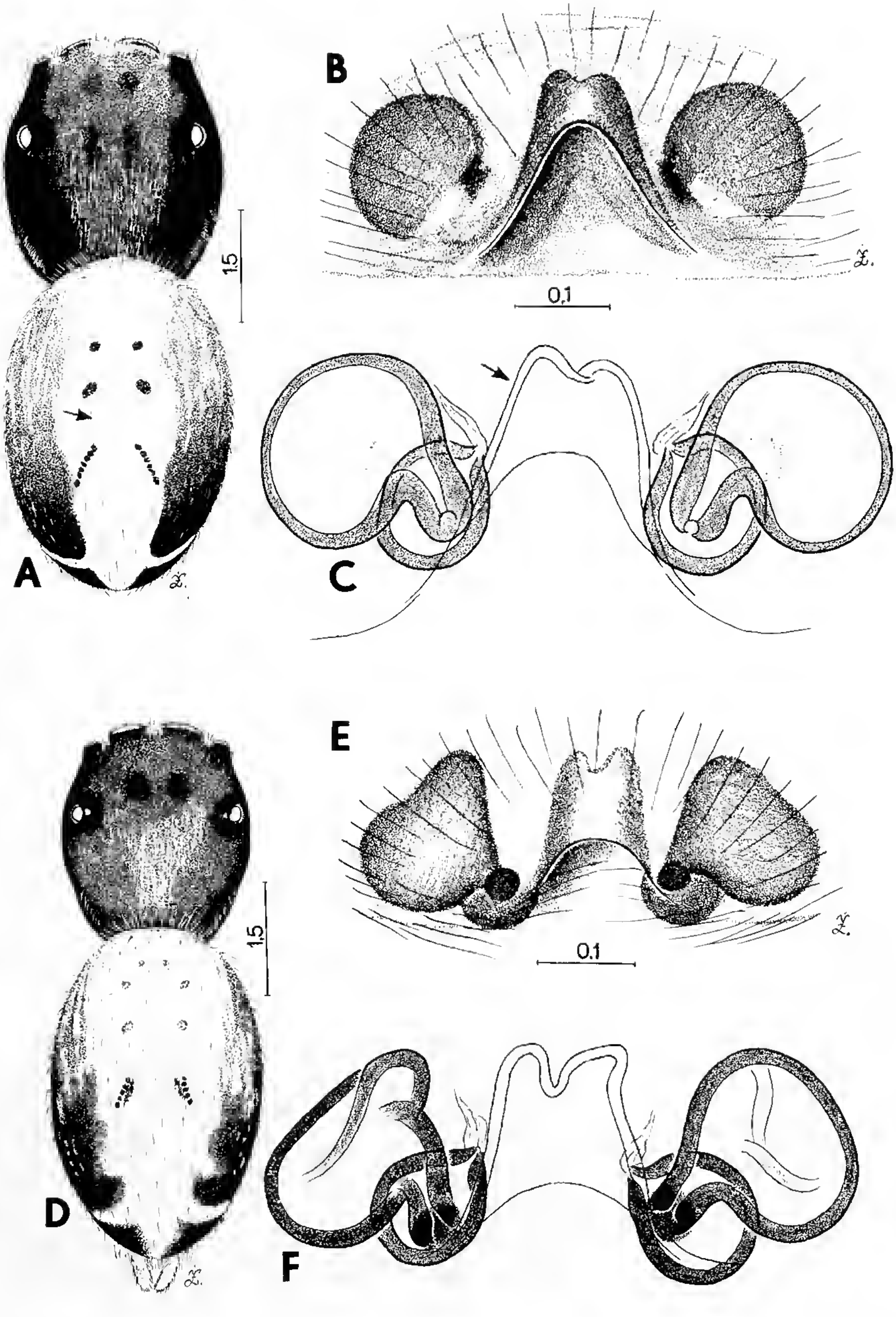


Figure 10 ♀ *Simaetha robustior* (Keyserling, 1882). A, D – general appearance. B–C, E–F – epigyne and internal genitalia.

Dimensions

CL 3.90 (3.20-3.90), EFL 1.60 (1.40-1.60), AEW 2.50 (2.30-2.50), PEW 3.00 (2.65-3.00), AL 4.70 (4.00-4.70).

Female (Figure 10A, D). Colour pattern and hairiness almost identical to that of the male.

Epigyne (Figure 10B-C, E-F) with large, bell-shaped central pocket. Insemination ducts distinctive, intermediate canals not visible.

Dimensions

CL 3.10-3.50, EFL 1.40-1.50, AEW 2.20-2.40, PEW 2.70-2.85, AL 4.00-5.20.

Simaetha knowlesi sp. nov.

Figures 11-12, Map 2

Holotype

1♂, Miling, Western Australia, Australia, 13 December 1974, A. Page (WAM 91/588).

Paratypes

Australia: Western Australia: 1♀, allotype, 23 km S Bungalbin Hill, on *Eremophila* flowers, 18 November 1990, D. Knowles (WAM 91/580). **Papua New Guinea:** 1♂, paratype, Laloki, Central Prov., ex *Citrus*, 3 December 1979, L. S. Mitkita (AM KS30818).

Diagnosis

In comparison with the related *Simaetha robustior* the abdominal light stripe is lacking, the subtegulum is smaller and the chelicerae have an additional anterior tooth. Epigynal pocket cone- rather than bell-shaped.

Description

Male (Figure 11C). Cephalothorax brown, darker on the eye field and around the eyes, clothed in numerous light hairs. Abdominal scutum greyish-brown with traces of lighter spots. Spinnerets brown. Clypeus orange, fringed with white hairs. Chelicerae (Figure 11D) brown with additional anterior tooth, maxillae, labium and sternum brown, venter grey-beige. Legs I long, dark-brown, remaining legs lighter.

Palpal organ (Figure 11A-B) similar to that of *S. robustior* but subtegulum is much smaller.

Dimensions

CL 3.20, EFL 1.40, AEW 2.20, PEW 2.70, AL 3.80.

Female (Figure 12A) robust and dark. Cephalothorax dark-brown, darker on eye field and black around eyes, clothed in numerous light-grey hairs. In the vicinity of the eyes dark-brown bristles are also present. Abdomen dark-grey, spinnerets dark-brown. Clypeus orange, fringed with numerous white hairs. Chelicerae, maxillae, labium and brown, sternum slightly lighter, venter greyish-brown. Legs I massive and long, dark-brown, remaining legs lighter – especially dorso-ventrally and distally.

Epigyne (Figure 12B-C) similar to that of *Simaetha robustior* but the central pocket cone-rather than bell-shaped.

Dimensions

CL 3.33, EFL 1.70, AEW 2.60, PEW 3.10, AL 5.00.

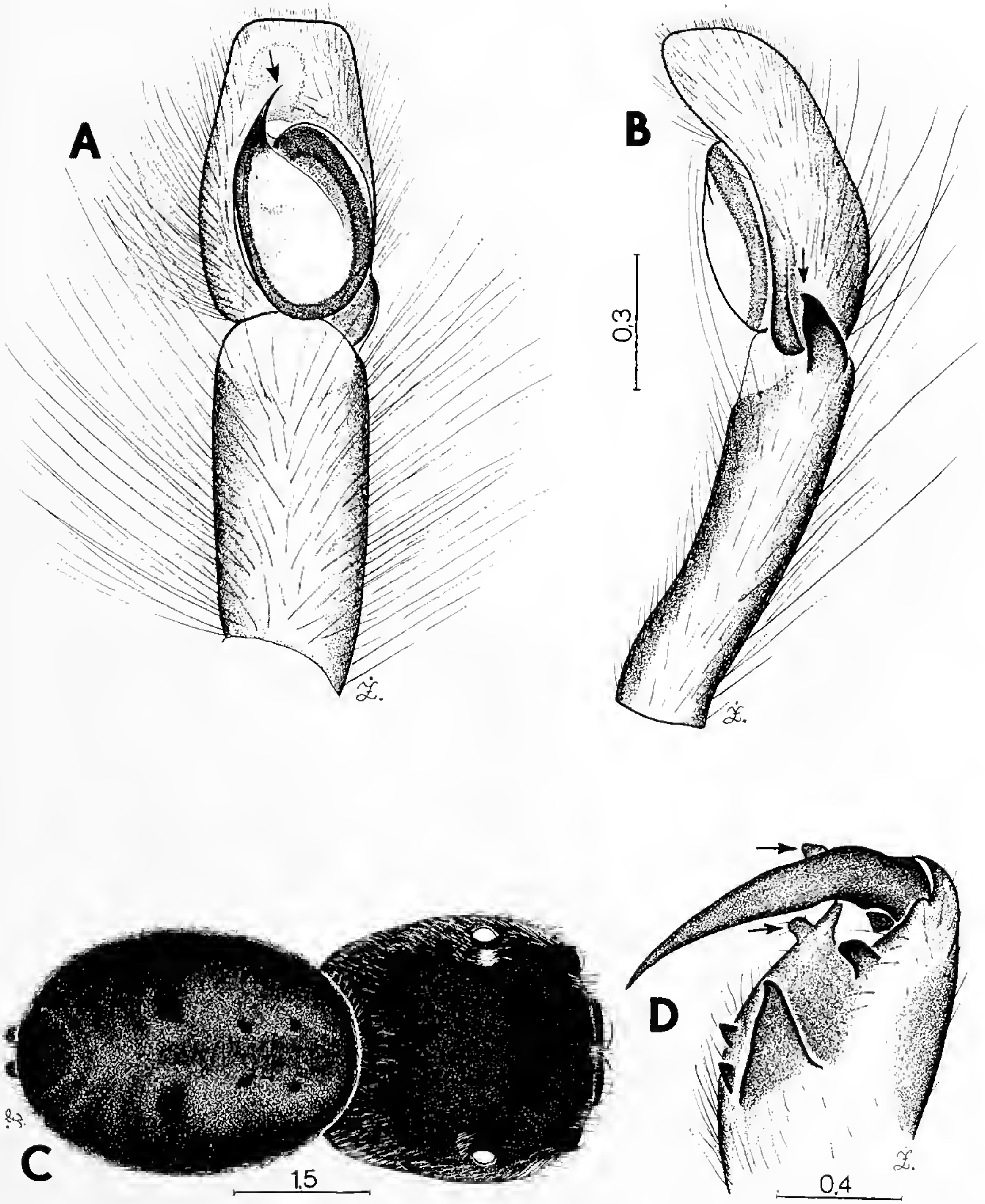


Figure 11 ♂ *Simaetha knowlesi* sp. nov. A–B – palpal organ: ventral and retrolateral aspects. C – general appearance. D – chelicera.

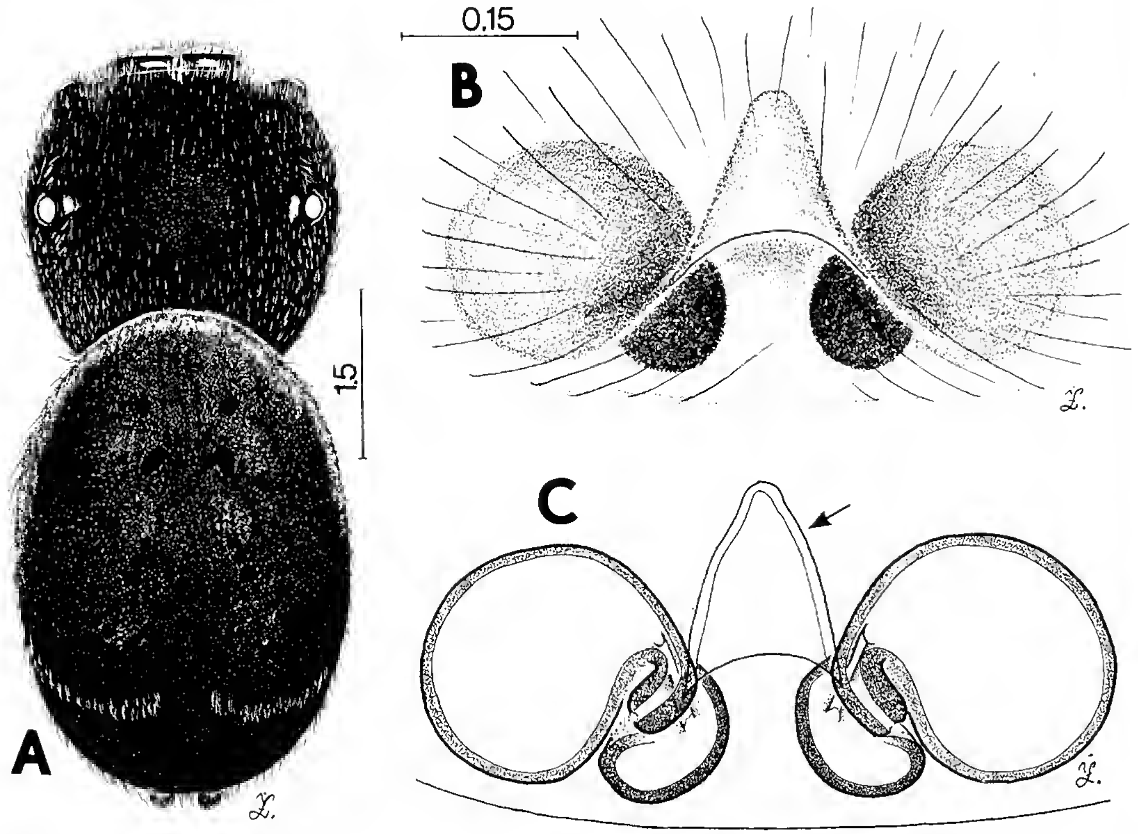


Figure 12 ♀ *Simaetha knowlesi* sp. nov. A – general appearance. B–C – epigyne and internal genitalia.

Etymology

The specific name is proposed in honour of Mr David Knowles (Trigg, Western Australia), Australian naturalist and photographer, collector of many rare species of Salticidae.

Simaetha paetula (Keyserling)

Figures 13-14, Map 2

Eulabes paetulus Keyserling, 1882: 1388.

Simaetha paetula: Simon, 1903: 832.

Syntypes

1♂, 1♀, Port Mackay, Queensland, Australia (ZMH, Mus. Godeffroy Nr. 8336).

Other material examined

Australia: Queensland: 1♂, 3♀, Molloy Road, 18 February 1972, N. C. Coleman (QM S4618). 4♂, 4♀, Davies Ck., summer 1971-72, N. C. Coleman (QM S4621). 1♀, Townsville, webs nest, 26 January 1981, R. R. Jackson (QM S4624). 3♂, 2♀, Clifton Beach, summer 1971-72, N. C. Coleman (QM S4620). 1♀, Koah Road, 2 April 1972, N. C. Coleman (QM S4622). 5♂, 3♀, 1 juv., Mt Garnet, 24 February 1974, N. C. Coleman (QM S4623). 1♀, 1 juv., Gin Gin, 8 August 71, N. C. Coleman (QM S4617). 1♂, 3 juv., Oak Forest, summer 1972, N.

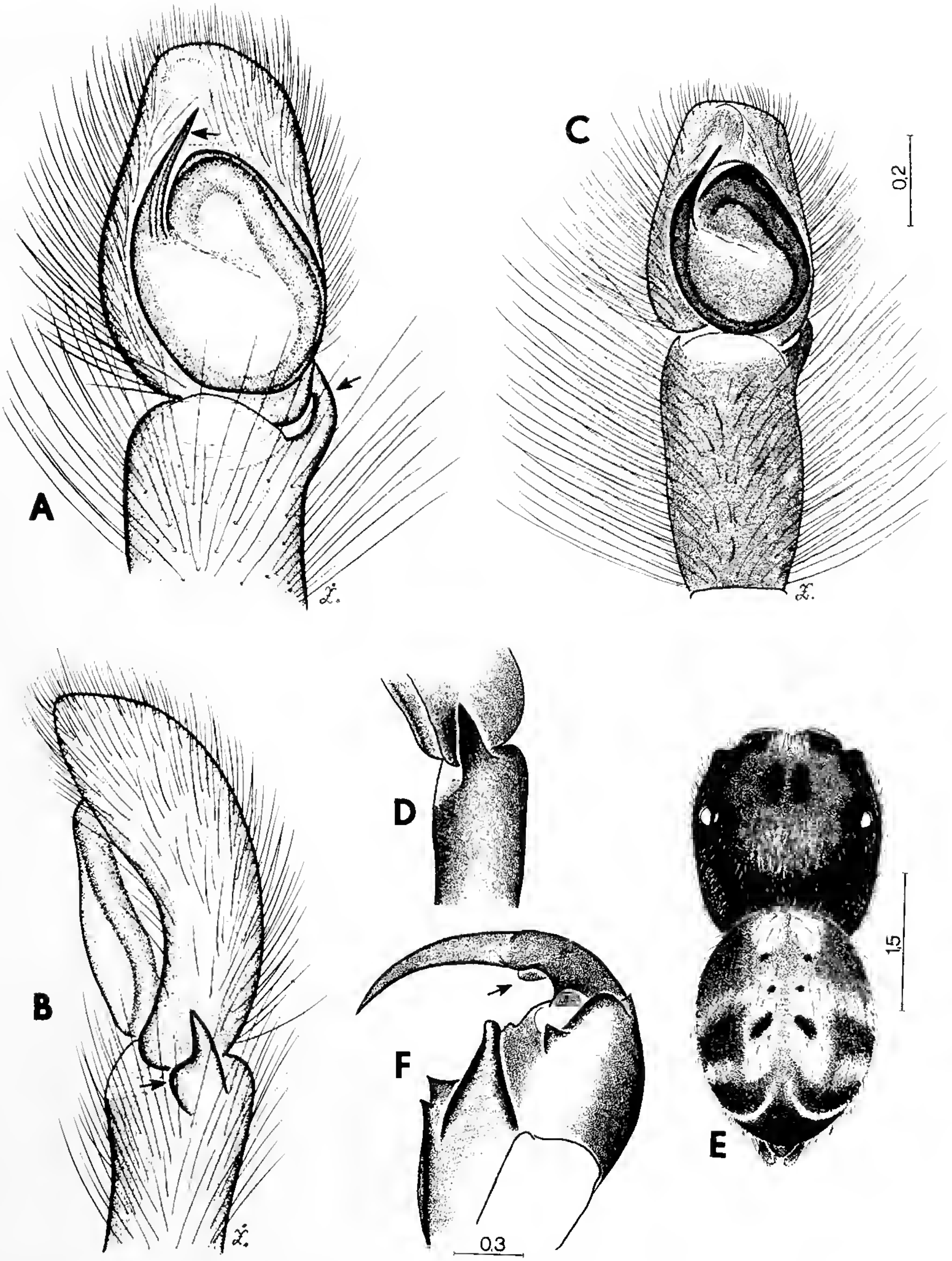


Figure 13 ♂ *Simaetha paetula* (Keyserling, 1882). A–D – palpal organ: ventral and retrolateral aspects. E – general appearance. F – chelicera. (A–B – syntype).

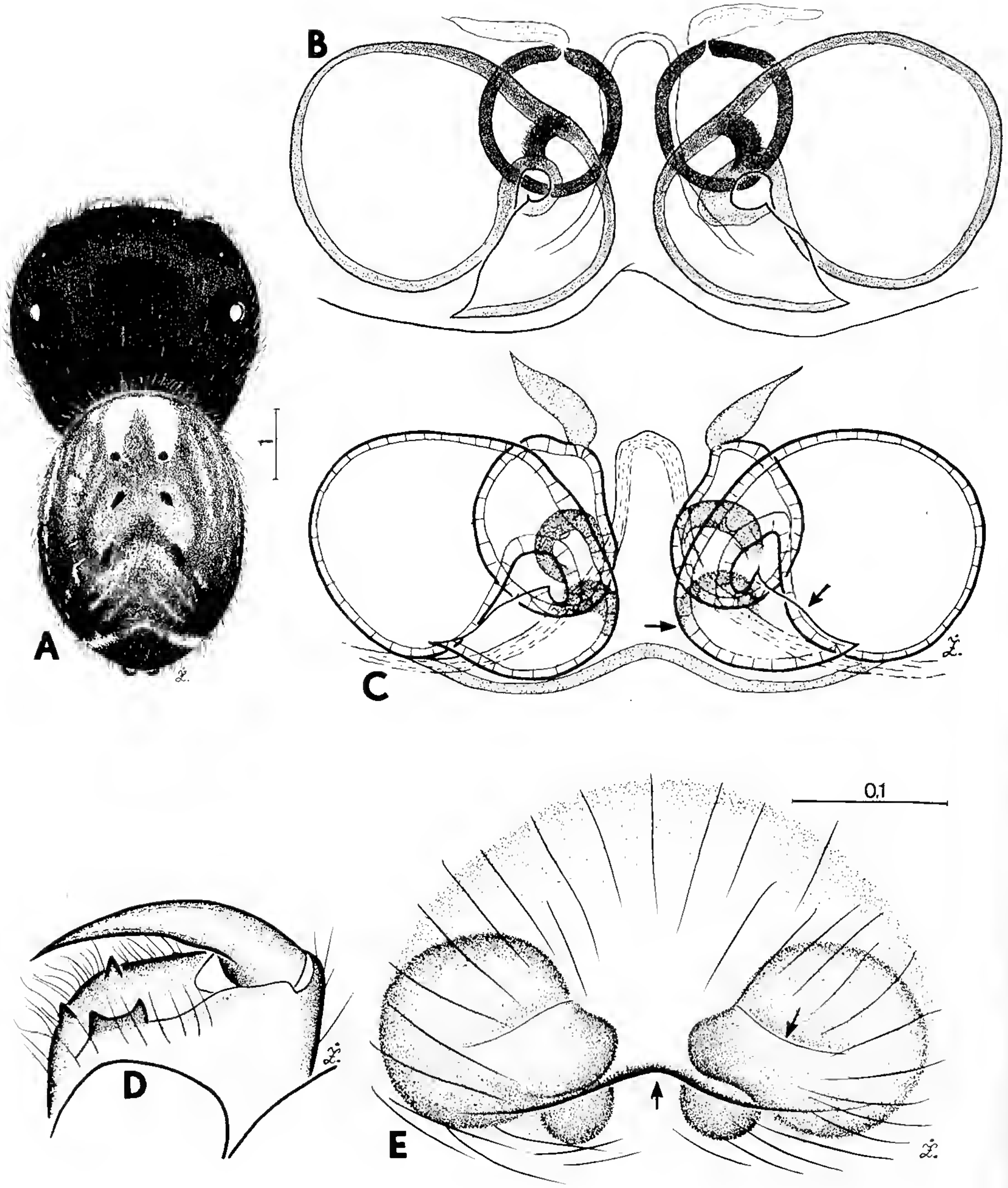


Figure 14 ♀ *Simaetha paetula* (Keyserling, 1882). A – general appearance. B–C, E – epigyne and internal genitalia. D – chelicera. (C–E – syntype).

C. Coleman (QM S4625). 1♀, 1 juv., Trinity Beach, summer 1971-72, N. C. Coleman (QM S4619). 1♀, Christies, Majors Ck., rainforest, general collection, 19 July 1986, J. Rienks, Cole (QM S3613). 1♀, Cairns, 13 June 1969, N. C. Coleman (AM KS18953). 1♀, Mareeba, 1951, J. G. Brooks (AM KS17899). 1♂, same locality, 15 February 1970, N. C. Coleman (AM KS22266). 1♀, North Camp Beagle, 45 km N Arakum, March 1982 (AM KS9062). **Western Australia:** 1♀, Drysdale River Station, wood house, 21 July 1990, A. F. Longbottom (WAM 91/582). 1♂, 4 km SW of Giles Ck. crossing, 17-18 January 1990, M. S. Harvey, T. F. Houston (WAM 91/584). 1♀, Dampier, mangroves, 24 May 1990, A. F. Longbottom (WAM 91/581). 1♀, 4 km E of Gallows Beach, in garden of 'Ironstone' house, 3 June 1986, J. Waldock (WAM 91/583). **Papua New Guinea:** 1♀, 1 juv., Izzy Dizzy, Morobe Prov., under bark of *Araucaria cunninghamii*, 24 September 1970, B. Gray (AM KS13274).

Diagnosis

Abdominal pattern similar to that of *S. thoracica* but the females are more robust. The embolus is longer than in the other species and the subtegulum is not visible. The epigyne has large, cup-like copulatory openings and the insemination ducts are definitely the longest of all the species.

Description

Male (Figure 13E). Cephalothorax robust and hairy, thoracic part light- to dark-brown, eye field lighter with two darker spots and darker eye surrounds. Hairs numerous: short white and longer brown, the first forming tufts between the anterior median eyes. Abdominal scutum light- to dark-brown, posteriorly and laterally darker, with lighter central pattern. Spinnerets dark-orange to brown. Clypeus orange- brown with sparse orange and brown hairs. Chelicerae (Figure 13F) brown, their armament similar to that of *S. robustior* (Keyserling), cheliceral fang with anterior outgrowth. Maxillae and labium orange-brown to dark-brown, scopular margins lighter. Sternum brown, venter grey-orange to grey. Legs I long and massive, brown, darker on prolateral surfaces (femora), remaining legs slightly lighter – especially their distal segments.

Palpal organ (Figure 13B, D) brown with numerous brownish hairs. Embolus relatively long and straight, subtegulum invisible, cymbial apophysis small, tibial apophysis laterally curved.

Dimensions

CL 2.76 (1.90-3.50), EFL 1.32 (1.10-1.50), AEW 2.04 (1.40-2.30), PEW 2.46 (1.60-2.80), AL 3.06 (2.10-3.90).

Female (Figure 14A). The shape and colouration of the cephalothorax as in the male. Abdomen lighter than in the male, light-brown to dark-grey-brown, central pattern and sides lighter. Spinnerets yellowish to grey-brown. Clypeus dark-orange to brown, fringed with long white hairs. Chelicerae, maxillae and labium orange to brown, sternum darker. Pedipalps orange, fringed with numerous white and dark hairs. Venter yellow-beige to grey. Legs I orange to brown, remaining legs yellow to orange, lighter distally, segments darker around the joints.

Epigyne (Figure 14B-C, E) with creviced copulatory openings, insemination ducts long, central pocket visible only after maceration.

Dimensions

CL 3.06 (2.70-3.10), EFL 1.32 (1.20-1.40), AEW 2.04 (2.00-2.10), PEW 2.58 (2.40-2.70), AL 4.58 (4.00-4.40).

Simaetha tenuior (Keyserling)

Figures 15-17, Map 3

Eulabes tenuior Keyserling, 1882: 1399.

Simaetha tenuior: Simon, 1903: 833.

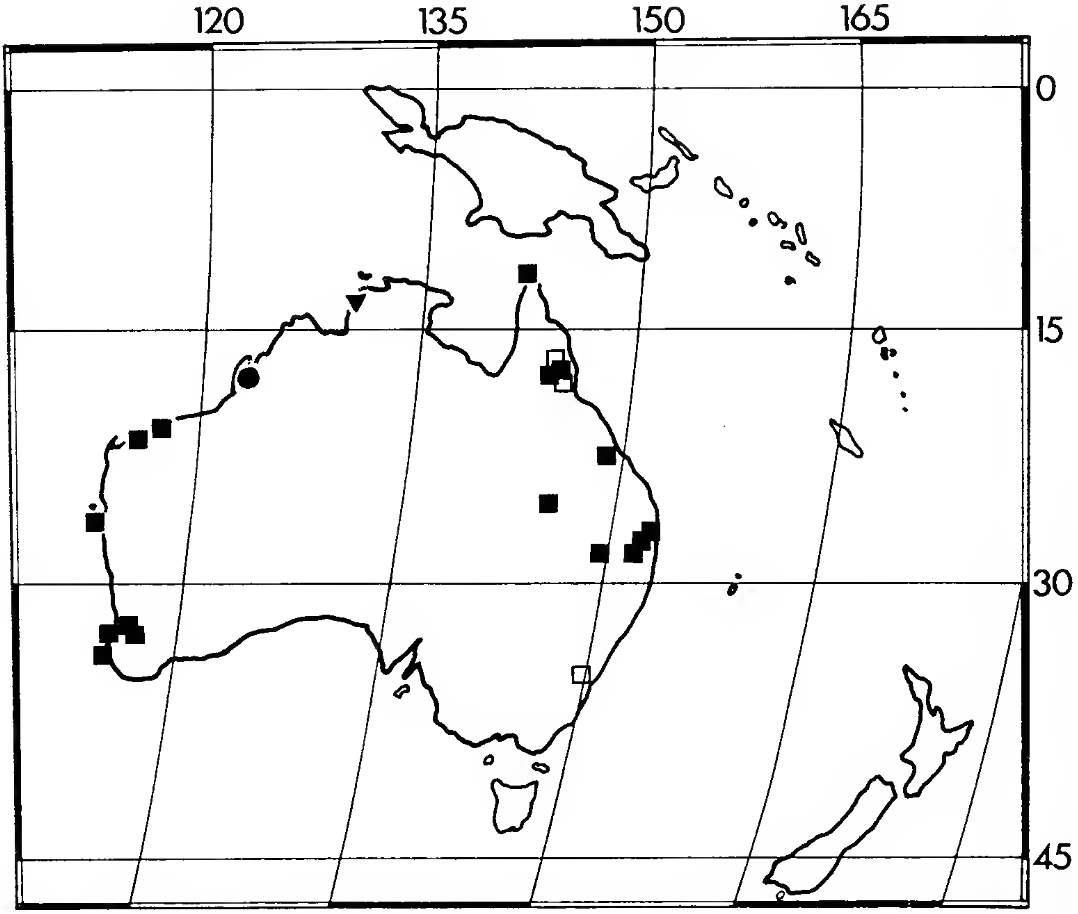
Simaethula tenuior: Rainbow, 1911: 312.

Syntypes

2♂, Peak Downs, Queensland, Australia (ZMH, Mus. Godeffroy Nr 7687).

Other material examined

Australia: Queensland: 1♀, Cape York, Sanamere Swamp near Jardine River, general collection, 3 September 1985, M. Bennie (QM S6917). 1♂, Camira, 4 December 1987, R. Raven (QM S2457). 1♀, Boobbin Head, 19 March 1970, A. B. Rose (AM KS30819). 1♂, Lake Broadwater via Dalby, sweeping, 22 February 1985, M. Bennie, V. Davies (QM S4649). 2♀, 1 juv., Brisbane (QM 4682). 2♂, 1 juv., Brisbane, Fig Tree Pocket, Roedean Street, 30 November 1977, 22 November 1980, V. Davies (QM S4677, S4637). 1♀, 4 juv., Mulgowie, 25 March 1981, M. D. Grant (QM S4630). 1♀, Oak Forest, summer 1972, N. C. Coleman (QM S6914). 1♂, Acacia Ridge, from wasp (*Scelephron formosum*, Sphecidae) nest, 10 December 1973, T. Dahms (QM S3615). 1♂, Altonvale



Map 3 Distribution of four species of *Simaetha* – *S. tenuior* (■); *S. almadenensis* (□); *S. atypica* (▼); *S. broomei* (●).

Stn., Horn, W Westmar, 10 January 1979, V. Davies, T. Adams, R. Raven (QM S6911). 2♂, Mt Molloy Road, 18 February 1972, N. C. Coleman (QM S6912). 1♀, same locality, September 1974, P. & F. Little (QM S6913). 1♂, 20 m E of Emerald, 6 April 1971, R. Monroe (QM S4689). 1♂, Koah Road, 2 April , N. C. Coleman (QM S4656). 1♂, Lake Broadwater, grass, 21 December, M. Bennie (QM S4635). 1♂, 1 juv., Laidley Ck., 28 September – 13 October 1981. M. Grant (QM S4657). **Western Australia:** 5♂, 12♀, 43 juv., Barrow Is., sweeping *Olearia axilaris*, *Acacia victoria*, *Acacia coriacea*, mixed shrubs, mangrove, 4-20 February 1977 (QM

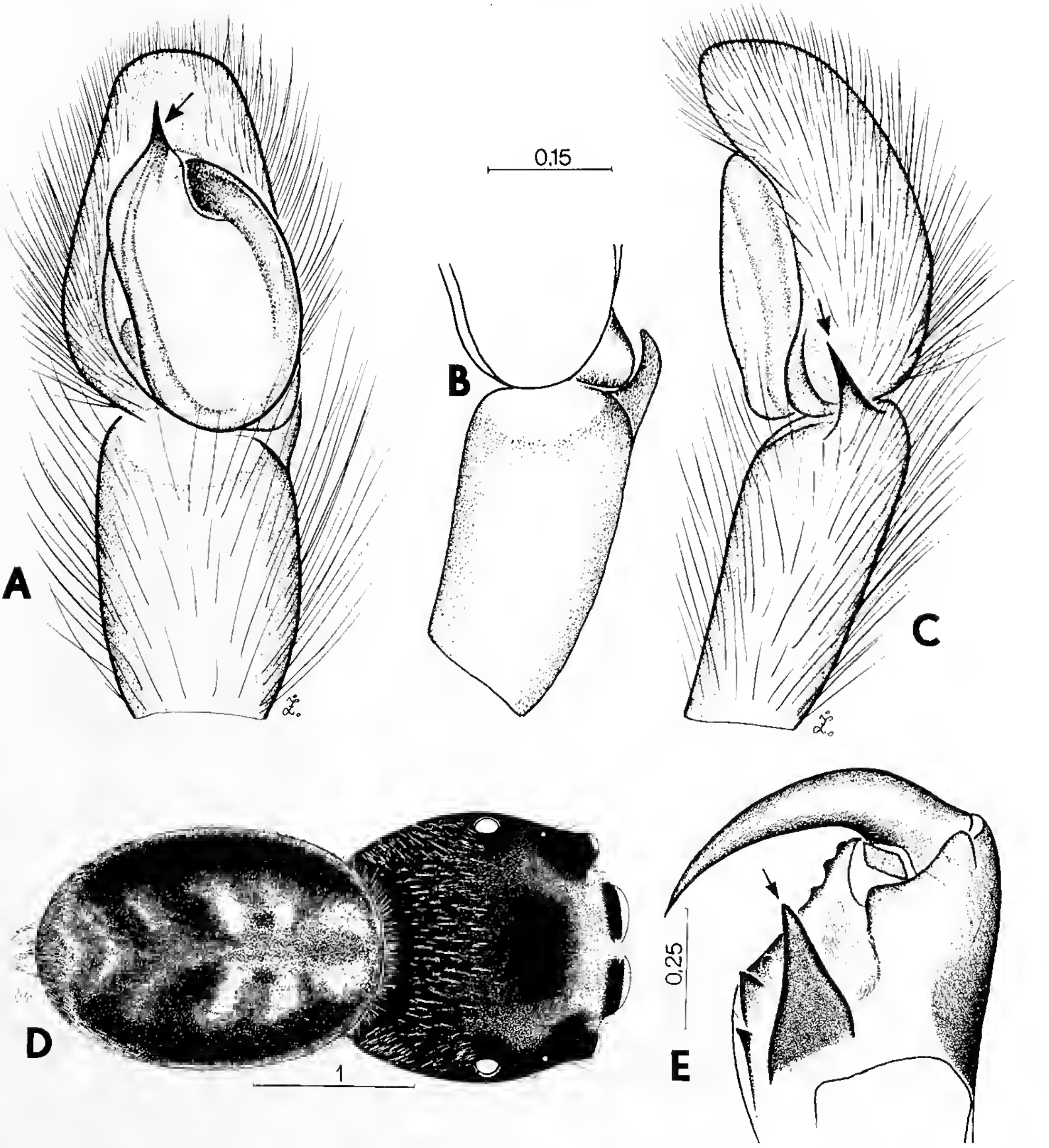


Figure 15 ♂ *Simaetha tenuior* (Keyserling, 1882). A–C – palpal organ: ventral, ventrolateral and retrolateral aspects. D – general appearance. E – chelicera. (A–C, E – syntype).

S3630, S4686, S4673, S4683, S3629, S4685). 1♂, Parmelia, on *Philodendron* leaf, 26 February 1987 (WAM 88/2152). 1♂, Parmelia near Kwinana, 6 April – 1 May 1989, A. E. de Jong (WAM 91/590). 1♂, Yangebup, 11 April 1985, D. Mead-Hunter (WAM 91/594). 1♂, Perth, WA Museum building, S. Slack-Smith, 11 April 1990 (WAM 91/591). 1♀, Karratha, NW of airport, mangrove, curled leaves with Clubionidae, 26 May 1990, A. F. Logbottom (WAM 91/586). **Papua New Guinea:** 1♂, Wau, Morobe Prov., 22 September 1970 (AM KS13252). 1♀, same data (AM KS13253). 1♂, Bulolo, Morobe Prov., 18 September 1970 (AM KS13237). 1♀, Izzy Dizzy, Morobe Prov., 24 September 1970 (AM KS13279).

Diagnosis

A relatively small spider. In comparison with the other species the embolus is straight and short and the tibial apophysis is set more dorsally. The epigyne has diagonal ridges (crevices), the pocket is distinctive and close to the epigastric furrow, insemination ducts are short.

Description

Male (Figure 15D). Cephalothorax orange to dark-brown, lighter anteriorly. Central eye field and eye surrounds black. Whole surface covered with white and less numerous brown

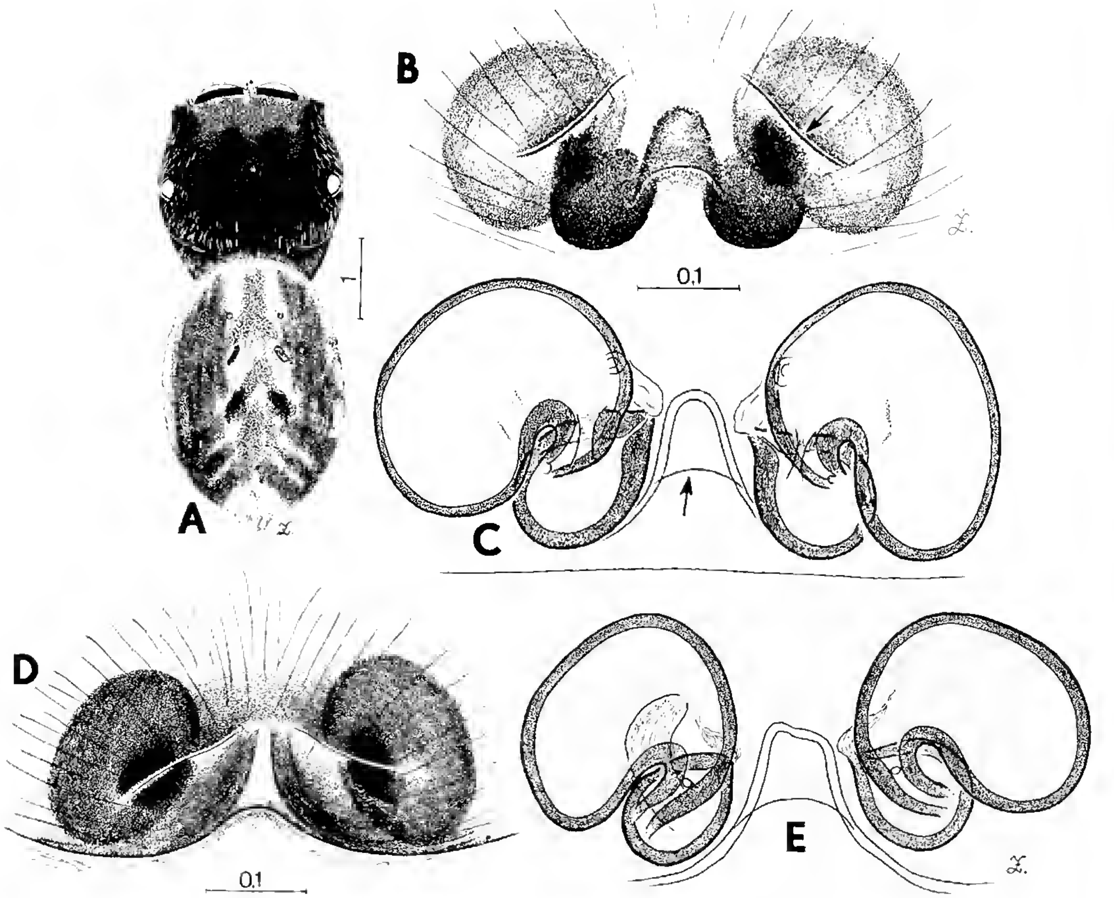


Figure 16 ♀ *Simaetha tenuior* (Keyserling, 1882). A – general appearance. B–E – variability of epigyne and internal genitalia.

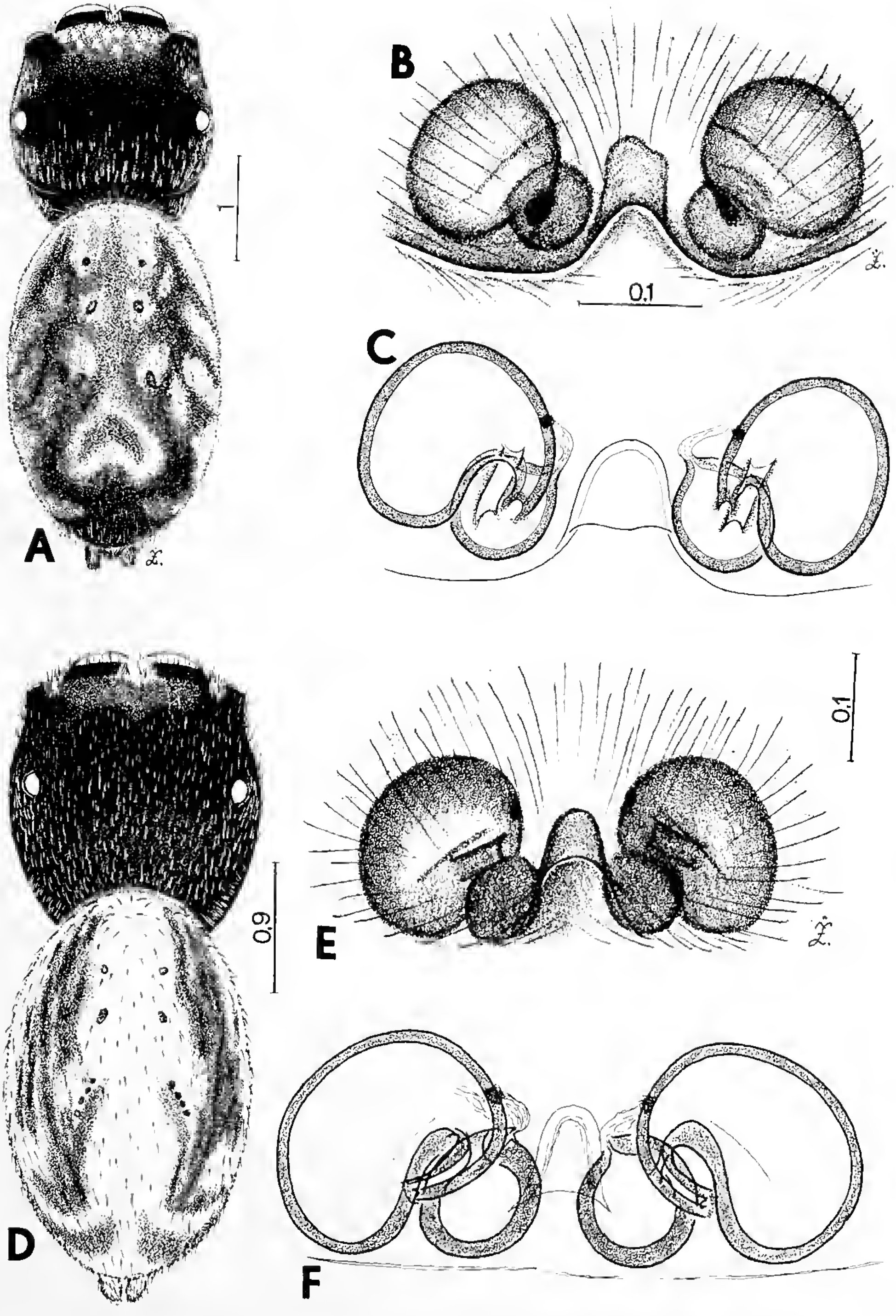


Figure 17 ♀ *Simaetha tenuior* (Keyserling, 1882). A, D – variability of general appearance. B–C, E–F – variability of epigyne and internal genitalia.

hairs. Abdominal scutum dirty-orange to grey-brown, darkening laterally and posteriorly, with more or less visible central pattern and with light sides. Spinnerets orange to brown. Clypeus brown, fringed with white hairs. Chelicerae (Figure 15E) orange to brown, distally lighter, with retromarginal single tooth, cheliceral fang with anterior outgrowth. Maxillae, labium and sternum brown, the first with light scopular margins. Venter orange to grey-brown with longitudinal rows of lighter spots. Legs I much longer than the others, rather slender, orange to dark-brown with darker femora. Remaining legs lighter with darker joint-areas.

Palpal organ (Figure 15A-C) with straight embolus, tibial apophysis curved and set more dorsally than in the other species.

Dimensions

CL 2.30 (1.75-2.30), EFL 1.00 (0.90-1.10), AEW 1.70 (1.45-1.70), PEW 1.90 (1.65-1.90), AL 2.65 (2.05-3.00).

Female (Figure 16A, 17A, D). Cephalothorax orange to brown with darker cephalic spots and dark eye surrounds. Whole surface clothed with numerous white and less numerous brown hairs. Abdomen grey-brown, centrally lighter, posteriorly darker, with mosaic of lighter spots and stripes. Spinnerets light-grey to grey-brown. Clypeus orange to brown, covered with white hairs. Chelicerae, maxillae and labium orange to brown. Pedipalps yellow to brown with numerous white and single brown hairs. Sternum yellow to brown. Venter light-grey to beige-brown. Legs I yellow-orange to dark-brown, femora darker, remaining legs lighter with darker terminal areas.

Epigyne (Figure 16B-E, 17B-C, E-F) with transverse ridges, pocket located posteriorly.

Dimensions

CL 1.65-2.50, EFL 0.85-1.15, AEW 1.20-1.85, PEW 1.20-2.10, AL 2.00-3.30.

Simaetha broomei sp. nov.

Figure 18, Map 3

Holotype

♀, 206 km E of Broome, Western Australia, Australia, 24 August 1987, A. E. de Jong (WAM 91/579).

Diagnosis

Proximal spermathecae relatively larger than in the other species, cephalothorax not flattened, "normal".

Description

Female (Figure 18A). Cephalothorax brown, anteriorly lighter, eye surrounds black. Anterior thorax and sides covered with white hairs. Around eyes white and longer, light-brown hairs. Abdomen macerated (colour pattern reconstructed), grey-brown with traces of a lighter central stripe. Spinnerets light-brown. Clypeus brown with single white hairs, chelicerae brown, maxillae and labium dark-brown, the latter with lighter tips. Sternum beige. Legs I brown with darker femora, remaining legs lighter, dirty-orange with darker joint-areas.

Epigyne (Figure 18B-C) similar to that of *S. tenuior* but proximal spermathecae relatively larger.

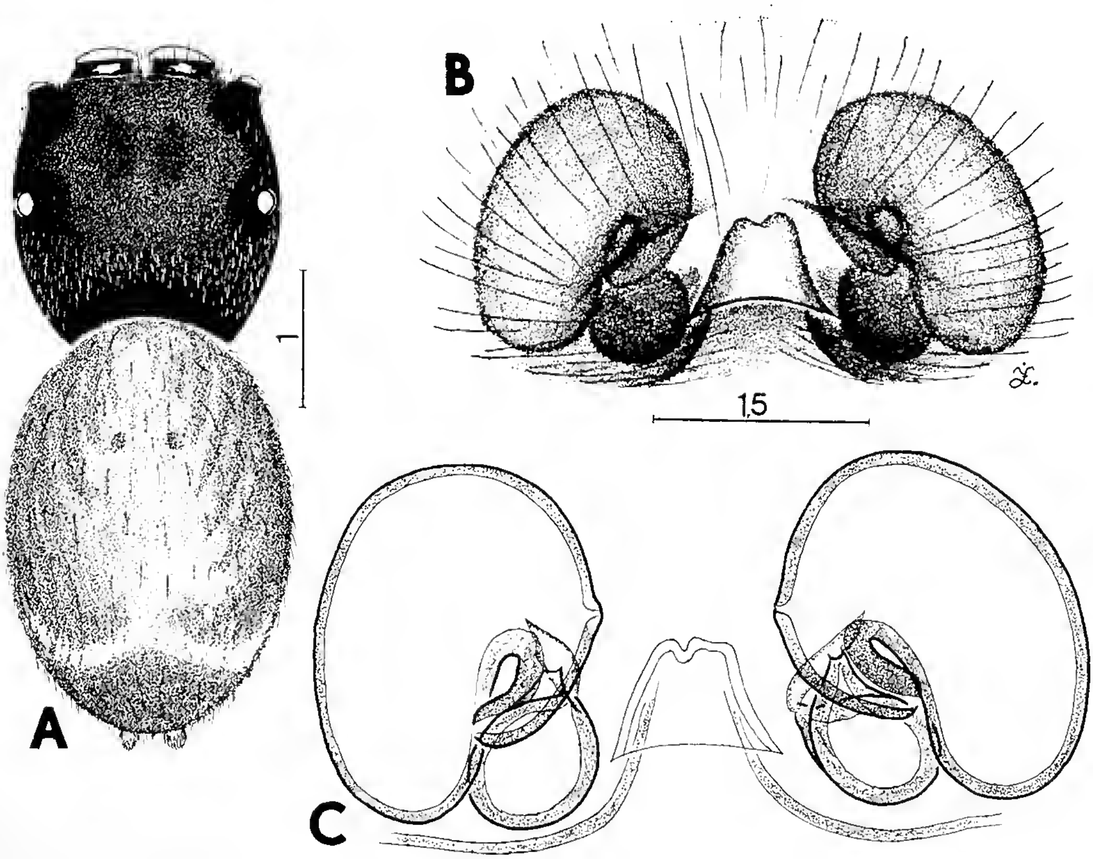


Figure 18 ♀ *Simaetha broomei* sp. nov. A – general appearance. B–C – epigyne and internal genitalia.

Dimensions

CL 2.15, EFL 0.95, AEW 1.60, PEW 1.80, AL 3.00.

Etymology

The name is derived from type locality.

Simaetha almadenensis sp. nov.

Figure 19, Map 3

Holotype

♂, Almaden, Chillagoe Distr., Queensland, Australia, 1928, W. D. Campbell (AM KS9036).

Paratypes

Australia: Queensland: 1♂, Eureka Ck, 11 February 1972, N. C. Coleman (QM S4616). **New South Wales:** 1♂, paratype, Tuross, 17-22 January 1936, K. C. McKeown (AM KS30820).

Diagnosis

A relatively small spider. Genitalia and cheliceral dentition similar to that of *S. atypica* but the body is almost uniform in colour and the spinnerets are much shorter.

Description

Male (Figure 19D). Cephalothorax brown, eye surrounds darker with scattered whitish hairs, similar hairs along lower margin. Abdominal scutum light-brown, darkening posteriorly and laterally, colour pattern very delicate. Sides light-grey, spinnerets greyish-brown. Clypeus

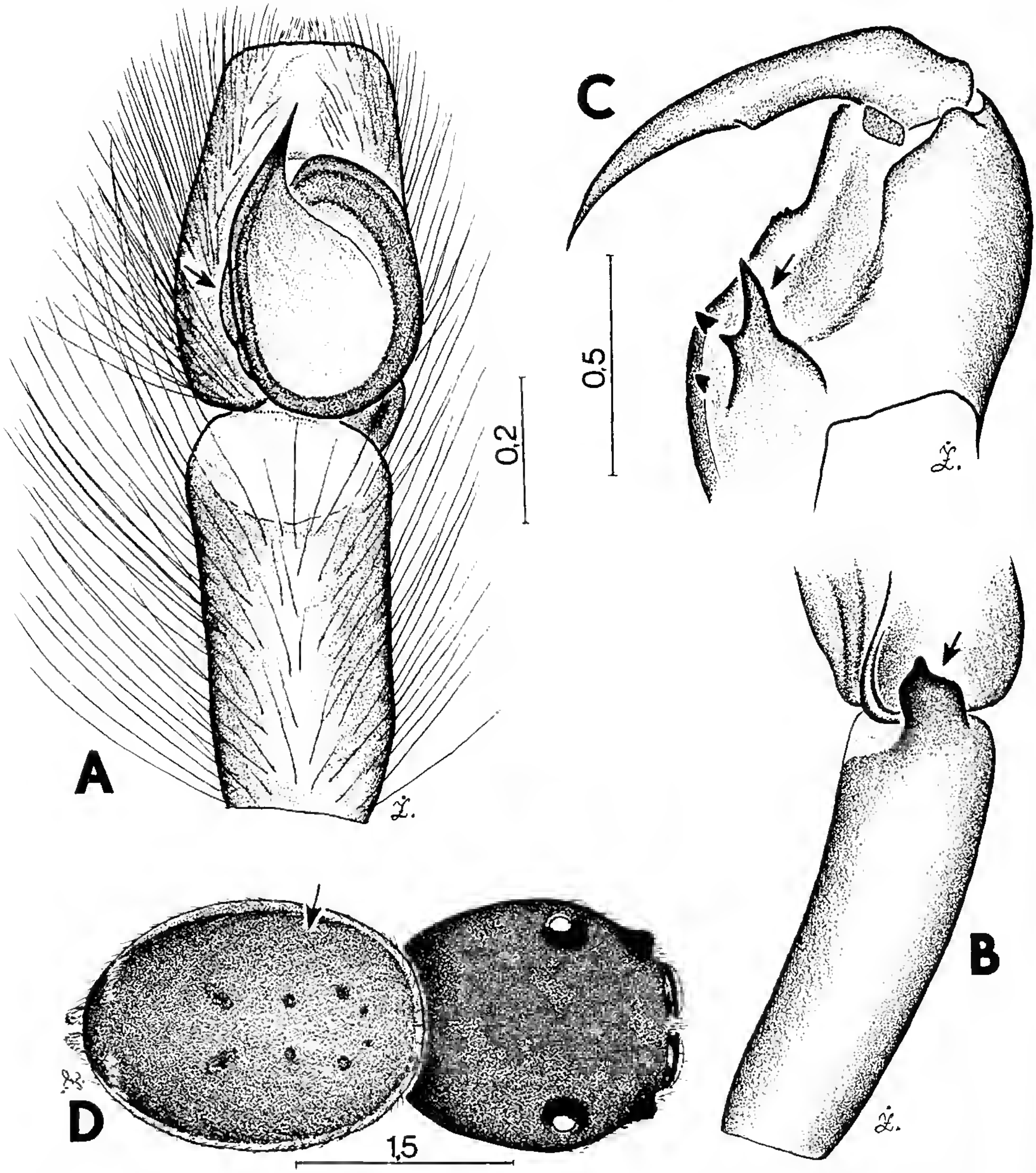


Figure 19 ♂ *Simaetha almadenensis* sp. nov. A–B – palpal organ: ventral and retrolateral aspects. C – chelicera. D – general appearance.

orange-brown, with very short scale-like hairs centrally. Chelicerae (Figure 19C) light-brown with a fissidentate retromarginal tooth. Maxillae and labium dark-brown with lighter scopular margins. Sternum orange-brown, venter beige. Legs I brown, remaining legs lighter and more delicate.

Palpal organ (Figure 19A-B). Embolus straight, subtegulum and cymbial apophysis relatively small, tibial apophysis spatular.

Dimensions

CL 2.70 (2.10-2.70), EFL 1.20 (0.90-1.20), AEW 1.90 (1.60-1.90), PEW 2.22 (1.80-2.22), AL 3.50 (2.15-3.50).

Etymology

The name is derived from type locality.

Simaetha atypica sp. nov.

Figures 20-21, Map 3

Holotype

♂, S Alligator Inn, Northern Territory, Australia, 7-9 July 1979, rainforest, G. B. Monteith, D. Cook (QM S4666).

Paratype

Australia: Northern Territory: 1♀, allotype, Peter Bridge Is., 28 June 1969, H. Heatwole (QM S6915).

Diagnosis

Spinnerets longer than in the other species, subtegulum more distinctive than in the closely related *S. almadenensis*, epigynal pocket located anteriorly.

Description

Male (Figure 20A). Cephalothorax orange-brown, lighter along the thorax and on the eye field, darker around eyes and towards lower margins. Hairs sparse, white and brownish. Abdominal scutum scarcely marked, centrally dirty-orange, posteriorly and laterally turning grey, anteriorly surrounded by a light band. Spinnerets rather long, greyish with lighter tips. Clypeus orange-brown with scarce yellowish hairs. Chelicerae (Figure 20D) orange with retromarginal fissidentate tooth. Maxillae and labium long, dark-brown, scopular margins orange. Sternum orange with dark-grey bump, venter light. Legs I dirty-orange with darker joint-areas, remaining legs lighter.

Palpal organ (Figure 20B-C) is similar to that of *S. almadenensis* but embolus shorter and the subtegulum more distinctive.

Dimensions

CL 2.05, EFL 1.00, AEW 1.70, PEW 1.90, AL 2.50.

Female (Figure 21A). Cephalothorax generally brown with black eye surrounds and a darker spot on the eye field. Whole surface, especially thorax covered with white and less numerous brown hairs. Abdomen with a light central stripe and with a mosaic of light and grey-brown irregular spots and stripes. Spinnerets longer than in the other species, greyish. Clypeus brown, fringed with long white hairs, around anterior median eyes tufts of white short setae. Chelicerae, maxillae and labium brown, the last with lighter scopular margins.

Pedipalps lighter with numerous light and dark hairs. Sternum brown, darker centrally, venter grey. Legs I light-brown, remaining legs lighter with grey joint-areas.

Epigyne (Figure 21B-C) similar to that of the other species but with pocket located anteriorly.

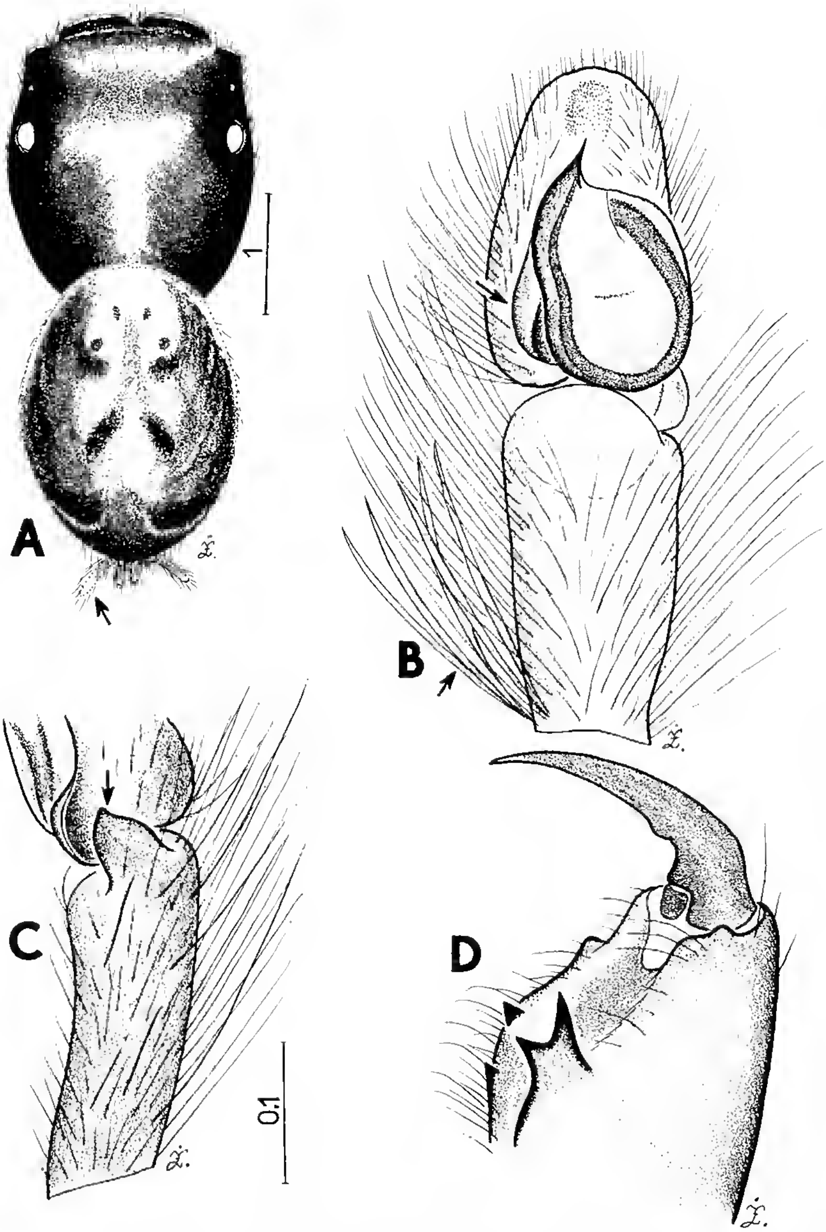


Figure 20 ♂ *Simaetha atypica* sp. nov. A – general appearance. B–C – palpal organ: ventral and retrolateral aspects. D – chelicera.

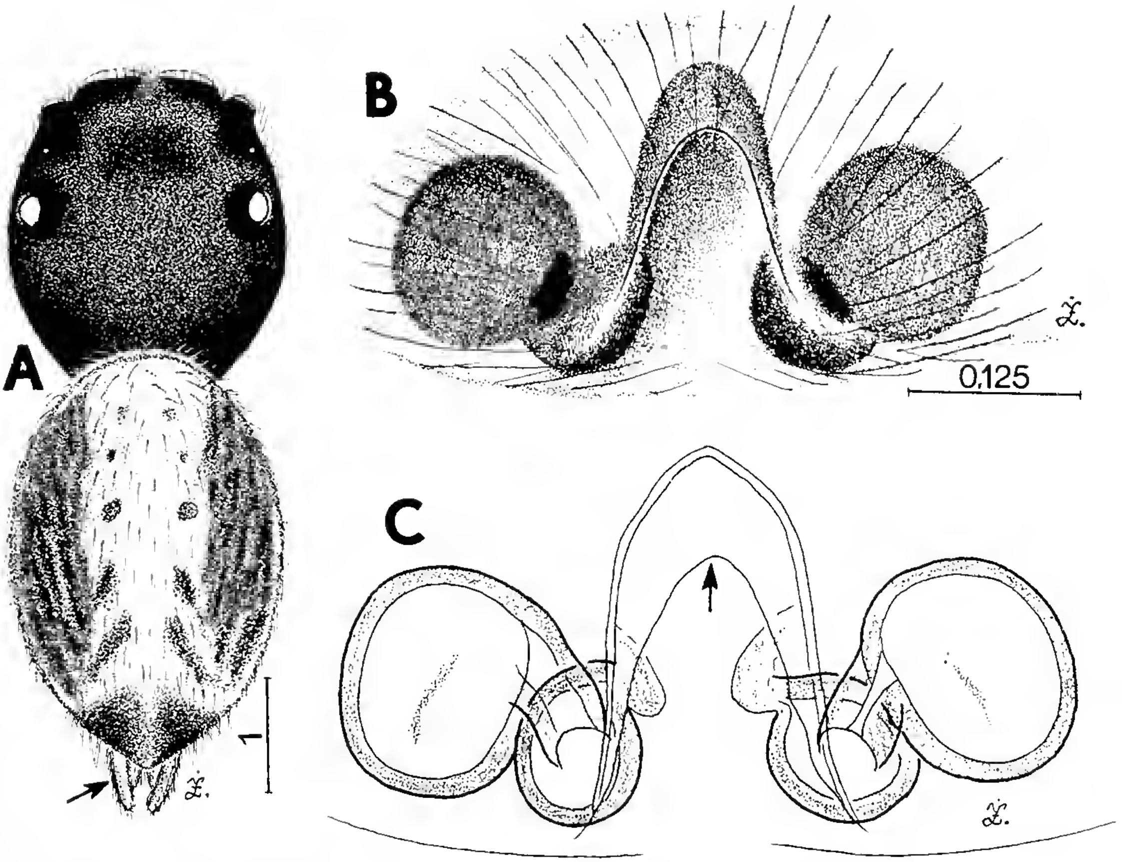


Figure 21 ♀ *Simaetha atypica* sp. nov. A – general appearance. B–C – epigyne and internal genitalia.

Dimensions

CL 2.50, EFL 1.10, AEW 1.65, PEW 2.20, AL 3.40.

Etymology

The species has (atypically) long spinnerets.

ACKNOWLEDGEMENTS

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Rec. West. Aust. Mus. 1994, **16**(4): 535–566

COPIDOGNATHUS (HALACARIDAE: ACARI) FROM WESTERN AUSTRALIA. DESCRIPTION OF TWELVE SPECIES OF THE *GIBBUS* GROUP

Ilse Bartsch*

ABSTRACT

Approximately 30 species of the genus *Copidognathus* were found in the intertidal and subtidal zones of Rottnest Island, southwestern Australia. Twelve new species are described in the present paper: *Copidognathus ampliatus* sp. nov., *C. bispinus* sp. nov., *C. bistriatus* sp. nov.. *C. caelatus* sp. nov., *C. canaliculifer* sp. nov., *C. crassispinus* sp. nov., *C. dubiosus* sp. nov., *C. laminifer* sp. nov., *C. multiporus* sp. nov., *C. nasutus* sp. nov., *C. punctellus* sp. nov., and *C. strigellus* sp. nov. They all belong to the *gibbus* group. A key to the species is presented. The majority of species have closely related congeners in the Atlantic and Pacific oceans. Two couples, *bispinus-laminifer* and *ampliatus-caelatus*, are almost identical in dorsal aspect.

INTRODUCTION

The genus *Copidognathus* presently includes nearly 300 species, which is about one-third of the halacarid mites described. Amongst the halacarids collected during the Fifth International Marine Biological Workshop: The Marine Flora and Fauna of Rottnest Island, Western Australia, the genus *Copidognathus* was represented by almost 30 species. The majority of species can be attributed to natural groups, and twelve species proved to belong to the *gibbus* group, these are *C. ampliatus* sp. nov., *C. bispinus* sp. nov., *C. bistriatus* sp. nov., *C. caelatus* sp. nov., *C. canaliculifer* sp. nov., *C. crassispinus* sp. nov., *C. dubiosus* sp. nov., *C. laminifer* sp. nov., *C. multiporus* sp. nov., *C. nasutus* sp. nov., *C. punctellus* sp. nov., and *C. strigellus* sp. nov.

MATERIALS AND METHODS

Samples of 100–500 cm^3 of various substrates such as green, brown and red algae, seagrasses, colonial and encrusting organisms, macrofauna, and sandy deposits, collected from various beaches and tidal and subtidal zones, were taken to the laboratory, washed with fresh water over a 100 μm sieve. The material retained in the sieve was scanned for halacarid mites. The mites were stored in ethanol, cleared in lactic acid and mounted in glycerine jelly.

The figures were drawn using a camera lucida. Each scale line represents 50 μm.

When indicating the position of appendages on the legs and palps, the terms 'medial' and 'lateral' are used in accordance with descriptions by Viets (1939/40) and Newell (1947). Compared with the terminology in Newell (1984), 'medial' corresponds to 'anterior' on palps, leg I and II, but a 'medial' position on leg III and IV corresponds to a 'posterior' site.

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Holotypes and other representatives are deposited in the Western Australian Museum in Perth (WAM), other specimens in the author's halacarid collection (IB).

SYSTEMATICS

Subfamily Copidognathinae Bartsch

Genus *Copidognathus* Trouessart

Diagnosis

Female and male similar in dorsal aspect. AD, OC and PD present. AE with epimeral pores. Female GA with 3 pairs of pgs and 1 pair of sgs. Male GA with 4 or more pairs of pgs and 3–4 (rarely 2) pairs of sgs. Palps 4-segmented. P-3 lacks seta or spine. P-4 with 3 setae in the basal whorl; apically with minute seta plus 2 spurs. Tibiae I and II each with 3 ventral bristles, tibiae III and IV each with 2 ventral bristles. All tarsi with parambulacral setae. Tarsus I with 3 ventral setae, tarsi II-IV lack ventral setae (occasionally, one of the pas may be moved to ventral position). Solenidion on tarsus I and II in dorsolateral position. Lateral claws generally large, median claw present though small.

Remarks

The majority of the 300 species described can be attributed to widely spread natural groups. One of these is the *gibbus* group (Newell 1971), characterized by the combination of: legs with large lamellae; trochanters III and IV with triangular dorsal process; basifemora with small ventral lamellae; telofemora with large ventrolateral and smaller ventromedial lamellae; tibiae with posterior articular lamellae; tarsi I and II with large lateral membranes of claw fossa; tarsi III and IV slender. General chaetotaxy, from trochanter to tibia: leg I, 1, 2, 5, 4, 7; leg II, 1, 2, 5, 4, 7; leg III, 1, 2, 2, 3, 5; leg IV, 0, 2, 2, 3, 5. I-5 and II-5 each with 2 bipectinate ventromedial setae, III-5 and IV-5 with one bipectinate ventromedial seta; glp-1 and ds-1 inserted more or less adjacent. Male genital sclerites with 3–4 pairs of sgs, 2–3 of them seta-like and one spur-like. In the majority of species the AD is characterized by an 'A'-shaped internal sclerite.

Key to Western Australian species of *Copidognathus*

1. Dorsal and ventral plates adjacent or fused 2
   Dorsal and ventral plates widely separated .... *C. dubiosus*

2. Dorsal plates with foveae and porose areolae 6
   Dorsal plates rather uniformly punctate, distinctly demarcated porose areolae lacking ... 3

3. AD with distinct frontal spine and anterolateral lamellae (Figures 16, 24, 38). Width of PD less than 1.5 times its length 4
   AD with minute frontal spine; anterolateral lamellae lacking. PD more than 1.5 times longer than wide .... *C. strigellus*

4. AE and PD fused, AE and GA separated .... *C. canaliculifer*
   AD and PD separated 5

5. AE and GA separated .... *C. bispinus*
   AE and GA fused .... *C. laminifer*

6. Porose areolae distinctly set off from reticulate or foveate remainder of plate 7
   Both porose areolae and remainder of AD and PD foveate (Figure 47) .... *C. punctellus*

7. AD with raised triangular area and without or with only small anterolateral lamellae which do not extend to tip of frontal spine (Figures 56, 68) 8
   Anterolateral lamellae extending from frontal spine almost to lateral corner of AD (Figures 83, 91, 105) 10

8. AD with small anterolateral lamellae, pair of areolae 2 pores wide 9
   AD without anterolateral lamellae. Pair of porose areolae triangular in outline, setae ds-4 to ds-6 generally conspicuously stout .... *C. nasutus*

9 AD with stout frontal spine; longitudinal costae on PD 2 pores wide .... *C. crassispinus*
   Frontal spine on AD present though small; longitudinal costae on PD 1 pore wide .... *C. bistriatus*

10. Median porose costae on PD 3–5 pores wide. AE, GA and PE fused .... *C. multiporus*
   Porose costae between ds-4 and ds-5 1(-2) rosette pores wide 11

11. AE and GA fused laterally but separated in the median .... *C. caelatus*
   AE and GA fused .... *C. ampliatus*

Description of species

The arrangement of description of the twelve species follows the sequence in the key.

Copidognathus dubiosus sp. nov.

Figures 1–8

Holotype

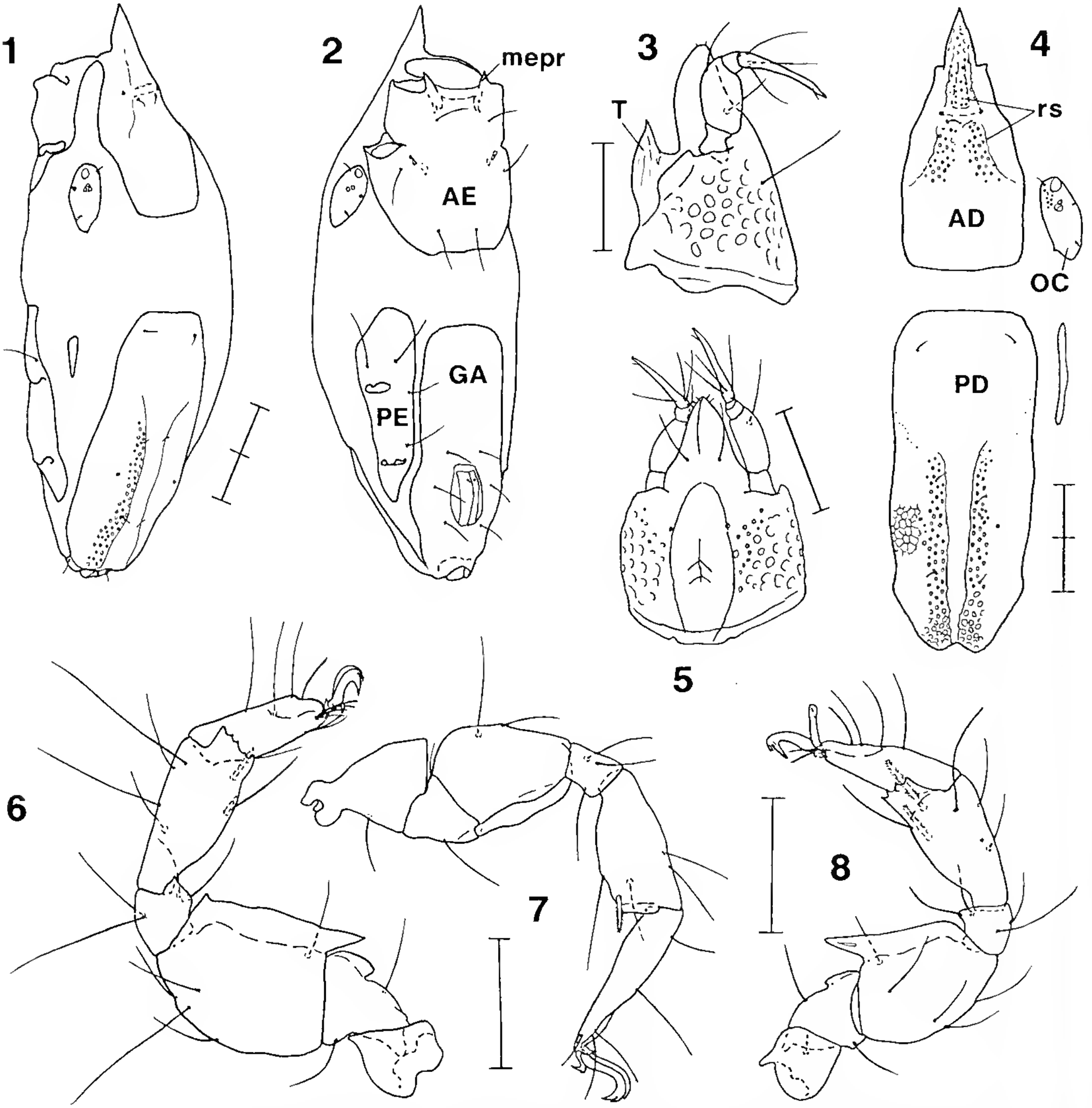
♀, Nancy Cove, Rottnest Island, Western Australia, Australia, sediment and algae on intertidal shore-line platform, 12 January 1991, I. Bartsch (WAM 93/2141).

Paratypes

Australia: Western Australia: 1 ♀, type locality and date (WAM 93/2142); 2 protonymphs, same data as holotype (IB Au372).

Description

Female: Idiosoma length 564 µm. Dorsum with wide areas of membraneous integument (Figure 1). AD 212 µm long; with median, gable-like portion slightly raised, areas lateral and posterior to raised portion reticulate, lateral part of AD coarsely reticulate and posterior part of AD minutely reticulate. Raised area extending into pointed frontal spine. Rosette-pores on gable-like area with rather wide ostia and canaliculi. AD with internal transverse bar level with insertion of leg I. Gland pores placed just lateral to that bar. Dorsal portion of AE surpassing insertion of leg I. OC 67 µm long. Posterior cornea divided into 2–3 lenses; gland pore level with posterior cornea, pore canaliculus separated from gland pore by slightly less than width of OC. Red eye pigment present beneath corneae. PD 266 µm long. Posterior part of PD with raised costae which anteriorly extend to level of insertion of leg III. Costae 2–3 rosette pores wide. Anterior rectangular part of PD with evenly scattered canaliculi, PD between costae delicately and lateral to costae coarsely reticulate (Figure 4). Narrow triangular (holotype) or oblong (paratype) sclerite present within striated integument and lateral to anterior part of PD.



Figures 1–8 *Copidognathus dubiosus* sp. nov., female, 1, idiosoma, dorsal aspect; 2, idiosoma, ventral aspect; 3, gnathosoma, lateral aspect; 4, dorsal plates; 5, gnathosoma, ventral aspect; 6, leg I, paratype, lateral aspect; 7, leg III, paratype, medial aspect; 8, leg I, holotype, lateral aspect.

AE and PE with dorsal portions reticulate; marginal portions of AE, PE and GA with wide rosette pores; ventral portions of the plates minutely reticulate, each mesh with 1–3 canaliculi. Medial eprI sharply pointed (Figure 2); lateral eprI present though inconspicuous. GA 253 μm long; GO 58 μm long. Distance from anterior margin of GO to that of GA twice length of GO; distance from posterior margin of GO to end of anal cone almost same as length of GO.

Gnathosoma 118 μm long. Ventral and marginal flank of gnathosoma with wide rosette pores (Figure 5). Tectum with sharp spine and slightly raised crest (Figure 3). P-4 somewhat longer than P-2. Ventral margin of P-2 crenulate.

Width of ventrolateral lamellae on telofemora less than half length of that segment (Figures 6, 7). Lamellae on telofemora I and II with reticulate sculpturing; ventral margin truncate, and with spine-like and backward directed process (Figure 8). Lateral articular lamellae on genua I and II small; that lamella on I-5 and II-5 quadrangular, on I-5 about half as long as high and with its distal margin bearing 6 lamellar dents (Figure 6), on II-5 about as long as high and ending in 4 lamellar dents. Medial articular lamellae on tibiae I and II much smaller. Posterior part of tibiae with short lateral and medial lamellae. Solenidion on tarsus I and II slender, seta-like. Tarsi III and IV slender, somewhat longer than both tibiae and telofemora; each with 4 dorsal setae.

Claws on tarsi I and II stout; claws on tarsi III and IV slightly longer. Accessory process with minute tines.

Protonymph: Idiosoma length 540 μm. Dorsal and ventral plates small, reticulate. AD with large frontal spine. OC in outline similar to that of female. Anterior PD ovate. Setae ds-2 and ds-3 inserted within membraneous integument. Tectum rounded, spine and crest lacking. Telofemora with ventrolateral lamellae; lamellae on I-3 and II-3 with backward directed spine-like process. Distolateral lamella on tibia I and II serrate.

Remarks

Copidognathus dubiosus differs from all other species in the *gibbus* group by the presence of a very stout frontal spine, dorsal and ventral plates being separated by large areas of striated integument, and unusually short OC.

The OC resemble those generally found in nymphs and larvae.

The pointed, backward extended process on I-3 and II-3 is supposed to be correlated with the mode of life and habitat and may help the specimens to anchor in the substrate.

***Copidognathus strigellus* sp. nov.**

Figures 9–15

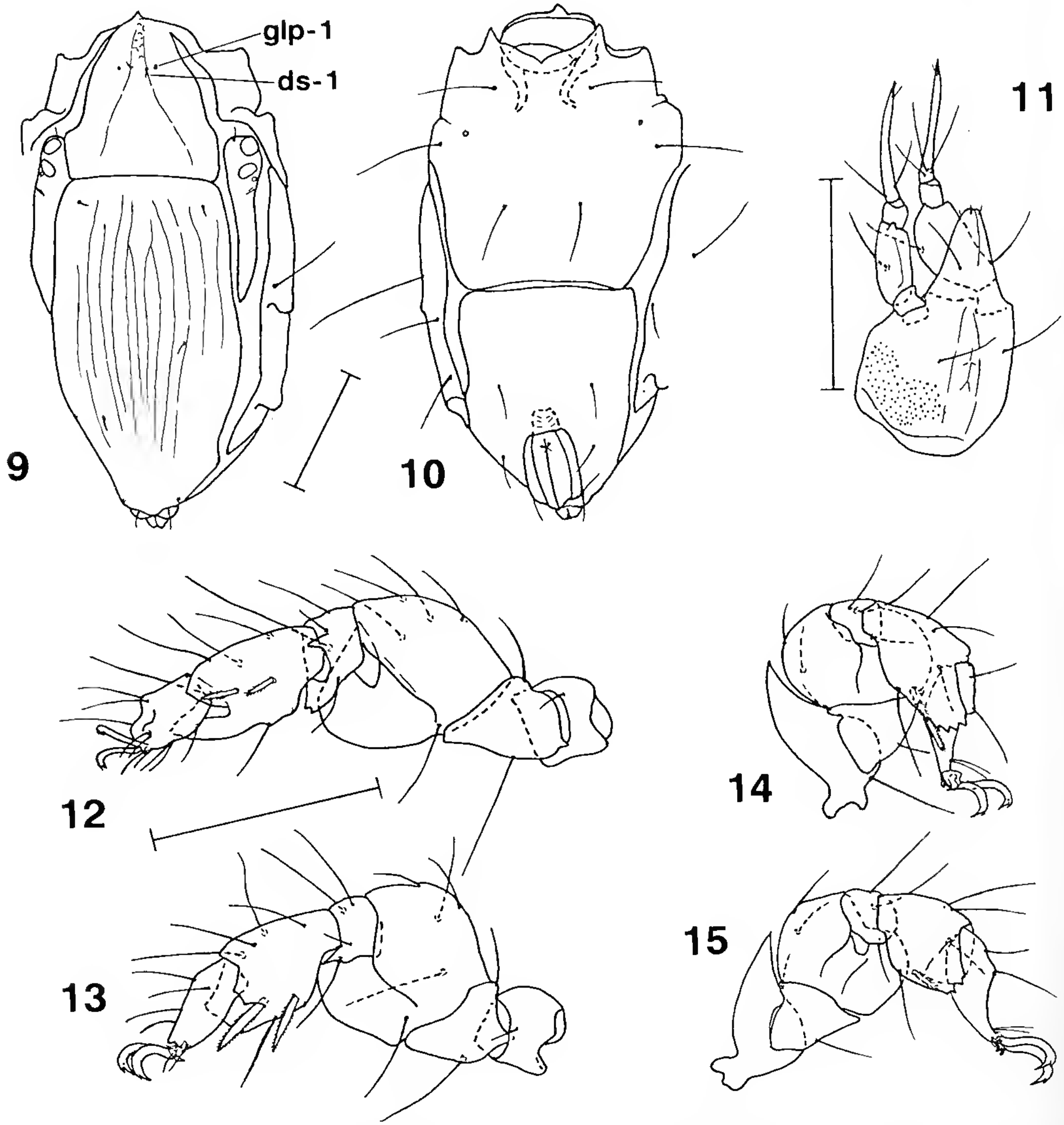
Holotype

♀, Fish Hook Bay, Rottnest Island, Western Australia, Australia, 1–1.5 cm thick corallines (*Amphiroa*) on edge of shore-line platform, 9 January 1991, I. Bartsch (WAM 93/2151).

Description

Female: Idiosoma length 202 μm. With narrow striae of membraneous integument between the plates. Dorsal plates delicately panelled. AD 64 μm long, 60 μm wide, with minute frontal spine and slightly raised gable-like portion (Figure 9). No internal transverse or gable-like sclerite present beneath anterior part of AD, instead there are faint sclerites along lateral margin of AD. Setae ds-1 and glp-1 close together. OC 68 μm long, 15 μm wide. Margins of posterior part of OC evenly tapering, not tail-like. Anterior cornea large, posterior cornea smaller; gland pore near posterolateral margin of posterior cornea, pore canaliculus just posterior to gland pore. Setae ds-2 at anterior margin of OC. PD 132 µm long, 75 µm wide, with longitudinal striae.

Ventral plates with canaliculi. All ventral plates separated. AE 80 µm long, 98 µm wide.



Figures 9–15 *Copidognathus strigellus* sp. nov., female, 9, idiosoma, dorsal aspect; 10, idiosoma, ventral aspect; 11, gnathosoma, lateral aspect; 12, leg I, ventromedial aspect; 13, leg II, medial aspect; 14, leg III, lateral aspect; 15, leg IV, lateral aspect.

Medial eprI large, pointed, medial eprII lamellar, lateral eprI and eprII inconspicuous. Apodemes posterior to camerostome large, crescentic (Figure 10). PE elongate, anteriorly extending beyond posterior cornea; portion anterior to insertion of leg III much longer than that between legs III and IV. GA 92 µm long, 68 µm wide. GO 29 µm long, 22 µm wide. Distance from anterior margin of GA to that of GO twice length of GO. Three pairs of pgs inserted as figured.

Ventral and marginal flanks of base of gnathosoma pierced by canaliculi (Figure 11). Tectum only slightly curved. Rostral sulcus extending just beyond pair of mxs. P-4 as long as P-2. The 3 basal setae on P-4 inserted adjacent. P-2 with stout seta situated near middle of segment.

Ventrolateral lamellae on telofemora I and II with delicately reticulate sculpturing. Lateral articular lamellae on genua I and II scale-like, that on II-4 longer than high, medial lamella triangular and pointed (Figures 12, 13). Lateral articular lamella on I-5 larger than medial one, both lamellae wide and triangular. Lateral articular lamella on II-5 subrectangular, medial lamella smaller. Medial lamella on III-5 and IV-5 slightly larger than lateral one. Ventral margin of tibiae I and II bulging and with very minute dent-like process. Ventromedial setae on II-5 remarkably wide, ensiform. Ventral setae on III-5 and IV-5 rather large, ventromedial bristle on III-5 long, on IV-5 short, both delicately bipectinate. Tarsi III and IV about as long as tibiae and telofemora; each tarsus with 4 dorsal setae (Figures 14, 15).

Claws with accessory process but no long pecten.

Remarks

Copidognathus strigellus is rather slender, the dorsal plates are panelled but lack porose areolae, and the tectum is not conspicuously enlarged. This combination of characters is also found in *C. felicis* Newell, *C. remipes* (Trouessart) and *C. subgibbus* Newell. *C. felicis* and *C. subgibbus* are known from the southeast Pacific (Newell 1971), *C. remipes* occurs in the eastern North Atlantic and the Mediterranean (Bartsch 1985a). *C. subgibbus* is separated from *C. strigellus* and the other three species in having shorter OC (relative to their width) which posteriorly extend less beyond anterior margin of PD.

C. felicis and *C. remipes* are closely related to *C. strigellus*. In *C. felicis*, the raised triangular area on the AD is much wider than in *C. strigellus* and *C. remipes*. *C. remipes* has a pair of short, narrow costae on the PD and the females have 2 pairs of pgs anterior to the GO, in contrast, *C. strigellus* has one pair of pgs anterior and 2 pairs on either side of the GO, and the PD lacks costae.

Copidognathus canaliculifer sp. nov.

Figures 16–23

Holotype

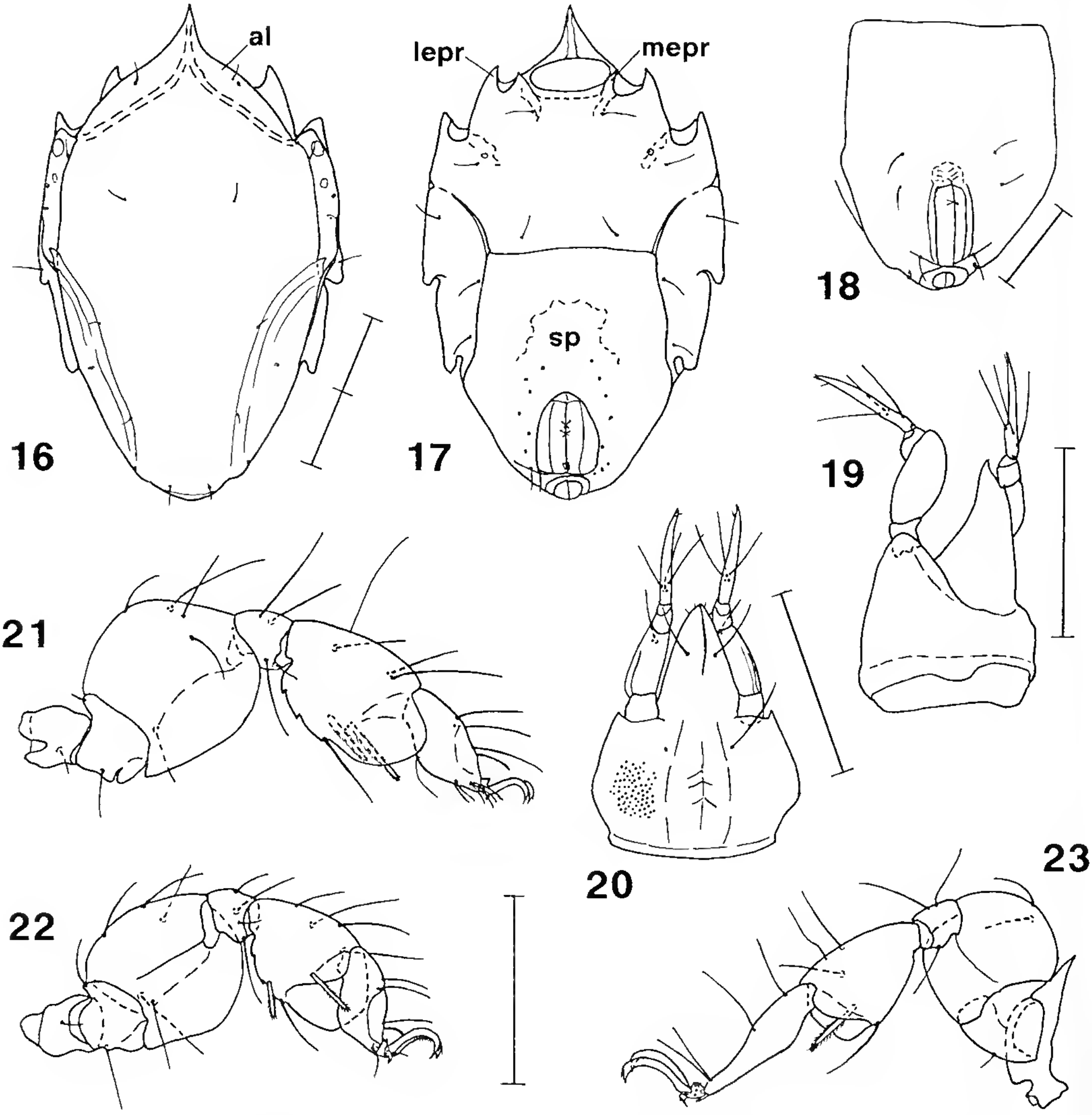
♂, Fish Hook Bay, Rottnest Island, Western Australia, Australia, small bushy algae (*Zonaria*, Phaeophyta) from edge of rocky platform, 0.5 m depth, 15 January 1991, I. Bartsch (WAM 93/2138).

Other Material Examined

Australia: Western Australia: 1 ♀, Salmon Point, sediment from 1.5 m depth, I. Bartsch, 18 January 1991 (WAM 93/2139).

Description

Male: Idiosoma 306 µm long, 186 µm wide. Dorsal and ventral plates densely and almost uniformly pierced by canaliculi. AD and PD completely fused (Figure 16); AD and OC joined, with sutures indicating outline of plates; striae with membraneous integument lacking. Idiosoma with pointed frontal spine. Area corresponding to AD with internal sclerite and large anterolateral lamellae. OC with large anterior and smaller posterior smooth area (corneae). Area of PD with diverging striae which, in form of very short lamellae, anteriorly extend beyond posterior part of OC. Dorsal setae small. Setae ds-1 and adjacent small glp-1



Figures 16–23 *Copidognathus canaliculifer* sp. nov., 16, idiosoma, dorsal aspect, male; 17, idiosoma, ventral aspect, male; 18, genitoanal plate, female; 19, gnathosoma, dorsolateral aspect, male (dorsal seta on P-2 omitted); 20, gnathosoma, ventral aspect, female; 21, leg I, lateral aspect, female; 22, leg II, medial aspect, female; 23, leg IV, medial aspect, female.

on margin of anterolateral lamella. Setae ds-2 on OC in medial position. Setae ds-3 to ds-6 on PD.

AE and GA contiguous, with distinct suture but without intermediate membraneous integument. PE and AE anteriorly fused and posteriorly with delicate striae of membraneous integument (Figure 17). AE 92 µm long, 174 µm wide. Epimeral processes present medially and laterally. Medial eprI pointed; medial eprII small, lamella-like; lateral eprI and eprII large. GA 156 µm long, 128 µm wide; with 7–8 pairs of slender pgs. GO 52 µm long. Spermatopositor large, extending beyond GO for length of GO.

Gnathosoma 75 µm long. Tectum enlarged, with median crest (Figure 19). Integument of tectum delicate when compared with that of gnathosoma base and rostrum. Insertiom of maxillary setae same as illustrated in Figure 20. Palps with small ventral lamella. P-4 slightly longer than P-2. Two of the setae in the basal whorl separated from basalmost seta by more than width of P-4.

Telofemur I with almost smooth ventrolateral lamella. Ventromedial lamella replaced by small crest. Articular lamellae on genua inconspicuous, those on tibiae large. Tibia I short, its ventral margin bulging and bearing 2 dent-like processes (cf. Figure 21); tibia II with less conspicuous processes (cf. Figure 22). Tarsi III and IV (cf. Figure 23) slender, each with 4 dorsal setae.

Pecten on tarsi II distinct, on tarsi III delicate and on tarsi I and IV inconspicuous.

Female: Idiosoma 290 µm long and 174 µm wide. In dorsal aspect similar to male. Ventral plates contiguous, similar to those of male. GA 142 µm long, 117 µm wide. GO 42 µm long, 22 µm wide. Interval between anterior margin of GA and that of GO equalling twice the length of GO. Second pair of of pgs inserted level with anterior end of GO (Figure 18).

Remarks

Copidognathus canaliculifer is very similar to *C. scutellus* Bartsch, a species recorded from the Philippines (Bartsch 1985a). Both species have a large, densely porose dorsal shield and contiguous ventral plates. The most marked difference between the two species is the length of the rostrum. The rostrum in *C. scutellus* is short, as long as wide, in *C. canaliculifer* it is 1.4 times longer than wide.

Copidognathus bispinus sp. nov.

Figures 24–35

Holotype

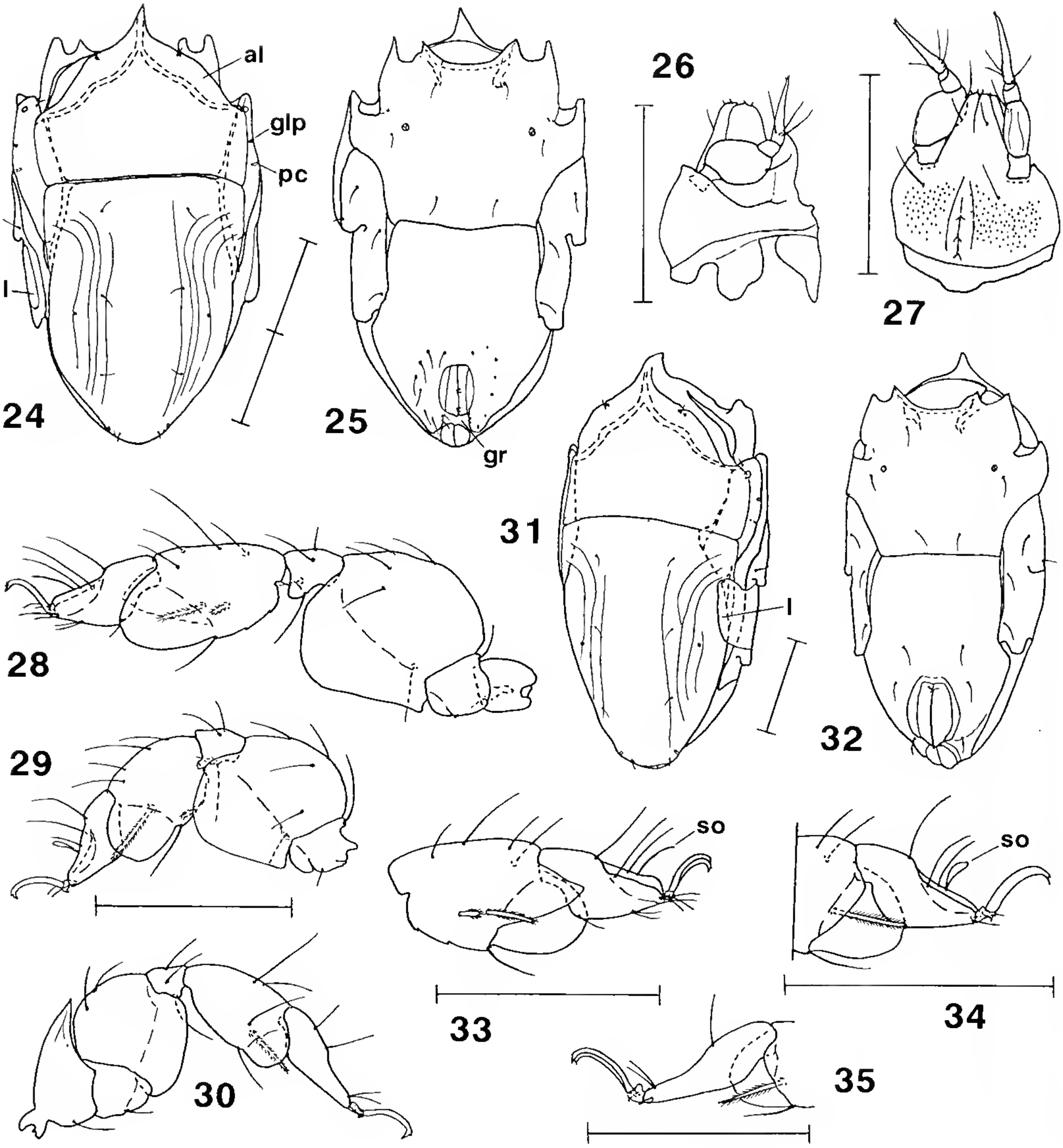
♂, Duffield Ridge, Rottnest Island, Western Australia, Australia, sediment from 30 m depth, 17 January 1991 sorted by I. Bartsch, (WAM 93/2129).

Paratypes

Australia: Western Australia: 1 ♀, type locality and date (WAM 93/2130); 3 ♀, type locality and date (IB Au323).

Description

Male: Idiosoma length 219 µm. Integument of dorsal plates with rather uniform and delicate porosity. AD 85 µm long, 93 µm wide; with gable-like internal sclerite extending anteriorly into lamellar frontal spine, and laterally into lamellae which surpass medial margin of OC (Figure 24). Anterolateral lamellae large, extending from frontal spine to lateral processes;



Figures 24–35 *Copidognathus bispinus* sp. nov., 24, idiosoma, dorsal aspect, male; 25, idiosoma, ventral aspect, male; 26, gnathosoma, dorsolateral aspect, female; 27, gnathosoma, ventral aspect, female; 28, leg I, lateral aspect, female; 29, basifemur to tarsus II, lateral aspect, female; 3O, leg III, lateral aspect, female; 31, idiosoma, dorsal aspect, female; 32, idiosoma, ventral aspect, female; 33; tibia, tarsus I, medial aspect, female; 34, distal tibia and tarsus II, medial aspect, female; 35, distal tibia and tarsus IV, medial aspect, female.

lamellae with gland pores and small ds-1. OC elongate, 94 µm long, 25 µm wide; posterior corner slightly set off from remainder of plate. OC with small and rather inconspicuous anterior cornea, gland pore and pore canaliculus in lateral margin, and ds-2 in anteromedial margin. Red-brown pigment present beneath OC and AD within the angle between internal sclerites. PD 130 µm long, 100 µm wide; with 4 pairs of sinuose longitudinal striae but without raised costae. AD and PD with thin lateral lamellae which surpass and cover medial margin of OC. Setae ds-3 to ds-5 inserted on PD; a pair of gland pores level with insertion of leg IV.

Ventral plates with rather delicate porosity. All ventral plates separated (Figure 25). AE 82 µm long, 122 µm wide. Lateral and medial epimeral processes prominent. Medial eprII lamellar, lateral eprII (in dorsolateral position) similar to lateral eprI. Posterior trochanters flanked by rounded lateral and small lamellar medial eprIII and eprIV. PE with dorsal lamella (Figure 24). GA 111 µm long, 88 µm wide; with deep groove posterior to GO. GO 26 µm long and 19 µm wide. Nine pgs on either side of GO and genital groove (Figure 25). Spermatopositor large, extending beyond GO for more than 1.5 times the length of GO.

Gnathosoma 50 µm wide, 52 µm long. Ventral and lateral flank of gnathosoma base with delicate porosity. Rostrum short and wide. Maxillary setae as illustrated in Figure 27. Rostral sulcus extending beyond mid of rostrum. Tectum with long but very narrow crest. Palps short. P-2 flattened (Figure 26), only slightly longer than high, with rather stout dorsal seta.

Lamellae on legs large but thin and without distinct ornamentation. Ventrolateral lamella on I-3 with ventral margin distally evenly rounded, otherwise truncate troughout its length (cf. Figure 28). Ventral seta on I-4 bristle-like; other 3 setae on I-4 delicate. Ventral margin of I-5 with 2 minute, dent-like processes. Ventromedial setae on I-5 bipectinate, ventral seta slightly smaller than bristle on I-4. Tibia II (cf. Figure 29) smaller but else similar to I-5. Solenidion on I-6 slender (cf. Figure 33), that on II-6 shorter and club-shaped (cf. Figure 34). III-6 with 4 (cf. Figure 30) and IV-6 with 3 dorsal setae (cf. Figure 35).

Claws slender. All with accessory process.

Female: Idiosoma length 219–242 µm. Dorsal and ventral plates separated, ornamented as in male, and AD, PD and PE with thin lamellae (Figure 31). GA (paratype, WAM) 108 µm long, 72 µm wide. GO 36 µm long, 28 µm wide, placed in posterior part of GA; distance from anterior margin of GO to that of GA 1.8 times the length of GO. Three pairs of pgs inserted as illustrated (Figure 32).

Remarks

Copidognathus bispinus is most similar to *C. laminifer*. Distinguishing characters are discussed below, after description of *C. laminifer*.

Copidognathus laminifer sp. nov.

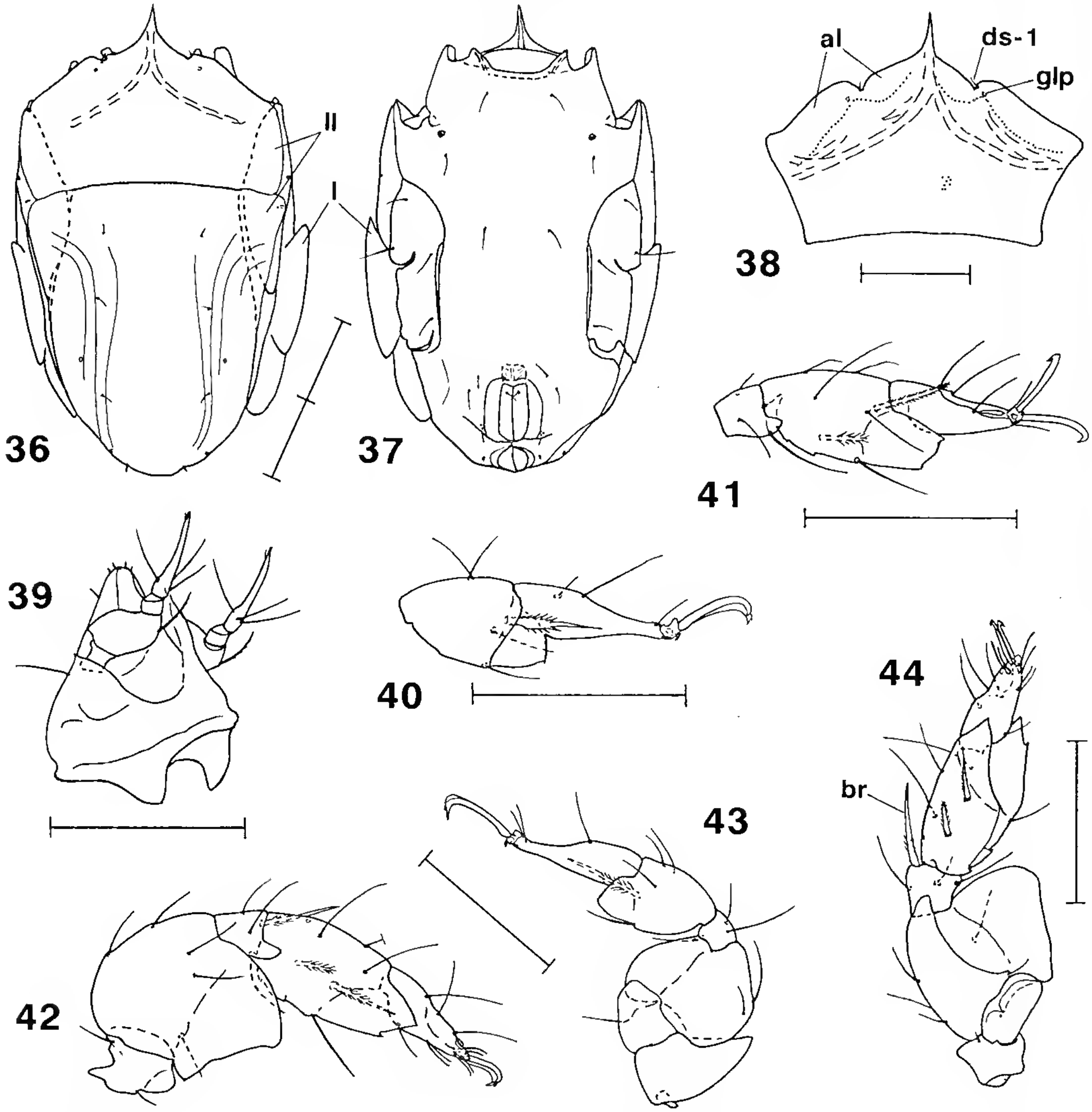
Figures 36–44

Holotype

♀, Duffield Ridge off Rottnest Island, Western Australia, Australia, sediment from 30 m depth, 17 January 1991, sorted by I. Bartsch (WAM 93/2143).

Description

Female: Idiosoma length 260 µm. Idiosoma with delicate marginal lamellae. Dorsal plates contiguous but not fused. Integument of all dorsal plates pierced by evenly scattered canaliculi. AD very wide, 92 μm long, 140 μm wide; with crest-like frontal spine, a rather narrow, gable-like internal sclerite, conspicuous anterolateral lamellae with distinct indentation level with ds-1 (Figure 38), and very delicate lateral lamellae partly concealing the OC (Figure 36). Pore glp-1 inserted on anterolateral lamellae; ds-1 situated at margin of these lamellae and adjacent to gland pores. OC elongate, anteriorly prolonged and extending beyond trochanter II. No



Figures 36–44 *Copidognathus laminifer* sp. nov., female, 36, idiosoma, dorsal aspect; 37, idiosoma, ventral aspect; 38, anterior dorsal plate (lateral lamellae omitted); 39, gnathosoma, dorsolateral aspect; 4O, tibia and tarsus III, medial aspect; 41, genu, tibia and tarsus II, lateral aspect; 42, basifemur to tarsus I, lateral aspect; 43, leg IV, lateral aspect; 44, leg I, ventromedial aspect.

cornea but faint brown eye pigment present beneath OC. Lateral margin of OC with gland pore and pore canaliculus. PD 169 µm long, 126 µm wide, with very delicate lateral lamellae and with longitudinal striae but no raised costae. Dorsal setae very delicate, arising from distinct pores. PD with a pair of gland pores level with insertion of leg IV, and a pair of delicate glp posteriorly.

AE and GA fused to a ventral shield (Figure 37). PE with thin lateral lamellae (Figure 37). Posterior part of PD (posterior to insertion of leg IV) may be joined with GA. Else, PE and ventral shield contiguous but not fused, with striae of membraneous integument present between area of GA and PE. Ventral plates with almost uniformly scattered canaliculi, porosity in marginal portions of the plates slightly denser and deeper than in median areas. Epimeral processes present. Lateral eprI in dorsolateral position; medial eprI triangular, slightly smaller than lateral eprI. Lateral eprII elongate, extending beyond trochanters II. Posterior epimera with rounded ventrolateral lamellae, medial epr forming small, raised crests posterior to insertion of legs. GO 36 µm long, 30 µm wide. Ventral setae delicate. Anterior pairs of pgs close together.

Gnathosoma short, 57 µm long. Venter of gnathosoma base with canaliculi, dorsum with faint reticulation. Tectum with narrow crest. Rostrum short. Maxillary setae slender, rostral setae spur-like. Palps short, flattened (Figure 39). P-2 with delicately plumose dorsal bristle. P-4 with all 3 setae inserted near base of segment.

Legs with huge lamellae which are delicate and only faintly reticulated. Ventrolateral lamella on I-3 with slightly sinuate ventral margin. Genua I (Figure 42) and II with small lateral articular lamellae; medial lamellae absent. Tibia I with large lateral and medial lamellae; lateral lamellae on tibiae II, III and IV moderately large, medial lamellae very small. Medial bristle on genu I very large, spine-like (Figure 44). Ventral margin of I-5 with 2 small dents; ventral bristle slender, ventromedial bristles bipectinate. Ventromedial bristle on tibiae III and IV stout, its basal shaft bipectinate, its apex sharply pointed; ventral bristle on tibiae III and IV slender. Tarsi III and IV slender, else outline resembling that of anterior tarsi. Tarsus III with 4 dorsal setae, tarsus IV (Figure 43) with 3 setae.

Claws very slender, with delicate accessory tooth but without pecten. Median claws minute.

Remarks

No other halacarid species is known to have such large lateral lamellae along the idiosoma.

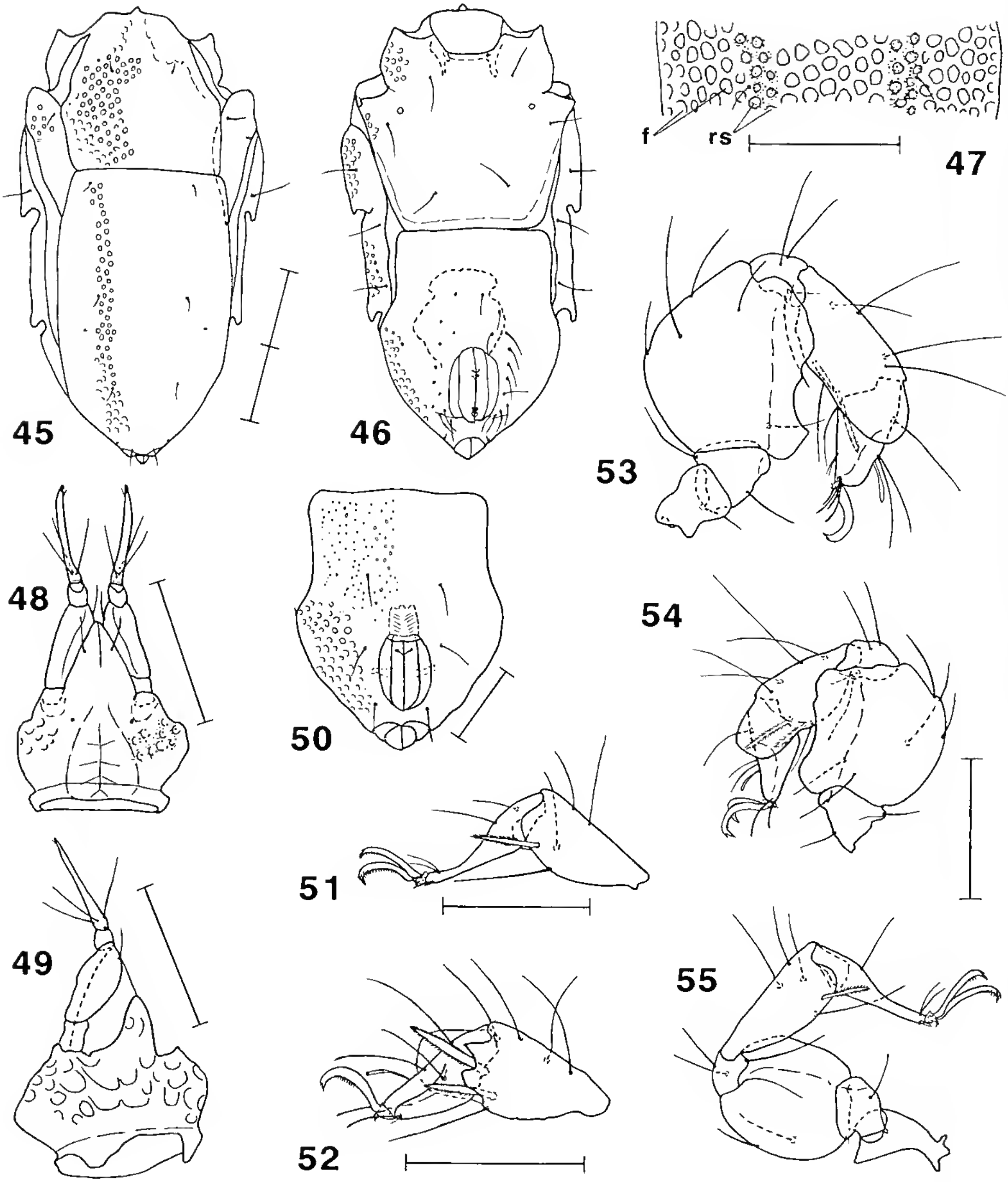
C. laminifer is closely related to *C. bispinus*. Adults are easily separated as AE and GA are fused in *C. laminifer* but separated in *C. bispinus*. Other distinguishing characters are: *C. laminifer* has a very prominent dorsal seta on P-2, whereas *C. bispinus* has a more slender seta and its P-2 is remarkably flattened and lamellar; in *C. laminifer* the medial seta on I-4 is unusually large. Such a large, spine-like seta on I-4 is unique within the *gibbus* group and may also help when identifying juveniles.

Copidognathus punctellus sp. nov.

Figures 45–55

Holotype

♂, Nancy Cove, Rottnest Island, Western Australia, Australia, shore-line platform, sand and algae (*Cystophora*, Fucales) with dense epiflora and epifauna, 12 January 1991, I. Bartsch (WAM 93/2149).



Figures 45–55 *Copidognathus punctellus* sp. nov., 45, idiosoma, dorsal aspect, male; 46, idiosoma, ventral aspect, male; 47, portion of PD level with ds-4, male; 48, gnathosoma, ventral aspect, male; 49, gnathosoma, dorsolateral aspect, female; 50, genitoanal plate, female; 51, tibia and tarsus III, medial aspect, male; 52, tibia and tarsus II, medial aspect, male; 53, leg I, lateral aspect, male; 54, basifemur to tarsus II, lateral aspect, male; 55, leg IV, medial aspect, male.

Other Material Examined

Australia: Western Australia: ♀, Little Armstrong Bay, Rottnest Island, sand from lower slope (near water table), 16 January 1991, I. Bartsch (WAM 93/2150).

Description

Male: Length of idiosoma 287 µm, width 152 µm. All dorsal plates contiguous though not fused. Plates foveate; integument within slightly raised areolae both foveate and densely punctate (canaliculi from rosette pores) (Figure 47). AD 102 µm long, 100 µm wide; with minute, delicately raised frontal spinelet (Figure 45); integument within arch-like areola pierced by numerous canaliculi. First pair of gland pores in anterolateral raised areola. OC 90 µm long, 28 µm wide, with small porose areola; remainder of plate reticulate. No cornea present. Gland pore almost inconspicuous. Pore canaliculus in lateral margin. PD 177 µm long, 115 µm wide. Two longitudinal areolae with foveae (ostia from rosette pores) surrounded by 12–14 canaliculi; areolae in anterior and posterior parts of PD 2–3 and 4 foveae wide. Foveae punctate. Pair of minute gland pores lateral to porose areolae, on level with insertion of leg IV. Dorsal setae small. Setae ds-1 on AD medial to gland pores; ds-2 on median margin of OC well removed from anterior margin of the plate; ds-3 to ds-6 on PD.

Ventral plates contiguous but not fused. Dorsal areas of AE and PE foveate, marginal areas with rosette pores. Porosity on median part of AE coarser than on GA, median part of AE with small pores arranged in groups (polygons). AE 112 µm long, 137 µm wide. Medial epimeral processes lacking, lateral epimeral processes inconspicuous. GA 147 µm long, 115 µm wide; marginal GA with rosette pores, median plate with very delicate pits but without deep canaliculi. GO 48 µm long, 39 µm wide; with 11–12 pairs of pgs. Spermatopositor large, surpassing GO for length of GO (Figure 46).

Gnathosoma 61 µm long, 58 µm wide. Tectum large, triangular (cf. Figure 49). Dorsum of gnathosoma base coarsely reticulate, venter with rosette pores (Figure 48) and sharp lateral carinae. Palps with ventral carinae.

Dorsal and lateral flank of I-3, II-3 and I-5 pierced by scattered canaliculi. Ventrolateral lamella on I-3 and II-3 with reticulate ornamentation; ventral margin of lamellae irregularly sinuate, with projecting lobes (Figures 53, 54). Ventrolateral lamellae on telofemora III and IV (Figure 55) with rather truncate ventral margin. Lateral articular lamella on I-5 about as long as wide, medial lamella slightly smaller. Medial lamella on tibia II with deep indentation for posterior pectinate seta (Figure 52). Solenidion on tarsi I and II slender, slightly clavate. Tarsus III with 4 dorsal setae (Figure 51), tarsus IV with 3 setae.

All lateral claws with accessory process and claw pecten. Tines of pecten largest near apex of claws.

Female: Idiosoma length 309 µm. In dorsal aspect similar to male. Median AE with coarser porosity than in male; pores resembling rosette pores. GA 157 µm long, 117 µm wide. Median GA with delicate pits, canaliculi lacking; marginal GA with rosette pores. GO 47 µm long, 31 µm wide. Ovipositor surpassing GO (Figure 50). Three pairs of pgs inserted as illustrated.

Remarks

Copidognathus punctellus is easily distinguished from the other representatives of the *gibbus* group on the basis of the rather uniformly foveate dorsal plates, with only slightly raised areas which are both foveate and pierced by canaliculi, the porose telofemora I and II, and the sinuose ventral margin of the ventrolateral lamellae. The ornamentation of the dorsal plates resembles that described for *C. simplipes* Newell, a species recorded from the southeastern Pacific near Chile (Newell 1984). The combination of: posterior margin of AD truncate, ds-4 inserted just anterior to insertion of leg IV, medial eprI absent, and ventrolateral lamella on I-3 sinuose, distinguish *C. punctellus* from *C. simplipes*.

C. punctellus is thought to inhabit water-logged sandy deposits. The ornamentation of the dorsal plates resembles that found in the epibenthic living *Copidognathus rhodostigma* (Gosse), a species common in the surface layers of shallow water sandy deposits (Bartsch 1979, 1985b, c); and both specimens may colonize similar habitats.

***Copidognathus nasutus* sp. nov.**

Figures 56–63

Holotype

♂, Fish Hook Bay, Rottnest Island, Western Australia, Australia, corallines (*Amphiroa*) from undercut of shore-line platform, just beneath low water edge, 15 January 1991, I. Bartsch (WAM 93/2146).

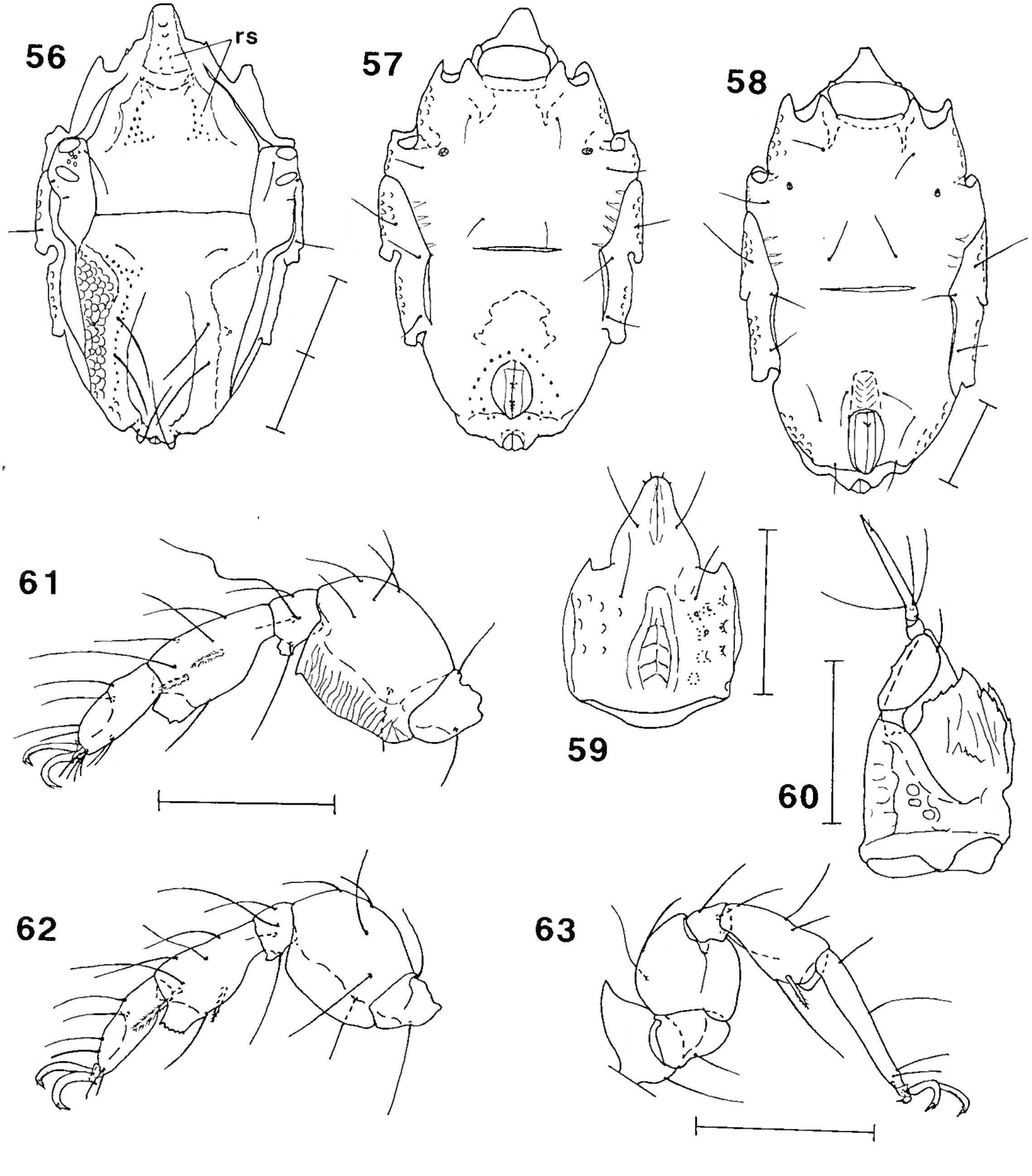
Other Material Examined

Australia: Western Australia: 1♀, 1♂, Nancy Cove, corallines from shore-line platform, low water, 20 January 1991, I. Bartsch (WAM 93/2147–2148); 2♀, Nancy Cove, 20 January 1991, I. Bartsch (IB Au97, Au351).

Description

Male: Idiosoma length 260–265 µm, holotype 265 µm. Dorsal plates contiguous, AD and OC, and OC and PD partly fused. AD 126 µm long, 105 µm wide; with raised, bluntly ending frontal process; raised area extending posterior, diverging, and ending level with ds-2. AD with internal 'A'-shaped structure. Pair of posterior porose areolae triangular in outline, with 12–13 rosette pores; unpaired anterior areola with 6 rosette pores (Figure 56). Frontal process with deep ostia but without canaliculi. Rosette pores on AD, OC and PD with small surficial ostia and canaliculi in deeper integumental layers. Reticulate integument lateral to raised area set off abruptly. OC 80 µm long, 30 µm wide; medial raised margin with 2 corneae; area between corneae with rosette pores; posterolateral margin of OC raised and with foveate sculpturing; large porus from gland pore on lateral protrusion of OC and small pore canaliculus just posterior to protrusion. Medial part of OC lacks distinct ornamentation. Posterior part of OC tail-like. PD and AD broadly contiguous but not fused. PD 135 µm long, 110 µm wide. Longitudinal costae anteriorly with narrow, curved crests which extend to lateral margins of PD. Arrangement of rosette pores as figured. Anterior part of PD with fine reticulate ornamention; lateral part of PD coarsely reticulate and rather abruptly set off from costae; median part of PD groove-like. Gland pore, level with insertion of leg IV, not included in costae. Setae ds-1 slender, inserted on AD, ds-2 in anteromedial part of OC, ds-3 on PD well removed from anterior margin. Setae ds-4, ds-5 and ds-6 conspicuously large, ds-4 and ds-5 turned backward, ds-6 forward (Figure 56).

AE and GA laterally fused but medially separated by striated integument; AE and PE contiguous; PE and GA partly separated by median wedge of striated integument (Figure 57). Ventral plates with rosette pores near margins whereas large ventral areas have scattered and very delicate canaliculi or are almost smooth. AE 95 µm long, 155 µm wide, with bulbous anterior apodemes. Dorsolateral margin of camerostome with small triangular processes. Lateral eprI enlarged dorsolaterally. Medial eprII lamellar, lateral eprII inconspicuous. GA



Figures 56–63 *Copidognathus nasutus* sp. nov., 56, idiosoma, dorsal aspect, male; 57, idiosoma, ventral aspect, male; 58, idiosoma, ventral aspect, female; 59, gnathosoma, ventral aspect, female; 60, gnathosoma, dorsolateral aspect, female; 61, basifemur to tarsus I, lateral aspect, male; 62, basifemur to tarsus II, lateral aspect, male; 63, leg III, medial aspect, female.

117 µm long, 108 µm wide; GO 33 µm long, 27 µm wide. GO in posterior part of GA, distance to anterior margin of GA equalling twice the length of GO. Genital sclerites with 3 pairs of sgs.

Gnathosoma 70 µm long. Venter of gnathosoma base foveate (ostia from rosette pores), canaliculi in holotype lacking (in a paratype female present). Maxillary setae inserted as illustrated in Figure 59. Tectum with abruptly raised large crest bearing a pair of carinae (cf. Figure 60). P-2 with small, lamellar ventral dent. P-4 slender, longer than P-2, with 3 setae inserted near base of P-4. Dorsal seta on P-2 stout.

Ventrolateral lamellae on all telofemora and ventral lamellae on basifemora reticulate and with transverse striae along ventral margin (Figure 61). Lateral articular lamellae on tibiae I and II with coarsely serrate edges (Figures 61, 62), their length less than half height of the segment. Lamellae on tibiae III (cf. Figure 63) and IV small. Right tarsus of holotype with 3, left tarsus (Figure 61) with 2 ventral seta. Tarsi III and IV slender, longer than telofemur and tibia, each tarsus with 4 dorsal setae.

Claws with accessory processes bearing tines. Claw pecten with delicate tines present on posterior half of claws.

Female: Idiosoma length 248–266 µm. In dorsal aspect similar to male. Ventral plates contiguous as in males, AE and GA separated medially but fused laterally (Figure 58). GA 113 µm long, 103 µm wide, separated from anterior margin of GA by almost twice the length of GO. Setae pgs inserted as illustrated. Ovipositor surpassing anterior pair of pgs.

Remarks

Copidognathus nasutus is characterized by its truncate frontal process and the ornamentation of the dorsal plates. A similar outline of porose areolae is known from *C. acanthophorus* Viets, *C. cristatus* Viets, *C. majusculus* (Trouessart), and *C. mesomorphus* André. *C. acanthophorus* lives in western Antarctica and adjacent areas (Viets 1950; Newell 1984), *C. cristatus* in the Caribbean area (Viets 1936), *C. majusculus* in the Mediterranean (Bartsch 1985a), and *C. mesomorphus* has been recorded from Egypt (André 1959). A long and truncate frontal spine as in *C. nasutus* is not found in any of the other species.

C. nasutus has remarkably large ds-4, ds-5 and ds-6. Slightly enlarged ds-5 are present in *Copidognathus gibbus* and *C. majusculus*. In populations of *C. gibbus* from the Mediterranean, studied by the author, both specimens with small ds-5 (of about same size as anterior setae) and with enlarged ds-5 were observed, in both males and females, independant of depth or season.

Enlarged ds-4 and ds-5, similar to those in *C. nasutus*, are recorded from *C. neptuneus* Bartsch. That species is not closely related to the *gibbus* group (Bartsch 1992).

Copidognathus crassispinus sp. nov.

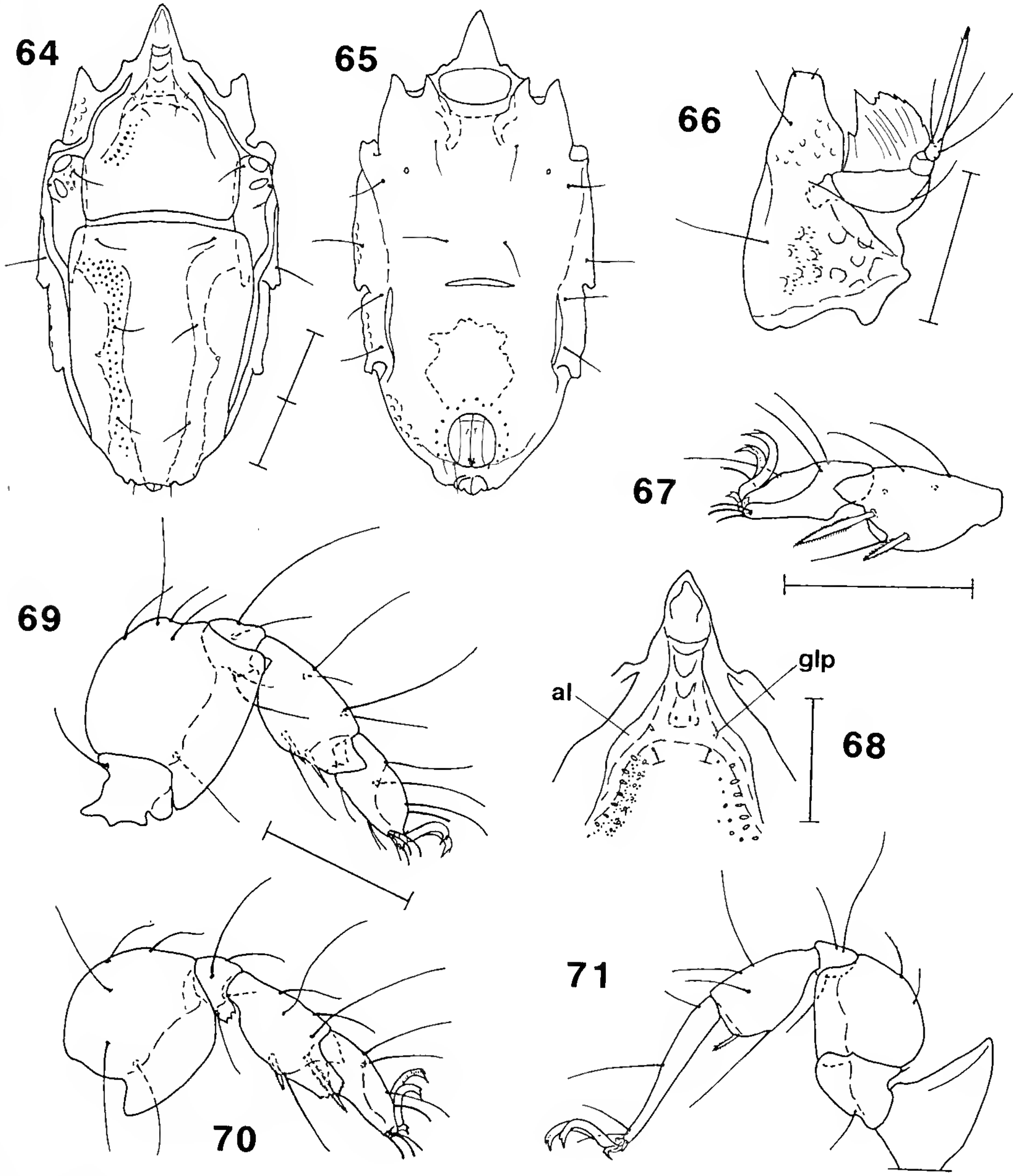
Figures 64–71

Holotype

♂, Little Armstrong Bay, Rottnest Island, Western Australia, Australia, sediment from slope, 30 cm sediment depth, 23 January 1991, I. Bartsch (WAM 93/2140).

Description

Male: Idiosoma length 335 µm. Dorsal plates adjacent, with narrow striae of membraneous



Figures 64–71 *Copidognathus crassispinus* sp. nov., male, 64, idiosoma, dorsal aspect; 65, idiosoma, ventral aspect; 66, gnathosoma, lateral aspect; 67, tibia and tarsus II, medial aspect; 68, anterior AD; 69, basifemur to tarsus I, lateral aspect; 70, telofemur to tarsus II, lateral aspect; 71, leg IV, lateral aspect.

integument between the plates. AD, OC and PD with porose areolae, remainder of plates reticulate. AD 145 µm long, 113 µm wide, with long and thick frontal spine (Figure 64). Internal sclerite anteriorly with 2 parallel longitudinal bars, followed by transverse bar and then diverging (Figure 68). Anterior portion of raised area with large foveae, posterior portion with porose longitudinal areolae that are 2 rosette pores wide, inner (medial) row of pores with small ostia at surface of plate and 5–7 canaliculi in deeper layers, lateral row of pores with ovate ostia each with 8–10 canaliculi. Narrow anterolateral lamellae present level with internal transverse bar (Figure 68); lamellae no more than 6 µm wide. Porus of first pair of glands opening beneath lamella. OC 84 µm long, 28 µm wide. Posterior part of OC tail-like. Anterior cornea large, posterior cornea smaller. Small porose area present medial to corneae. Gland pore on lateral edge of OC, pore canaliculus posterior to gland pore. Setae ds-2 placed near anterior cornea. PD 177 µm long, 115 µm wide, with 2 raised and sinuose porose areolae. Porose costae anteriorly 4 rosette pores wide, posteriorly 1–2 pores wide. Pair of gland pores at margin of costae, level with insertion of leg IV and in posterior part of PD. Plate lateral to costae coarsely reticulate, median part of PD faintly reticulate.

Dorsal areas of ventral plates foveate, marginal areas with rosette pores, ventral areas with scattered delicate canaliculi. AE 112 µm long, 159 µm wide, GA 145 µm long, 117 µm wide, with 50 µm wide wedge of striated integument between AE and GA, else plates fused (Figure 65). Medial eprI triangular, slightly smaller than eprI in dorsolateral position. Two blunt dents on dorsolateral margin of camerostome. Lamellar medial eprII and lateral eprII (in dorsolateral position) prominent. Pair of vs-3 inserted distinctly removed from posterior margin of AE (Figure 65). GO 40 µm long, 36 µm wide, 11–12 pairs of pgs arranged very close around GO. Genital sclerites in the single male available with one anterior and two posterior pairs of sgs. Spermatopositor large. GO removed from anterior margin of GA for somewhat more than 2 times the length of GO.

Gnathosoma 82 µm long. Ventral and marginal areas of gnathosoma base with rosette pores. Tectum spine-like, with large crest (Figure 66). P-4 slender, longer than P-2. P-4 with 3 long setae inserted near base of segment. P-2 with small ventral dent.

Ventrolateral lamellae on I-3 and II-3 rather smooth, with slightly convex ventral margin (Figures 69, 70). Lateral articular lamella on I-4 scale-like, that on I-5 slightly shorter than high. Lamellae on II-4 and II-5 about as long as corresponding lamellae on leg I but with coarsely serrate margin. Distal bipectinate setae on tibia II enlarged. Tarsus II with small ventral knob (Figure 67). Solenidion on both tarsus I and II slender and seta-like. Tarsi III and IV (Figure 71) slender, much longer than tibiae and telofemora, each with 4 dorsal setae.

Claws rather long and slender. Pecten with few delicate tines.

Remarks

Copidognathus crassispinus is distinguished from other species found around Rottnest Island on the basis of the long spine. *C. nasutus* has a stout frontal spine, too, but that of *C. crassispinus* is longer, the spine lacks rosette pores, there are small anterolateral lamellae level with the transverse internal bar, and the outline of the porose areolae is different from that of *C. nasutus*.

C. crassispinus is very similar to *C. longispinus* Bartsch and Iliffe, a species recorded from the islands of Bermuda (Bartsch and Iliffe 1985). *C. longispinus* differs from *C. crassispinus* in having the anterior pair of gland pores and ds-1 being widely separated and bearing rosette pores anterior to the ds-1.

Copidognathus bistriatus sp. nov.

Figures 72–82

Holotype

♂. Fish Hook Bay, Rottnest Island, Western Australia, Australia, 1–1.5 cm high corallines, edge of rocky platform, tidal low water edge, 9 January 1991, I. Bartsch (WAM 93/2131).

Paratypes

Australia: Western Australia: 1 ♀, type locality and date (WAM 93/2132); 1 ♀, 1 ♂, type locality and date (WAM 93/2133–2134).

Other Material Examined

Australia: Western Australia: 2 ♀, 2 ♀, 1 protonymph, Nancy Cove, corallines and colonies of polychaetes on concrete piers, lower tidal edge, 12 January 1991, I. Bartsch (IB Au368); 1 ♀, 1 ♂, Little Armstrong Bay, epiflora on the seagrass *Amphibolis*, 0.5–1.5 m depth, 16 January 1991, I. Bartsch (IB Au360). 1 ♀, Nancy Cove, corallines, tidal low water edge, 20 January 1991, I. Bartsch (IB Au351).

Description

Male: Length of idiosoma 248–263 µm, that of holotype 248 µm. Dorsal aspect similar to female (cf. Figure 72). Dorsal plates separate, with narrow striae of membraneous integument between plates. AD (holotype) 97 µm long, 93 µm wide. Median part of AD and frontal spine prominently raised, with 'A'-shaped porose areolae and 'A'-shaped internal sclerite. Porose areolae with rosette pores, posterior 'legs' of 'A' 2 pores wide. Remainder of plate lightly reticulated. Pair of glp-1 level with transverse internal bar. OC elongate, 73 µm long, 20 µm wide (holotype), with 2–3 rosette pores medial to the 2 corneae; gland pore and pore canaliculus in lateral margin. PD 144 µm long, 105 µm wide. Pair of costae with rosette pores, costae anteriorly 2(–3) pores wide, else 1 pore wide (cf. Figure 75). Plate lateral to costae coarsely foveate; median and anterior PD lightly reticulate. Pair of gland pores present in lateral, foveate plate, level with insertion of leg IV. Dorsal setae delicate, ds-1 adjacent to glp-1, ds-2 in anteromedial margin of OC, ds-3 near anterior margin of PD, ds-4 and ds-5 within costae anterior and posterior to level of gland pore.

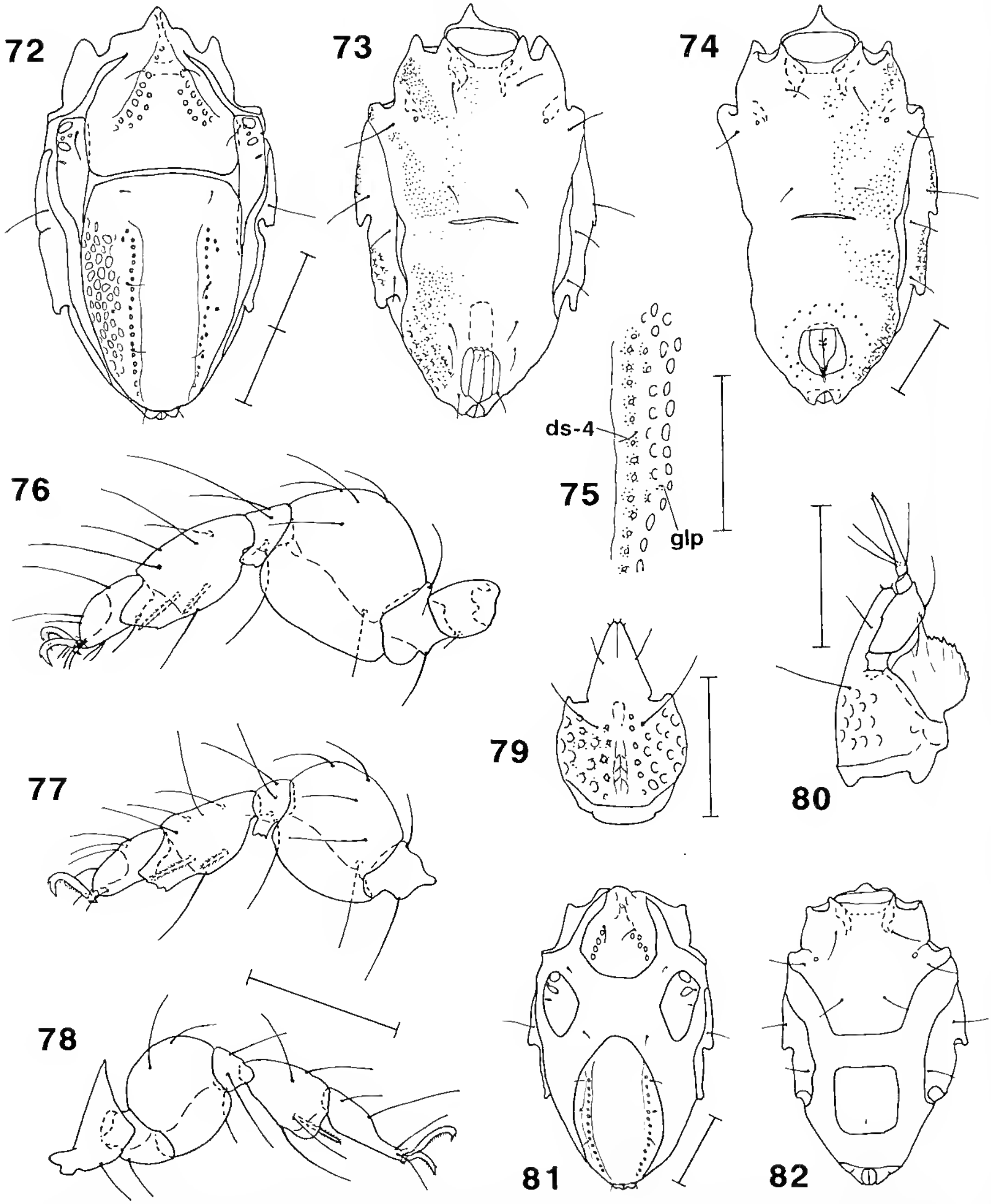
Median part of AE and GA separated by striae of membraneous integument but fused in posterolateral and anterolateral corners (Figure 74). AE and GA with rosette pores near margin, adjacent areas with canaliculi, median part of AE and GA with almost smooth integument. GA 117 µm long, 96 µm wide. GO 32 µm long, 30 µm wide, surrounded by 13–14 pairs of pgs. Distance from GO to anterior margin of GA almost twice the length of GO.

Gnathosoma 73 µm long. Tectum with huge serrate crest (Figure 80). Ventral flank of gnathosoma base with rosette pores (Figure 79), dorsal flank roughly reticulate and with dorsolateral lamellae. P-4 with 3 setae in basal whorl inserted adjacent to each other.

All telofemora with large ventrolateral lamellae (Figures 76–78); these lamellae delicately and finely reticulate; anteromedial flank of I-3 with numerous delicate striae. Height of telofemora more than length of segment. Tibiae shorter than telofemora. Tibiae I and II with large lateral and distinctly smaller medial articular lamella. Tarsi III with 4 and tarsi IV with 3 dorsal setae.

Claws with accessory process and long pecten.

Female: Idiosoma length 248–254 µm. Similar to male except for genital region. AE and GA as in male fused laterally but separated in the median (Figure 73). GA (paratype) 121 µm long, 102 µm wide. GO 38 µm long, 25 µm wide, its distance to anterior margin of GA equalling twice the length of GO. Setae pgs inserted as figured. Ovipositor surpassing GO for less than length of GO, but extending beyond anterior pair of pgs.



Figures 72–82 *Copidognathus bistriatus* sp. nov., 72, idiosoma, dorsal aspect, female; 73, idiosoma, ventral aspect, female; 74, idiosoma, ventral aspect, male; 75, portion of right PD with ds-4, female; 76, leg I, lateral aspect, male; 77, basifemur to tarsus II, lateral aspect, male; 78, leg III, lateral aspect, male; 79, gnathosoma, ventral aspect, male; 80, gnathosoma, lateral aspect, male; 81, idiosoma, dorsal aspect, protonymph; 82, idiosoma, ventral aspect, protonymph.

Protonymph: Idiosoma length 198–201 µm. Dorsal plates smaller than those of adults. AD and PD with rounded posterior and anterior margin (Figure 81). Setae ds-3 inserted within striated integument. Ventral plates delicately and minutely reticulate. Outline of plates as illustrated (Figure 82). Gnathosoma similar to that of adults. Telofemora with ventrolateral lamellae. Tibiae I and II with a single (the distal one) bipectinate seta.

Remarks

Copidognathus bistriatus is closely related to *C. incarinatus* Newell and *C. areolatus* Bartsch. The two latter species are known from the eastern Pacific Ocean near Chile (*C. incarinatus*) and the Hawaiian Islands (*C. areolatus*) (Newell 1984; Bartsch 1989). *C. incarinatus* has wider costae on the PD (costae two pores wide). The AD of *C. areolatus* shows a second transverse bar with a sculpturing differing from remainder of the plate; such bar is lacking in *C. bistriatus*.

In the samples taken around Rottnest Island, *C. bistriatus* is an abundant representative of the *gibbus* group. The species was found within scrubs of corallines and colonies of tube-building polychaetes in tidal and shallow subtidal areas.

Copidognathus multiporus sp. nov.

Figures 83–90

Holotype

♂, Little Armstrong Bay, Rottnest Island, Western Australia, Australia, seagrass *Amphibolis* with dense epiflora and epifauna and sediment, 0.5–1.0 m depth, 16 January 1991, I. Bartsch (WAM 93/2144).

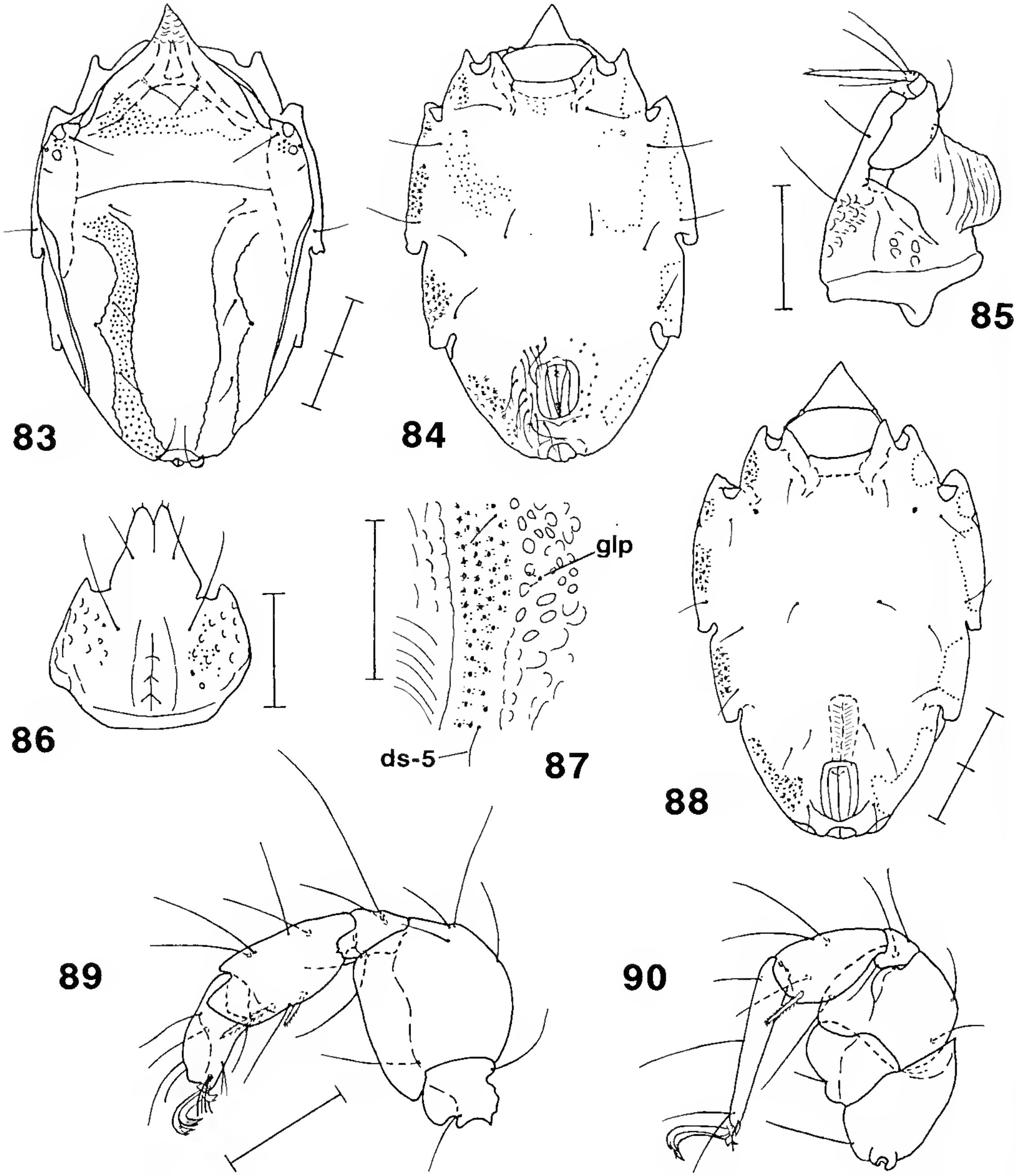
Paratypes

Australia: Western Australia: 1 ♀, type locality, date and collector (WAM 93/2145); 1 ♂, 1 ♀, type locality, date and collector (IB Au389).

Description

Male: Idiosoma length 372–396 µm, holotype 396 µm. Dorsal plates contiguous, partly but not completely fused. AD (holotype) 155 µm long, 179 µm wide. Frontal spine and median AD raised, with 'A'-shaped internal sclerite, porose areolae with rosette pores and wide anterolateral lamellae (Figure 83). Integument of frontal spine foveolate. Each rosette pore with very small surficial ostium and 3–4 canaliculi in deeper layers. OC 130 µm long; with large anterior and small posterior cornea, 10–12 rosette pores medial to corneae, and gland pore and pore canaliculus in lateral margin. PD 235 µm long, 204 µm wide; with 2 sinuose, sharply raised and porose costae. Gland pore at margin of costae (Figure 87). Anterior part of costae 3–4 pores wide; costae just posterior to gland pores 2 rosette pores wide; posterior part of costae 4–5 pores wide. Lateral part of PD with reticulate sculpturing. Median part of PD with very delicate, scattered canaliculi, else rather smooth. Dorsal setae long and slender; ds-1 inserted on AD on one level with transverse bar of 'A'-shaped internal sclerite; ds-2 on anteromedial margin of OC; ds-3 to ds-5 on PD, ds-3 anterior to raised costae, ds-4 and ds-5 within raised costae.

All ventral plates fused to a ventral shield (Figure 84); only internal apodemes from muscle strings give evidence of margins of plates. Marginal areas of ventral shield with rosette pores, adjacent areas with groups of canaliculi, median shield with scattered, very delicate canaliculi. Epimeral processes large, medial and lateral eprI triangular, median process slightly shorter



Figures 83–90 *Copidognathus multiporus* sp. nov., 83, idiosoma, dorsal aspect, male; 84, idiosoma, ventral aspect, male; 85, gnathosoma, lateral aspect, male; 86, gnathosoma, ventral aspect, male; 87, portion of right PD with ds-4 and ds-5, male; 88, idiosoma, ventral aspect, female; 89, basifemur to tarsus I, lateral aspect, male; 90, leg III, medial aspect, male.

than lateral process. Lateral eprII distinct. GO 52 μm long, 35 μm wide; 13–14 pairs of pgs arranged around GO; two posterior pairs of pgs bristle-like. Spermatopositor large.

Gnathosoma very wide, 97 μm long, 82 μm wide. Gnathosoma base with rosette pores (Figure 86). Tectum with large, sharply raised crest (Figure 85). Palp with small ventral process. P-4 with 3 long setae inserted near base of segment.

Dorsal projection on trochanters III and IV large. Basifemora III and IV with large ventral lamellae. Telofemora slightly longer than high; with large, very delicately reticulated ventrolateral lamellae. Lateral articular lamella on I-5 distinctly larger than medial lamella. II-5 with small, triangular and flap-like medial lamella; lateral lamella long and wide (Figure 89). Tibiae III and IV with lateral lamellae somewhat smaller than medial lamellae. Ventromedial (bipectinate) seta on III-5 short when compared with very long ventral bristle-like seta. Tarsi III (Figure 90) and IV conspicuously long and slender, longer than tibiae plus genua; each tarsus with 4 dorsal setae.

Claws slender. Accessory process with delicate tines.

Female: Idiosoma length 378–390 μm. In dorsal aspect similar to male. Ventral plates fused to a ventral shield (Figure 88). GO 48 μm long, 30 μm wide. Ovipositor surpassing GO for slightly more than length of GO.

Remarks

Copidognathus multiporus is most easily identified on the basis of the combination of: all ventral plates fused to a ventral shield; AD with transverse bar, PD with 2 longitudinal areolae, each with numerous rosette pores, rosette pores having small ostia at the surface of the plates and 3–4 canaliculi in deeper layers; tarsi III and IV very long and slender.

In dorsal aspect, there is a slight similarity with *C. cataphractus* (Trouessart), a species recorded from the western Indian Ocean (André 1959). The shape of the AD, its anterolateral lamellae and the transverse porose areola are similar in both species, but the outline of the porose costae on the PD is distinctly different.

Copidognathus caelatus sp. nov.

Figures 91–99

Holotype

♂, Bickley Point, Rottnest Island, Western Australia, Australia, *Amphiroa* and other corallines from vertical rock surface, 0.5 m depth, 18 January 1991, I. Bartsch (WAM 93/2135).

Paratypes

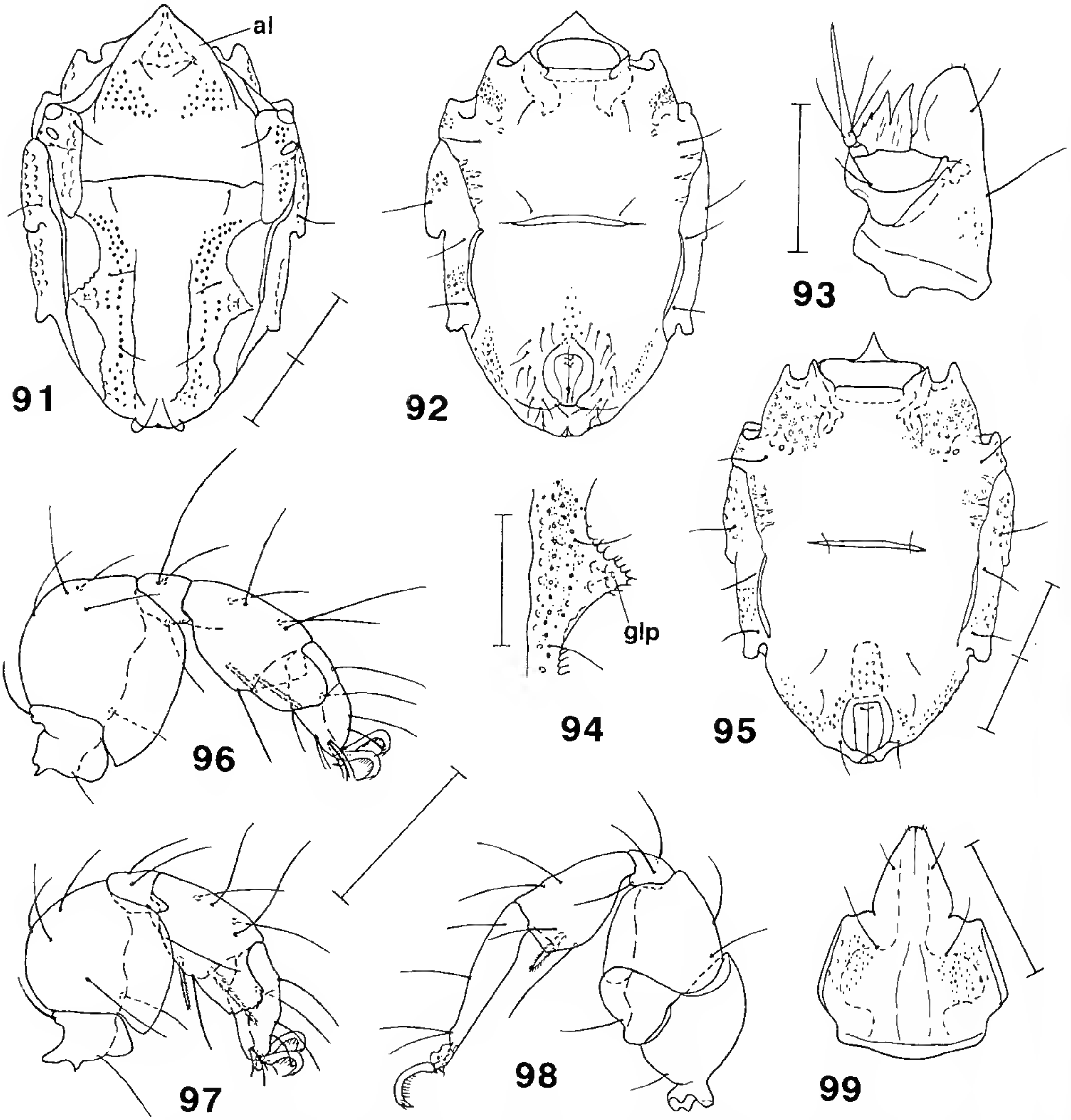
Australia: Western Australia: 1 ♀, same data and collector as for holotype (WAM 93/2136); 1 ♂, type locality and date (WAM 93/2137).

Other Material Examined

Australia: Western Australia: 2 ♂, Little Armstrong Bay, seagrass *Amphibolis*, 0.5 m depth, 16 January 1991, I. Bartsch (IB Au390).

Description

Male: Idiosoma 276–278 μm long, holotype 278 μm long. Idiosoma intensely armoured; dorsal plates contiguous, partly overlapping, margins of plates present but plates often not separated by striated integument. Porose areolae generally with small surficial ostia and numerous canaliculi in deeper integumental layers. Remainder of plates (outside porose areolae) with very faint reticulate ornamentation. AD (holotype) 122 μm long, 117 μm wide, with 'A'-shaped, solid internal sclerite. Wide anterolateral lamellae extending from frontal spine almost to level of ds-2 (Figure 91). Scattered canaliculi within anterior angle of 'A'-



Figures 91–99 *Copidognathus caelatus* sp. nov., 91, idiosoma, dorsal aspect, male; 92, idiosoma, ventral aspect, male; 93, gnathosoma, lateral aspect, male; 94, portion of right PD with ds-4 and ds-5, male; 95, idiosoma, ventral aspect, female; 96, basifemur to tarsus I, lateral aspect, male; 97, basifemur to tarsus II, lateral aspect, male; 98, leg III, lateral aspect, male; 99, gnathosoma, ventral aspect, male.

shaped sclerite. The 2 triangular areolae each with about 25 rosette pores. First pair of gland pores rather inconspicuous, level with transverse bar of internal 'A'-shaped sclerite. OC 89 μm long, 30 μm wide, not distinctly separated from AD and PD, and linked with dorsal AE; posterior part of OC tail-like. Lateral part of OC raised; with 2 large corneae, rosette pores between corneae and on 2 rows along lateral margin of OC. Medial part of OC excavated and without prominent sculpturing. Gland pore and pore canaliculus lateral to posterior cornea. PD 149 μm long, 117 μm wide. With longitudinal sinuose porose costae; costae with lateral protrusions both level with insertion of leg III and leg IV (Figure 91); median part of PD slightly excavated, lateral part of PD abruptly set off from raised costae. Solid internal sclerites present beneath costae. Anterior porose areolae with small ostia; posterior areolae with larger ostia. Large gland pore within lateral protrusion (Figure 94). Dorsal setae long, ds-1 inserted adjacent to 'A'-shaped sclerite, ds-2 in medial margin of OC, ds-3 close to anterior margin of PD, ds-4 and ds-5 within costae just anterior and posterior to level of leg IV.

AE 96 μm long, 174 μm wide. Anterior apodemes very prominent (Figure 92). Medial eprI triangular, lateral eprI somewhat larger and extending dorsolaterally, medial eprII scale-like. Dorsal and marginal parts of AE and PE with rosette pores; ventral plates with distinctly demarcated porose areolae. AE with pair of triangular areolae posterior to leg I, small areolae posterior to leg II and scattered canaliculi posterior to camerostome. PE with ventral porose areolae both anterior to leg III and leg IV. Lateral part of GA with pair of porose areolae and few scattered pores anterior to GO. Remainder of AE and anterior part of PE incompletely fused, with margins of the plates still visible and epicuticula somewhat overlapping. GA 140 μm long, 137 μm wide. AE and GA fused posterolaterally and anterolaterally for about 30 μm; median 70 μm wide wedge with striated integument (Figure 92). GO 45 μm long, 32 μm wide; anterior foramen overlaid by a membrane. Pgs slender, 11–12 on either side of foramen. Spermatopositor large.

Gnathosoma 80 μm long. Ventral and lateral base of gnathosoma with rosette pores and canaculiculi (Figure 99). Tectum with long spine which bears a high crest (Figure 93). P-4 slender, longer than P-2; 3 setae inserted near base of segment. Dorsal seta on P-2 rather stout.

Ventrolateral lamella on I-3 and II-3 with very delicate reticulate sculpturing, both with ventral margin somewhat convex (Figures 96, 97). Lateral articular lamellae on I-5 and II-5 much larger than small medial lamellae. Articular lamellae on posterior tibiae rather small (Figure 98). Solenidion on both tarsus I and II slender, seta-like. Tarsi III and IV slender, longer than tibiae and telofemora, tarsus III with 4 dorsal setae, tarsus IV with 3 setae.

Claws with accessory process and pecten. Tines on pecten long and rather delicate.

Female: Idiosoma length 266–267 μm. Dorsal aspect similar to male. AE with apodemes flanking camerostome smaller than in male. Porose areolae on ventral plates larger than in male. AE and PE partly fused, GA and PE separated via striated integument (Figure 95). AE and GA fused in their outer edges but separated in the median. GA 135 μm long and 120 μm wide. GO 38 μm long, 32 μm wide, distance to anterior margin of GA about 2.5 times the length of GO. Ovipositor extending beyond GO for about length of GO.

Remarks

With the wide idiosoma, the anterolateral lamellae on the PD and the porose areolae on the dorsal plates, *C. caelatus* resembles *C. cataphractus* (Trouessart), a species recorded from

Djibouti (Trouessart 1899), and *C. mesomorphus* André, recorded from Egypt (André 1959). In *C. cataphractus*, the integument outside the raised porose areolae is coarsely foveate whereas in *C. caelatus* the integument is smooth or delicately reticulate. In *C. mesomorphus* the raised area on the AD is much more narrow and extends posteriorly distinctly beyond the mid of the AD.

In *C. caelatus*, as in several other species of the *gibbus* group, the lateral PD is deeply excavated, the excavations are flanked by the raised longitudinal costae. The excavations are fitted to take up trochanters and telofemora of leg III and IV. Trochanters and telofemora of the anterior legs can be hidden beneath the anterolateral membrane of the raised AD.

Copidognathus ampliatus sp. nov.

Figures 100–109

Holotype

♂, Little Armstrong Bay, Rottnest Island, Western Australia, Australia, seagrass *Amphibolis* overgrown with epiflora and epifauna, 0.5 m depth, 16 January 1991, I. Bartsch (WAM 93/2127).

Paratypes

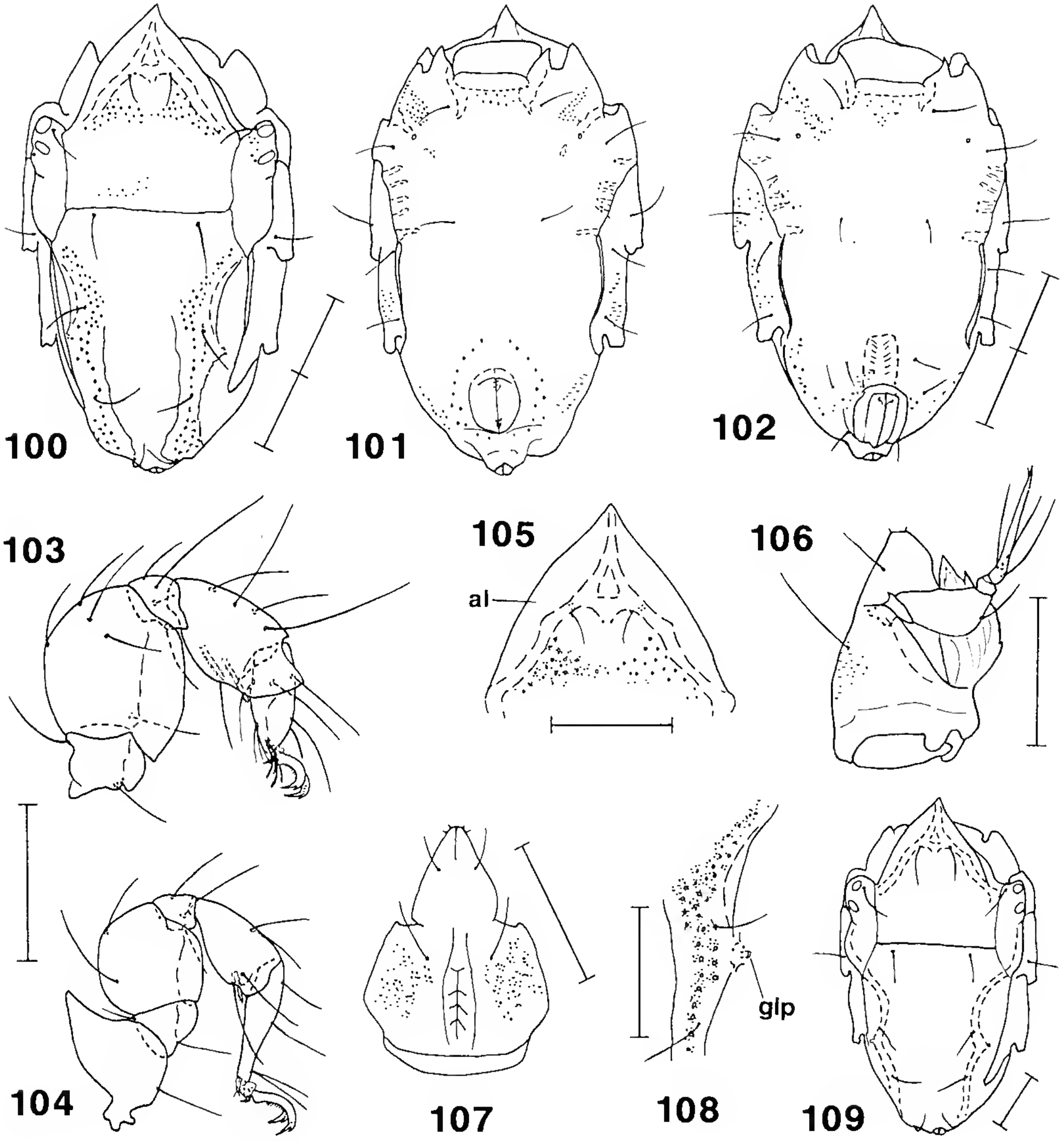
Australia: Western Australia: 1 ♀, same data as for holotype (WAM 93/2128); 2 ♂ and 3 ♀, same data as for holotype (IB Au359, Au360, Au390).

Description

Male: Idiosoma length 276–281 μm, that of holotype 281 μm. AD (holotype) 123 μm long, 135 μm wide. Anterolateral lamellae extending from frontal spine to level of ds-2. Internal sclerite as figured (Figure 105). Pair of triangular porose areolae almost fused medially. Porose areolae with small ostia at surface and 5-7 canaliculi in deeper layers. Posterior part of AD with groups of canaliculi (Figure 100). AD and OC contiguous. OC 98 μm long, with 2 large corneae; anterior porose areola with about 15 rosette pores; posterolateral margin of OC raised and with foveate sculpturing but without rosette pores. Medial part of OC not raised, its ornamentation faint. Posterior part of OC tail-like. Anterior part of PD and posterior part of OC fused though margin of plates still present. PD 145 μm long, 122 μm wide; with 2 pairs of longitudinal sinuose costae. Lateral part of PD with reticulate sculpturing set off abruptly from longitudinal costae. Anterior part of PD faintly reticulate, median and posterior parts of PD excavated and only delicately ornamented. Internal sinuose sclerites beneath costae (Figure 109). Rosette pores in anterior part of costae with small ostia; middle part of costae 1–2 rosette pores wide (Figure 108), ostia slightly larger than in anterior part of costae. Gland pore level with insertion of leg IV. Dorsal setae long. Setae ds-3 inserted near anterior margin of PD.

AE and GA completely fused, with only 10 μm long lateral apodemes indicating margin between plates (Figure 101). Ventral shield 230 μm long, 162 μm wide. AE and PE contiguous though margins of plates still present. GA separated from PE by striae of membraneous integument. AE with rather large triangular porose areolae, moreover, scattered canaliculi present posterior to leg II. PE with small porose areolae anterior to legs III and IV. Camerostome surrounded by internal sclerites. Medial eprI large, triangular, as long as lateral (dorsolateral) cprI. GO 42 μm long, 33 μm wide; with 11–12 pairs of slender pgs.

Gnathosoma 78 μm long. Tectum with crest-like spine (cf. Figure 106). Ventral and marginal flank of gnathosoma base porose (cf. Figure 107). P-4 slender, longer than P-2. Seta



Figures 100–109 *Copidognathus ampliatus* sp. nov., 100, idiosoma, dorsal aspect, male; 101, idiosoma, ventral aspect, male; 102, idiosoma, ventral aspect, female; 103, basifemur to tarsus I, lateral aspect, female; 104, leg III, lateral aspect, female; 105, anterior AD, male; 106, gnathosoma, lateral aspect, female; 107, gnathosoma, ventral aspect, female; 108, portion of right PD with ds-4 and ds-5, male; 109, idiosoma, internal sclerites at dorsal aspect, male (porose areolae omitted).

on P-2 bristle-like. Basal whorl of setae inserted near base of P-4.

Ventrolateral lamellae on I-3 and II-3 delicately reticulate, ventral margin evenly convex (cf. Fig 103). Lateral articular lamellae on I-5 large, and triangular, those on II-5 rounded-rectangular, medial lamellae on both tibiae small. Lateral and medial lamellae on tibiae III (cf. Figure 104) and IV small. Tarsi III and IV slender, longer than tibiae and telofemora. III-6 with 4 dorsal setae, IV-6 with 3 setae.

Claws with accessory process and pecten. Pecten almost reaching to base of claws.

Female: Idiosoma length 278–308 µm. Similar to male in dorsal and ventral aspect. AE, PE and GA fused, but PE and GA separated by wedge of striae (Figure 102). Lateral apodemes from PE extending medially. GO 40 µm long and 35 µm wide. Ovipositor extending beyond GO for slightly less than length of GO, and surpassing anterior pairs of pgs.

Remarks

In dorsal aspect, *C. ampliatus* is very similar to *C. caelatus*. There are small differences in outline of the porose areolae and the number of rosette pores; *C. caelatus* has larger porose areolae than *C. ampliatus*, and several rosette pores along the lateral margin of the OC posterior to the corneae. At ventral aspect, adults of the two species are easily distinguished; *C. caelatus* has a median wedge with membraneous integument between AE and GA whereas in *C. ampliatus* the two plates are completely fused. Intermediate forms have not been found in the material examined. Outline of porose areolae with rosette pores and presence or absence of sutures between the plates may be influenced by sclerotization of the plates, which in turn is influenced by environmental parameters (unpublished observations). Detailed studies on more material is needed.

DISCUSSION

Bartsch (1985a) gave a brief survey on species of the *gibbus* group, 19 species were known at that time, since then, another eight species have been described, viz., *C. areolatus* Bartsch, *C. chilensis* Newell, *C. glareus* Newell, *C. incarinatus* Newell, *C. longispinus* Bartsch and Iliffe, *C. lubricus* Bartsch, *C. simplipes* Newell, *C. ventriscutatus* Bartsch (Newell 1984; Bartsch and Iliffe 1985; Bartsch 1986, 1989).

Around Rottnest Island, 12 species of this group have been found. *C. dubiosus* is unique in several characters, with no closely allied species described as yet. *C. canaliculifer* is very similar to the Philippine species *C. scutellus*. Even when sorting a sample at low magnification, both species are discriminated from all the others on the basis of the wide dorsal shield which lacks surficial sculpturing. *C. bispinus* and *C. laminifer* resemble *C. canaliculifer* in general facies such as wide idiosoma and the plates being rather smooth except for canaliculi and longitudinal striae, but, *C. bispinus* and *C. laminifer* have lateral lamellae arising from the PE. Similar lamellae have not been recorded from any other *Copidognathus*.

The other species found around Rottnest Island have closely related congeners in other regions of the world. *C. strigellus* is allied to *C. felicis* and *C. remipes*; *C. felicis* was collected in the southeastern Pacific, *C. remipes* is rather abundant in the northeastern Atlantic and the Mediterranean. *C. punctellus* demonstrates close similarity with the Chilean *C. simplipes*, and *C. crassipinus* with the Bermudian *C. longispinus*. *C. bistriatus* resembles the Pacific species *C. incarinatus* and *C. areolatus*. *C. ampliatus* and *C. caelatus* are most similar to *C. cataphractus* and *C. mesomorphus*, both recorded from the eastern African coast.

Amongst the halacarid material collected around Rottnest Island is a high number of sibling species (unpublished). Amongst others, the pairs *C. laminifer/C. bispinus*, and *C. ampliatus/ C. caelatus* are almost identical in dorsal aspect, but *C. laminifer* and *C. ampliatus* have AE and GA fused whereas in *C. bispinus* and *C. caelatus* AE and GA are separated at least in the median. Though the dorsal aspect of the idiosoma, the form of plates, their ornamentation and outline of porose areolae and size of pores is higly characteristic for a given species, the dorsal aspect alone is insufficient when determining halacarid species.

ACKNOWLEDGEMENTS

Thanks are due to Dr Fred E. Wells and his colleagues for organizing the Fifth International Marine Biological Workshop and their constant assistance throughout the days on Rottnest Island. I also wish to thank the participants of the Workshop for enjoyable days on Rottnest and help with sublittoral deposits.

Abbreviations used in text and figures

AD	anterior dorsal plate
AE	anterior epimeral plate
al	anterolateral lamella
br	bristle
ds	dorsal setae on idiosoma, ds-1, first pair of dorsal setae
epr	epimeral process, eprI, epimeral process of first epimeron
f	foveae
GA	genitoanal plate
glp	gland pore, glp-1, first (anteriormost) gland pore
GO	genital opening
gr	groove
l	lamella
lepr	lateral epimeral process
ll	lateral lamella
mepr	medial epimeral process
mxs	maxillary setae
OC	ocular plate(s)
P	palp, P-2, 2nd palpal segment
pas	parambulacral setae
pc	pore canaliculus
PD	posterior dorsal plate
PE	posterior epimeral plate
pgs	perigenital setae
rs	rosette pores
sgs	subgenital setae
so	solenidion
T	tectum with crest
vs	ventral seta on idiosoma.

Legs numbered I to IV, leg segments 1 to 6, I-1 to I-6, trochanter, basifemur, telofemur, genu, tibia and tarsus on leg I.

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DESCRIPTION OF A NEW GENUS AND SPECIES OF MONACANTHID FISH FROM INDIA

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ABSTRACT

A new genus and species of monacanthid fish, *Lalmohania velutina*, is described from six specimens collected in the Kilakkarai region of south-eastern India. The taxon appears to be most similar to members of the genus *Stephanolepis*, but differs in scale structures, fin shapes, fin ray counts, lateral line sensory system, and structure of the pelvic fin rudiment.

INTRODUCTION

Hutchins (1988) investigated the morphology and phylogeny of the monacanthid fishes, following the cladistic approach of Hennig. Collections from many parts of the world were examined, resulting in the discovery of several new taxa. One of these is known from only six specimens collected in a small area of south-eastern India. This paper presents a description of this new form, and examines its relationships with other members of the family.

Methods of counting and measuring follow those of Hutchins (1977, 1986). Abbreviations for institutions are recorded in the Acknowledgements.

SYSTEMATICS

Family Monacanthidae Nardo, 1844

Genus *Lalmohania* gen. nov.

Type species

Lalmohania velutina sp. nov. (see below).

Diagnosis

Distinguished from all other Group A genera (i.e., those possessing a pelvic fin rudiment movably articulated with the pelvis, see Table 1) of Hutchins (1988) by its unique scale structures. All scales on the anterior one-quarter of the body, not including the head, are very small, each possessing several posteriorly curved spinules (up to five) arranged in a transverse line, whereas the scales on the posterior three-quarters are much larger, particularly those midlaterally, each supporting a single, elongate spinule (Figure 1); spinules of the male are more robust, bristlelike, extremities curving anteriorly, but not forming a prominent midlateral

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Table 1 Monacanthid genera belonging to Group A (Hutchins 1988)

Acreichthys Fraser-Brunner, 1941
Arotrolepis Fraser-Brunner, 1941
Chaetodermis Swainson, 1939
Colurodontis Hutchins, 1977
Laputa Whitley, 1930
Leprogaster Fraser-Brunner, 1941
Monacanthus Oken, 1817
Paramonacanthus Bleeker, 1865
Pervagor Whitley, 1930
Stephanolepis Gill, 1861
"Genus a" (described herein)
"Genus b" (genus and species are undescribed)

patch of bristles. Other distinctive characters include a moderately deep body with interdorsal space prominently concave in lateral profile, moderately large pelvic fin rudiment with a prominent space ventrally between the encasing scales, anterior portion of soft dorsal fin elevated in the male (but without filamentous rays), soft dorsal and anal fin ray counts low (25–27 and 25–28 respectively), pectoral fin ray counts low (10–11), caudal fin of male with an arrowhead-like shape to the rear margin, and 19 (7+12) vertebrae.

Relationships

In overall appearance, the genus is most similar to *Stephanolepis*, both taxa being relatively deep bodied with small ventral flaps. The lateral profiles of their interdorsal spaces and snouts are mostly concave (snout of male *Stephanolepis* is usually straight to slightly concave), and the anterior portion of the soft dorsal fins are somewhat elevated. In both *Lalmohania* and *Stephanolepis*, the caudal peduncles are not deep, and the pelvic fin rudiments are not large. Internally, both genera possess very similar skeletal structures, particularly in the skull and the pelvis. However, none of these similarities is considered to be synapomorphic (Hutchins 1988). The two genera differ noticeably in squamation, fin shapes, fin ray counts, lateral line sensory system, and structure of the pelvic fin rudiment. *Stephanolepis* is characterised by its distinctive lozenge-shaped cluster of spinules on a single, broad-based pedicle (spinule cluster is more circular and mushroom-shaped in small examples) on each body scale. Scales on the middle portion of the caudal peduncle of the male each possess an elongate spinule, distal extremity curving anteriorly in mature individuals, forming a well defined elongate patch of bristles extending a short distance anteriorly along the side of the body. In contrast, *Lalmohania* has no body scales with spinule clusters, and all scales on the posterior three-quarters of the body have single spinules which do not form a distinct bristle patch. The male of *Stephanolepis* has an elongate filamentous ray anteriorly in the soft dorsal fin (absent in *Lalmohania*) and has a rounded posterior margin to the caudal fin (more arrowhead-shaped in *Lalmohania*). Most members of *Stephanolepis* usually possess soft dorsal and anal fin ray counts of 30 or more, and pectoral fin ray counts of 12–14 (the exception is *S. setifer* from the Atlantic Ocean which has counts of, respectively, 26–30 and 11–13). In contrast, *Lalmohania* has much lower counts (soft dorsal 25–27, anal 25–28, and pectoral 10–11). *Stephanolepis* has the most primitive lateral line system of the family, especially in the retention of mandibular pores. Like all other monacanthids, however, *Lalmohania* has no mandibular

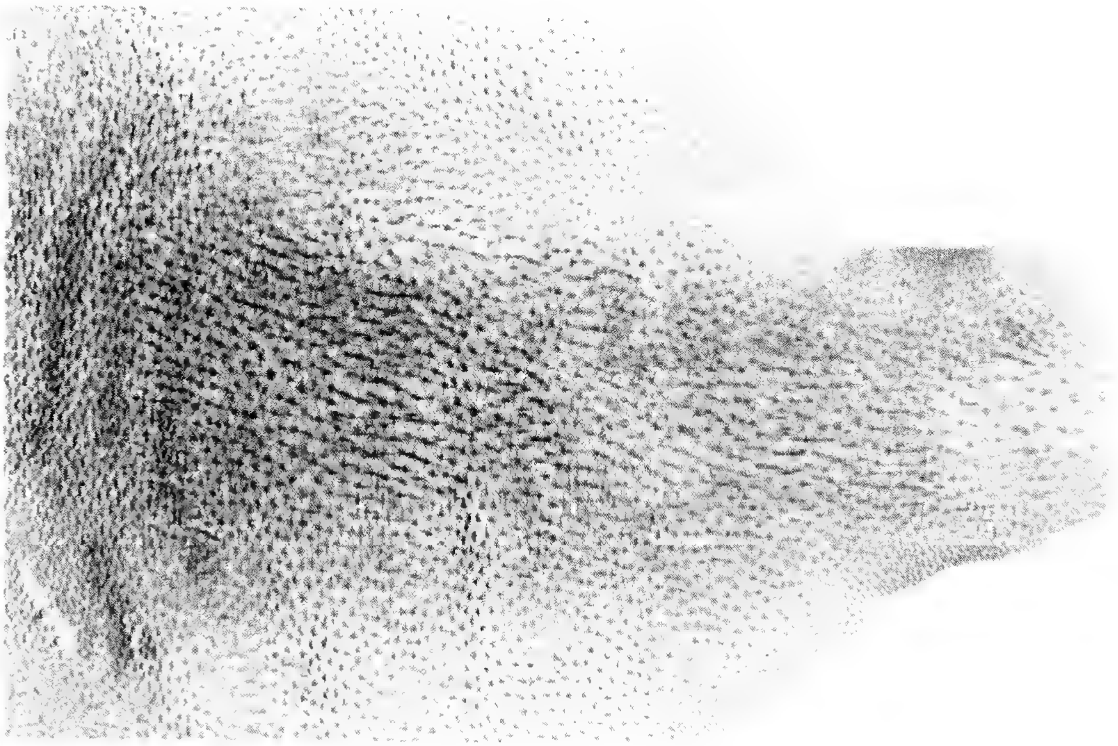

Figure 1 Cleared and stained skin (left hand side) of *Lalmohania velutina*, paratype, WAM P.30671–001, 55 mm SL, showing body scales in region posterior to pectoral fin.

pores. The pelvic fin rudiment of *Stephanolepis* lacks a prominent space between segments 2 and 3 (a small one is sometimes present), a feature which always occurs in *Lalmohania*. In addition, the rudiment is broadly joined dorsally to the ventral flap in *Stephanolepis*, but only very narrowly attached in *Lalmohania*.

This new form is similar in appearance to several other deep-bodied monacanthid genera but can be easily distinguished on several features. *Lalmohania* lacks the greatly enlarged ventral flap that characterises *Monacanthus* and *Leprogaster*. It differs from *Acreichthys* and *Chaetodermis* in having only 19 vertebrae (latter both have 20), from *Colurodontis* in having four predorsal neural spines, a robust pelvis, and pointed teeth (latter possesses three predorsal neural spines, a very slender pelvis, and truncate teeth), and from *Arotrolepis* by lacking both a dorsal ridge on the midline of the male's snout and a unique ventral expansion of the basioccipital for swim bladder support.

Etymology

This new taxon is named after R.S. Lal Mohan, Central Marine Fisheries Institute (CMFRI), Mandapam Camp. Not only was he involved in the collection of the type series, but he also provided invaluable assistance to me and other foreign participants during the FAO/DANIDA consultation at Cochin in 1980.

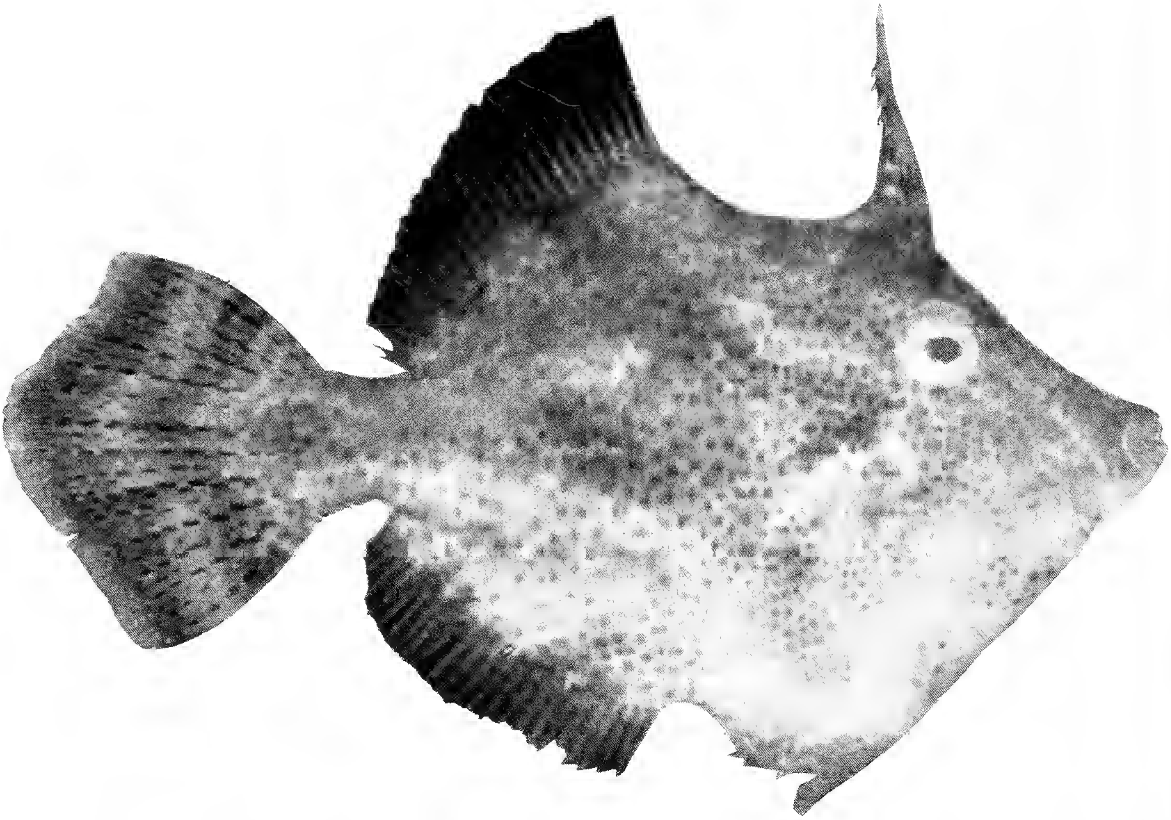

Figure 2 *Lalmohania velutina*, holotype, BPBM 20617, 72 mm SL (hyaline soft dorsal and anal fins appear black as specimen originally photographed on dark background).

Lalmohania velutina sp. nov.

Figures 1, 2 and 3; Tables 1 and 2

Stephanolepis diaspros (*non* Fraser-Brunner?) Munro, 1955: 275.

"Genus a species 1" Hutchins, 1988.

Holotype

BPBM 20617, 72 mm SL, male, Kilakkarai (approximately 9°16'N, 78°48'E), Gulf of Mannar, India, purchased from market, J.E. Randall, K. Rama Rao, and R.S. Lal Mohan, 4 March 1975.

Paratypes

BPBM 35756, 2 specimens, 62–73 mm SL, collected with holotype; WAM P.30671-001, 55 mm SL, collected with holotype, cleared and stained; CMFRI uncatalogued, 2 specimens, 68–83 mm SL, Kilakkarai, trawl net at 5 m, 12 December 1979.

Diagnosis

See generic account above.

Description

Measurements and counts of the holotype and paratypes are presented in Table 2. The following counts and proportions in parentheses represent the ranges for the paratypes when they differ from those of the holotype.

Soft dorsal rays 26 (25–27); anal rays 26 (25–28), normally equal to or one more than soft dorsal count; pectoral rays 11 (10–11), although left hand side count of 7 considered a deformity; vertebrae 7+12=19 (one paratype with 7+13=20) (from radiographs and cleared and stained material); branchiostegals 1+4=5.

Body compressed but deep, width 2.2 (1.9–2.3) in head length and depth 1.5 (1.5–1.6) in SL; lateral profile of interdorsal space very concave, rising noticeably to origin of soft dorsal fin (Figure 2); head relatively short, length 3.0 (2.8–3.2) in SL; lateral profile of snout prominently concave, length 4.0 (4.1–4.3) in SL; eye diameter 3.4 (3.0–3.6) in head length, 1.0 (0.9–1.2) in interorbital width; gill opening a short slit, length 5.2 (4.0–4.9) in head length, positioned in advance of pectoral fin base, centred below posterior one-quarter of eye; pelvic flap small in size.

Mouth small, terminal, lips somewhat fleshy; dentition consisting of three outer and two inner teeth on each side of upper jaw (exposed portion of first inner tooth small but obvious, with rounded extremity, second inner tooth mostly covered by outer teeth); three teeth on each

Table 2 Measurements and counts of the holotype and paratypes of *Lalmohania velutina.*

	Holotype			Paratypes		
	BPBM 20617	CMFRI Uncat.	BPBM 35756	CMFRI Uncat.	BPBM 35756	WAM P30671-001
Standard length	72	83	73	68	62	55
Head length	24	26	24	23	21	20
Body depth	47	56	50	45	38	36
Body width	11	13	12	12	10	8.7
Snout length	18	20	17	16	15	13
Eye diameter	7	7.6	7.1	6.4	7.1	6.3
Interorbital width	7	8.4	7.4	7.8	6.8	5.7
Gill slit length	4.6	6.2	4.9	4.8	5.3	4.5
Snout to dorsal spine	25	27	25	24	21	#
Lower jaw to pelvic fin rudiment	45	54	48	47	42	#
Dorsal spine length	19	22	18	18	17	16
Interdorsal space	23	26	22	19	18	15
Longest dorsal ray	13	#	14	#	6.8	7.8
Longest anal ray	7.9	#	11	#	5.2	6.5
Longest pectoral ray	9	#	9.7	#	7.9	#
Length of caudal fin	28	31	29	23	21	20
Length of dorsal fin base	29	32	31	26	24	21
Length of anal fin base	28	35	31	26	23	21
Length of caudal peduncle	7.3	8.1	7.8	6.6	6.9	6.1
Depth of caudal peduncle	10	13	11	10	8.8	8.2
Length of pelvic fin rudiment	5.1	#	4.9	#	4.8	4
Soft dorsal fin ray count	26	25	26	26	27	26
Anal fin ray count	26	26	26	26	28	25
Pectoral fin ray count	11/7	11/11	11/11	10/10	11/11	11/11
Sex	Male	Male	Male	Female	Female	Male

\# Measurement not taken due to damage.

side of lower jaw; anterior pair of teeth in both jaws with pointed extremities; gill rakers on first gill arch 16 (from 73 mm SL paratype).

First dorsal spine originating over centre to slightly behind centre of eye; spine rather long, slightly shorter than interdorsal space, length 1.3 (1.2–1.3) in head length; spine robust, circular in cross-section, somewhat sinuous in shape, tapering to acute tip; spine of smallest available specimen (55 mm SL) with four rows of barbs, consisting of two adjacent rows of small barbs on anterior face (barbs mostly upward-directed, some with small downward-directed branch, prominent on proximal half but indistinguishable distally from spinules that cover anterior face of spine), and two rows of large downward-directed barbs on posterior face, projecting mostly posterolaterally; with increasing SL, anterior barbs become obsolete; second dorsal spine small, hidden in skin at rear base of first spine; interdorsal space without groove for receiving first dorsal spine when folded rearwards; soft dorsal fin elevated anteriorly in male, outer margin convex (Figure 2), longest dorsal ray 1.8 (1.7–3.1); anal fin not elevated anteriorly in either sex, outer margin convex, longest anal ray 3.0 (2.2–4.0); length of soft dorsal base 2.5 (2.4–2.6) in SL, equal to or slightly longer than anal fin base (bases of fin membranes not perforated); origin of soft dorsal fin directly above origin of anal fin; base of pectoral fin below a point ranging from slightly in advance of to slightly behind rear border of eye; caudal fin moderately long, length 0.9 (0.8–1.0) in head length, middle rays noticeably longer in male producing somewhat arrowhead appearance to posterior margin

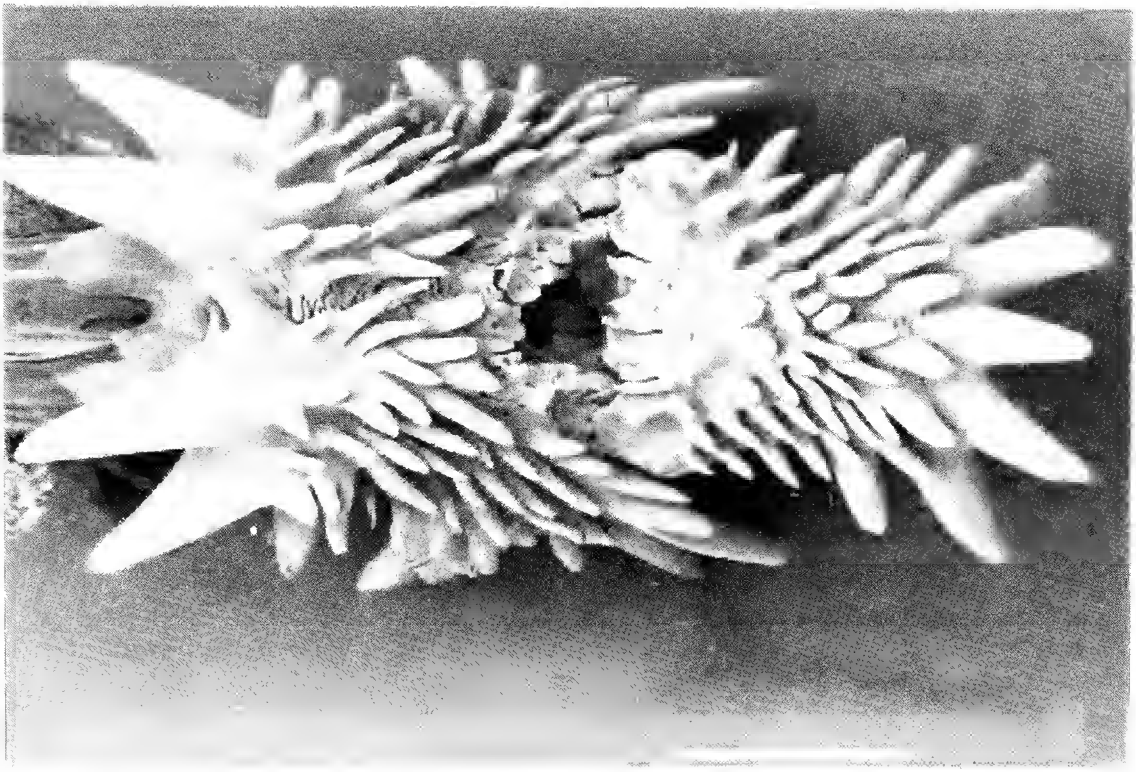

Figure 3 Pelvic fin rudiment (ventral view) of *Lalmohania velutina*, paratype, WAM P.30671-001, 55 mm SL (scanning electron micrograph: integumentary sheath removed to make encasing scales more visible; anterior end of rudiment facing left; white bar = 1 mm)

of fin; caudal peduncle length 3.3 (3.0–3.5) in head length, 1.4 (1.3–1.6) in caudal peduncle depth; pelvic fin rudiment (Figure 3) relatively large in size, length 1.4 (1.4–1.6) in eye diameter, consisting of five encasing scales with prominent barbs, an anterior pair (segment 1), a middle pair (segment 2), a single posterior scale (segment 3); scales of segment 2 separated from each other along ventral midline of rudiment by a prominent gap (Figure 3); segment 3 movably articulated with segment 2 and rear end of pelvis; pelvic fin rudiment not broadly joined to rear margin of ventral flap.

Anterior midbody scales small to moderate in size, mostly imbricate, elliptical in shape, with 1–5 slender, simple, posteriorly curved spinules supported by transverse ridge on each scale. spinules becoming longer posteriorly, reducing to one per scale (all scales on posterior three-quarters of body with only one spinule, except on base of soft dorsal and anal fins, see Figure 1); scale spinules on posterior portion of caudal peduncle of male moderately enlarged, robust, distal extremity curving anteriorly, spinules becoming smaller and more flexible anteriorly; scales on forehead with short, robust spinules, some rather flattened; spinules on breast scales similar but not flattened; skin velvety to slightly coarse; numerous moderately sized cutaneous tentacles on body, dorsal spine, and pelvic fin rudiment.

Colour of holotype in alcohol

Ground colour brown with many dark brown closely packed spots; head and body also with darker blotches, those on body tending to form two oblique, curved cross bands, first from anterior portion of second dorsal base to gill slit, second from midside of body above centre of anal fin base to ventral flap; indications of several dark bands across breast, two across interorbital space, two on bases of soft dorsal and anal fins; soft dorsal and anal fins hyaline, some body spotting extending onto basal portions; caudal fin pale brown to hyaline, with two wide curved dark cross bars, posterior bar subterminal; body spotting continuing onto membranes of caudal fin, but caudal spots slightly larger, more crowded, and more elliptical in shape; paratypes similar in colour to holotype, except dark spots on largest specimen forming short lines in region of pectoral fin.

Colour when fresh is not known, but based on colour transparencies of specimens taken after preservation in formalin for one month, ground colour is probably a pale greenish grey. Figure 2 is a black and white photograph of the holotype taken by J.E. Randall (BPBM) shortly after capture. Features now not visible in the preserved specimen include pale wavy lines on the snout, several whitish elongate blotches on the body, particularly one behind the gill opening, and several series of dark-edged white spots following the posterior margin of the caudal fin.

Etymology

This species is named *velutina* in reference to its velvet-like skin.

Distribution

Lalmohania velutina has so far been collected only from the Kilakkarai region of south-eastern India, where it apparently inhabits shallow weedy bottoms.

Remarks

Lalmohania velutina is a poorly known species, but is probably more widespread in southern India than is indicated by the available material. It may even occur in Sri Lanka. Munro

(1955) recorded *Stephanolepis diaspros* Fraser-Brunner, 1940 from Sri Lanka based on material trawled in the Gulf of Mannar (the type locality for *Lalmohania velutina* occurs on the Indian side of this gulf). However, it has not been reported from this region since, nor have any other members of the genus. Munro's brief account closely follows the type description of *S. diaspros*, which suggests that his specimens were not thoroughly examined. Perhaps they were in fact representatives of *L. velutina*, but at the time were not recognised as being undescribed.

ACKNOWLEDGEMENTS

I would like to thank Dr John E. Randall, Bishop Museum, Honolulu (BPBM) for sending specimens and photographs of this species. I participated in the FAO/DANIDA consultation through the invitation of Dr Walter Fischer (FAO, Rome), and was able to examine specimens at the Central Marine Fisheries Research Institute (CMFRI), Cochin, through the courtesy of its Director, Dr E.G. Silas. The scanning electron micrograph of the pelvic fin rudiment was made by Mr C.W. Bryce, Western Australian Museum (WAM).

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REVISION OF THE GENUS *CRASSIFOENUS* CROSSKEY (HYMENOPTERA: GASTERUPTIIDAE), WITH A DESCRIPTION OF A NEW SPECIES FROM WESTERN AUSTRALIA

John T. Jennings* and Andrew D. Austin*

ABSTRACT

The endemic Australian gasteruptiid genus *Crassifoenus* Crosskey is revised and the included species, *C. grossitarsis* (Kieffer) and *C. macronyx* (Schletterer), are redescribed. A striking new species from Western Australia is described and an illustrated key to separate it from the other two species is presented. The taxonomic history, monophyly and biology of the genus are discussed.

INTRODUCTION

The Gasteruptiidae are among the most easily recognised parasitic Hymenoptera because of their elongate, subclavate metasoma, and very high position of its attachment on the mesosoma. The family comprises two subfamilies, the Gasteruptiinae and Hyptiogastrinae; the former containing only the cosmopolitan and commonly collected *Gasteruption* L., a genus that is readily identified in Australia by having an exserted ovipositor, propleura produced to form a distinct neck between the mesosoma and head, short mandibles, and low position of fore wing vein 1-Rs+M (i.e. in line with M+Cu). Alternatively, the Hyptiogastrinae are collected less often and they have a Gondwanan distribution. The group comprises five valid genera of which *Aulacofoenus* Kieffer is known from both Australia and South America, *Pseudofoenus* Kieffer is restricted to New Zealand, *Crassifoenus* Crosskey and *Hyptiogaster* Kieffer are restricted to Australia, while the predominantly Australian *Eufoenus* Szépligeti with more than 20 described species is also known from Fiji, Vanuatu (Crosskey 1953, 1962), New Guinea and New Caledonia (new records – AEIC, ANIC, BMNH). To date, 39 species of hyptiogastrine wasps are recognised (Crosskey 1953, 1962), of which 32 are from Australia. However, recently available material indicates that this figure represents only about 40% of the true size of the Australian fauna.

As a group, the Hyptiogastrinae is characterised by having long overlapping mandibles, and the trochantellus absent. Also, they usually have the fore wing vein 1-Rs+M intersecting the basal cell about half way between M+Cu and Sc+R+Rs (all genera except *Pseudofoenus*), and a short ovipositor (all genera except *Hyptiogaster*). As for *Gasteruption*, hyptiogastrine wasps are parasitic or predator-inquilines in the nests of bees (Houston 1969, 1984b, 1987; Naumann 1983) and vespid wasps (Houston 1984a; Naumann and Cardale 1987), though the biology of most species is unknown.

Although up to nine genera of hyptiogastrines have been recognised, Crosskey (1953, 1962) provided substantial generic stability after partly revising the subfamily and reducing the

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number of genera to five (Crosskey 1962). However, his study was based on only limited material, and over the last 30 years, particularly with the advent of mass-collecting techniques such as malaise traps, the amount of available material in Australian and other collections has increased by more than ten fold. From this we have recognised a large number of new species and have been able to reassess the limits of described species and genera. Apparent from this work is that the Hyptiogastrinae is probably paraphyletic without the inclusion of *Gasteruption*.

Our overall aim is to revise the genera of the Gasteruptiidae, analyse their relationships to provide a stable classification, and compare the resultant phylogeny to their known distribution to determine whether it can be wholly explained by continental drift theory. This paper revises the smallest of the genera recorded from Australia, *Crassifoenus*, and, at the same time, describes a striking new species from Western Australia. We present an illustrated key to the included species, and discuss the taxonomic history, monophyly, biology and distribution of the genus.

METHODS, TERMINOLOGY AND ABBREVIATIONS

Specimens used for ovipositor examination were partly dissected prior to the removal from the metasoma, and hydrated in distilled water for up to 24 h. The ovipositor was then teased from the sheaths with a fine needle. Specimens for SEM study were cleaned by removing obvious dirt and other debris with a fine brush; they were sputter-coated with platinum, and then examined under a Cambridge Stereoscan 250 (Mk 3B) scanning electron microscope.

Terminology for morphology, except for wing venation, generally follows Crosskey (1951, 1953, 1962), although a few terms have been changed to standardise them with recent studies on other groups of large-sized parasitic wasps (see Gauld and Bolton 1988; Naumann 1991; Figures 1, 2, 17). As for the most recent taxonomic studies on parasitic Hymenoptera, we used the term 'metasoma' rather than 'gaster' or 'abdomen'. Terminology for wing venation follows the modified Comstock-Needham system after Sharkey (1988), but with some modifications and using the nomenclature of van Achterberg (1979) for cells (Figures 15, 16). Terminology used for surface sculpturing follows Harris (1979).

Abbreviations of institutions follow Arnett *et al.* (1986), except for WARI which is not included in that publication. AEIC, American Entomological Institute, Gainesville; AMSA, Australian Museum, Sydney; ANIC, Australian National Insect Collection, Canberra; BMNH, The Natural History Museum, London; MCZC, Museum of Comparative Zoology, Cambridge, Massachusetts; MHNG, Museum d'Histoire Naturelle, Geneva; QMBA, Queensland Museum, Brisbane; SAMA, South Australian Museum, Adelaide; WAMP, Western Australian Museum, Perth; WARI, Waite Campus Collection, University of Adelaide, Adelaide.

SYSTEMATICS

Gasteruptiidae: Hyptiogastrinae

Genus *Crassifoenus* Crosskey

Crassifoenus Crosskey, 1953: 355; Muesebeck and Walkley, 1956: 344; Crosskey, 1962: 393; Naumann, 1991: 942.

Type species

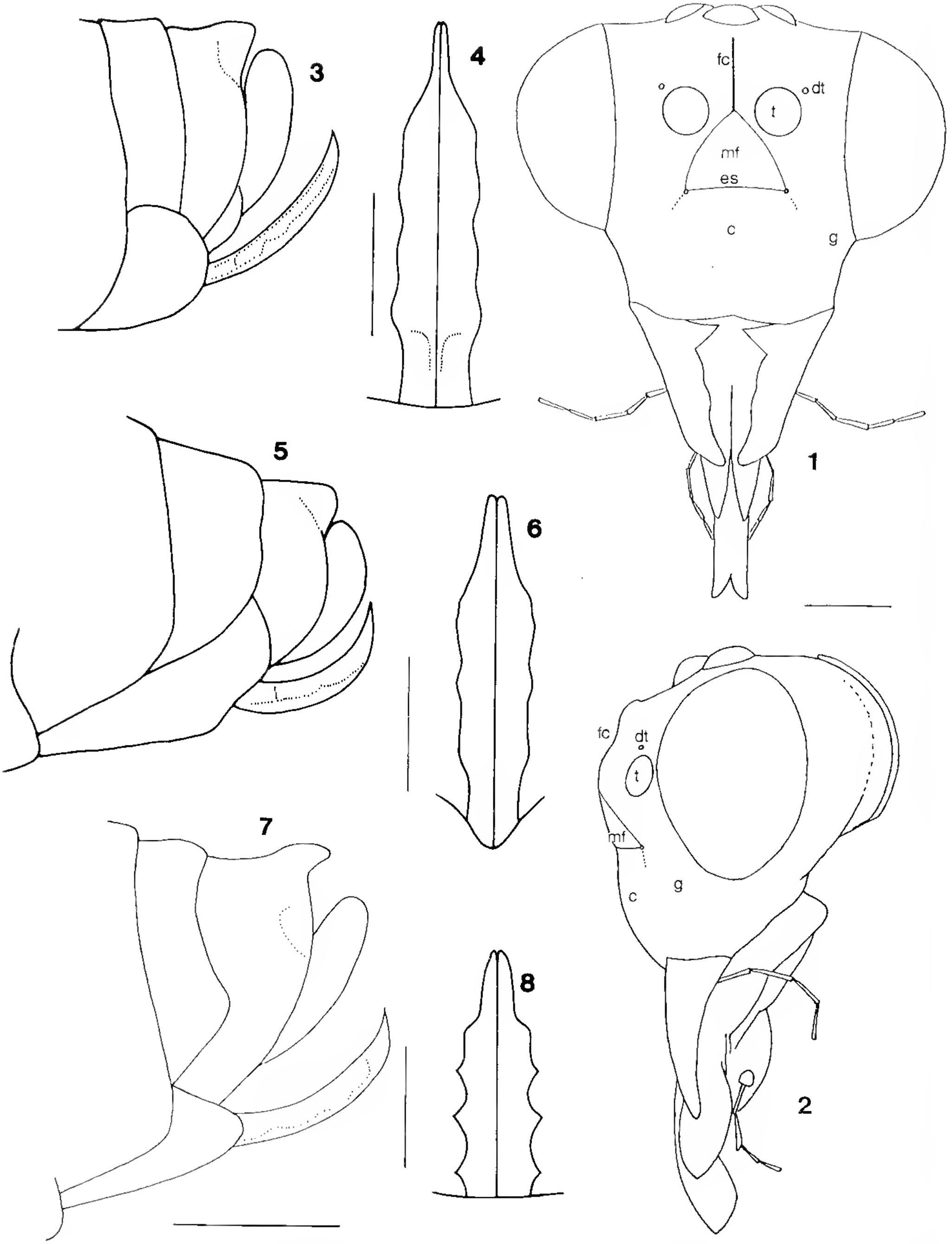
Gasteruption macronyx Schletterer, 1889 (by original designation).

Diagnosis

Gasteruptiid wasps of large, stout form; head about equal in width to or slightly wider than mesosoma; head elongate ventrally, length of malar space plus mandibles about as long or longer than height of eye (Figure 1); lateral epistomal suture absent so that clypeus is continuous with gena; clypeus greater than 0.75 x as high as wide; malar space large, about one-third height of eye; mandibles elongate, about as long as clypeus; labio-maxillary complex elongate, protruding well below mandibles; frontal carina strongly raised; antennal scrobes (beside frontal carina) deeply excavate and reaching almost to level of median ocellus; dorsal tentorial pits present on frons, one each above toruli; subantennal sutures present, indistinct to clearly visible, defining small triangular subantennal area on face (the medial face); first flagellomere longer than second; female antenna 14-segmented, male antenna 13-segmented; pronotum without processes; propleuron with prominent ventro-lateral carina (Figure 17); mesoscutum almost as broad as long, with faint median and admedian lines anteriorly; notauli percurrent, punctate or scrobiculate (Figure 9); parapsidal lines indistinct; pit of metapleural apophysis deep; propodeal spiracle elongate, surrounded by dense pilosity (Figure 12); propodeum separated from metapleuron by carinate furrow, with short or percurrent medial longitudinal carina; inner surface of mid tibia in female with subapical notch, absent in male; outer surface of mid tibia with scattered short stout spines and apical pecten of short teeth; hind trochanter with transverse groove (Figures 13, 14); hind femur and tibia strongly incrassate, about equal in length; outer hind tibial spur shorter and more robust than inner spur; in female first four hind tarsal segments very strongly contracted, deeply bilobed and tightly fitting, fifth segment about equal in length to preceding four combined, strongly swollen apically, hind claws very large, as long as four basal tarsal segments combined (Figures 18, 28, 29); in male first four hind tarsal segments not strongly contracted, fifth segment only slightly larger than each basal segment, much narrower than basal three segments, hind claws small, about equal in length to fourth segment (Figure 19); fore wing vein 1-Rs+M intersecting basal cell about one-quarter to one-third distance from M+Cu (Figure 15); hind wing with 4-7 hamuli, r-m and 2-M pigmented (Figure 16); first metasomal tergum transversely strigate-rugose; ovipositor short, robust, upwardly curved, lateral margins of ventral valves dentate or undulate (Figures 3–8), normally hidden by ovipositor sheaths (Figures 26, 27).

Comments

Crassifoenus was erected by Crosskey (1953) to include two species (*C. grossitarsis* (Kieffer) and *C. macronyx* (Schletterer)) which have a long malar space, the first four hind tarsal segments strongly contracted and deeply bilobed, and the hind femur and tibia incrassate. Not obvious from the original description of the genus is that it is only females that possess modified hind tarsi; in males they are normally elongate and not strongly bilobed. When compared with other gasteruptiid genera these characters are autapomorphic for *Crassifoenus* and define it as a monophyletic group. Although some species of *Hyptiogaster* have the second to fourth hind tarsal segments significantly shortened they are not bilobed, and thus have probably evolved independently of the condition in *Crassifoenus*.



Figures 1–8 (1–4) *Crassifoenus houstoni*, ♀: (1) anterior view of head; (2) lateral view of head; (3) lateral view of posterior metasoma; (4) ventral view of ovipositor; (5, 6) *Crassifoenus macronyx*, ♀: (5) lateral view of posterior metasoma; (6) ventral view of ovipositor; (7, 8) *Crassifoenus grossitarsis*, ♀: (7) lateral view of posterior metasoma; (8) ventral view of ovipositor. Scale lines: 1.0 mm (1–3, 5, 7); 0.5 mm (4, 6, 8). (c = clypeus, es = epistomal suture, fc = frontal carina, g = gena, mf = medial face, t = torulus, dt = dorsal tentorial pit).

This study has revealed a further three characters that are unique to *Crassifoenus*. These are the presence of a subapical notch on the inner surface of the mid tibia of females, the dentate or undulate lateral margins of the ventral ovipositor valves, and the presence of a distinct ventro-lateral carina on the propleuron. In all other genera of gasteruptiids the mid tibia is tubular, the margin of the ventral ovipositor valves are smooth and straight, and the ventro-lateral propleuron is smoothly rounded. An exception to the latter condition is known only in two species of *Hyptiogaster* (*H. humeralis* (Schletterer) and *H. flavosignata* (Kieffer)). However, these species have paired ventro-lateral carinae which bound a narrow crenulate groove. This groove appears to lock against the sharp anterior margin and ventral process of the lateral pronotum. This is not the case in *Crassifoenus* where the propleuron is more elongate, so that the ventro-lateral carina is distant from the anterior margin of the lateral pronotum.

Crassifoenus species all possess small dorsal tentorial pits, one above each torulus, which apparently have not been reported previously for any members of the family. However, our preliminary observations show that this structure exists in all genera of Gasteruptiidae, as well as members of the Aulacidae, but is absent in other families of parasitic Hymenoptera examined, with the exception of some Ichneumonidae (Cryptinae). A more extensive survey of these groups is required but, conditionally, the presence of these pits may represent a synapomorphy for the Gasteruptiidae + Aulacidae.

The sister-group to *Crassifoenus* is not resolved, but superficially it is most similar to *Aulacofoenus* and *Hyptiogaster*. All three genera comprise large robust wasps, possess an elongate labio-maxillary complex and trochanteral groove (a character also shared by *Gasteruption* and Aulacidae, but absent in *Eufoenus* and *Pseudofoenus*; Crosskey, 1962). However, potentially more definitive characters do not provide an unequivocal pattern of relationships. For example, *Crassifoenus* and *Aulacofoenus* possess a short hidden upwardly curved ovipositor, while *Hyptiogaster* has a long exposed ovipositor. Alternatively, *Crassifoenus* and at least some *Hyptiogaster* share greatly shortened hind tarsal segments in females and the presence of carinae on the ventro-lateral propleuron. Also, members of these two genera lack a lateral epistomal suture so that the clypeus and gena are continuous. Hopefully, a more exhaustive search for informative characters in the future will resolve the pattern of relationships among gasteruptiid genera.

Distribution

Crassifoenus species are endemic to the Australian mainland and, with the exception of two records from the Brisbane region, are apparently restricted to the drier central and western regions of the continent (Figure 25).

Biology

Members of this genus are parasitic or predator-inquilines in the nest of bees, and host records for two species indicate that the genus may be restricted to stenotritine bees. The structure of the labio-maxillary complex, particularly the 'sieve'-like arrangement of the distal glossae (Figures 23, 24), indicate that adult *Crassifoenus* are probably nectar rather than pollen feeders. This is supported by a general paucity or absence of pollen grains on the mouthparts of wasps collected at flowers.

Key to Species of *Crassifoenus*

1. Mandible strongly curved distally, with two distinct medial teeth (Figures 21, 22); hypopygium in lateral view elongate, either truncate or broadly pointed apically (Figures 5, 7); vertex very finely transversely substrigulate to imbricate or longitudinally strigate to carinate; occipital margin smooth or very faintly crenulate; mat of long setae present on ventral surface of fifth hind tarsal segment; body predominantly red-brown, sometimes with dark markings 2

   Mandible weakly curved distally, with indistinct medial teeth (Figure 20, 23); hypopygium in lateral view short and rounded (Figure 3); vertex coarsely scrobiculate to reticulate punctate, often smooth or finely reticulate-strigate towards occipital carina; occipital margin scrobiculate; without mat of long setae on ventral surface of fifth hind tarsal segment; body uniformly dark, often black with very dark red markings .... *C. houstoni* sp. nov.

2. Hypopygium in lateral view truncate apically (Figure 5); ventral ovipositor valves with undulate margins (Figure 6); vertex very finely transversely substrigulate to imbricate with minute punctures, sometimes with single row of large punctures directly behind ocelli; median longitudinal carina present in posterior one-third to one-quarter of propodeum .... *C. macronyx* (Schletterer)

   Hypopygium in lateral view broadly pointed apically (Figure 7); ventral ovipositor valves with dentate margins (Figure 8); vertex longitudinally strigate or carinate, becoming very finely strigate-punctate; median longitudinal carina on propodeum percurrent .... *C. grossitarsis* (Kieffer)

Crassifoenus grossitarsis (Kieffer)

Figures 7, 8, 22, 25

Hyptiogaster grossitarsis Kieffer, 1911: 179; 1912: 194, 197; Hedicke, 1939: 48.

Crassifoenus grossitarsis (Kieffer): Crosskey, 1953: 356, 357; 1962: 385, 389.

Holotype

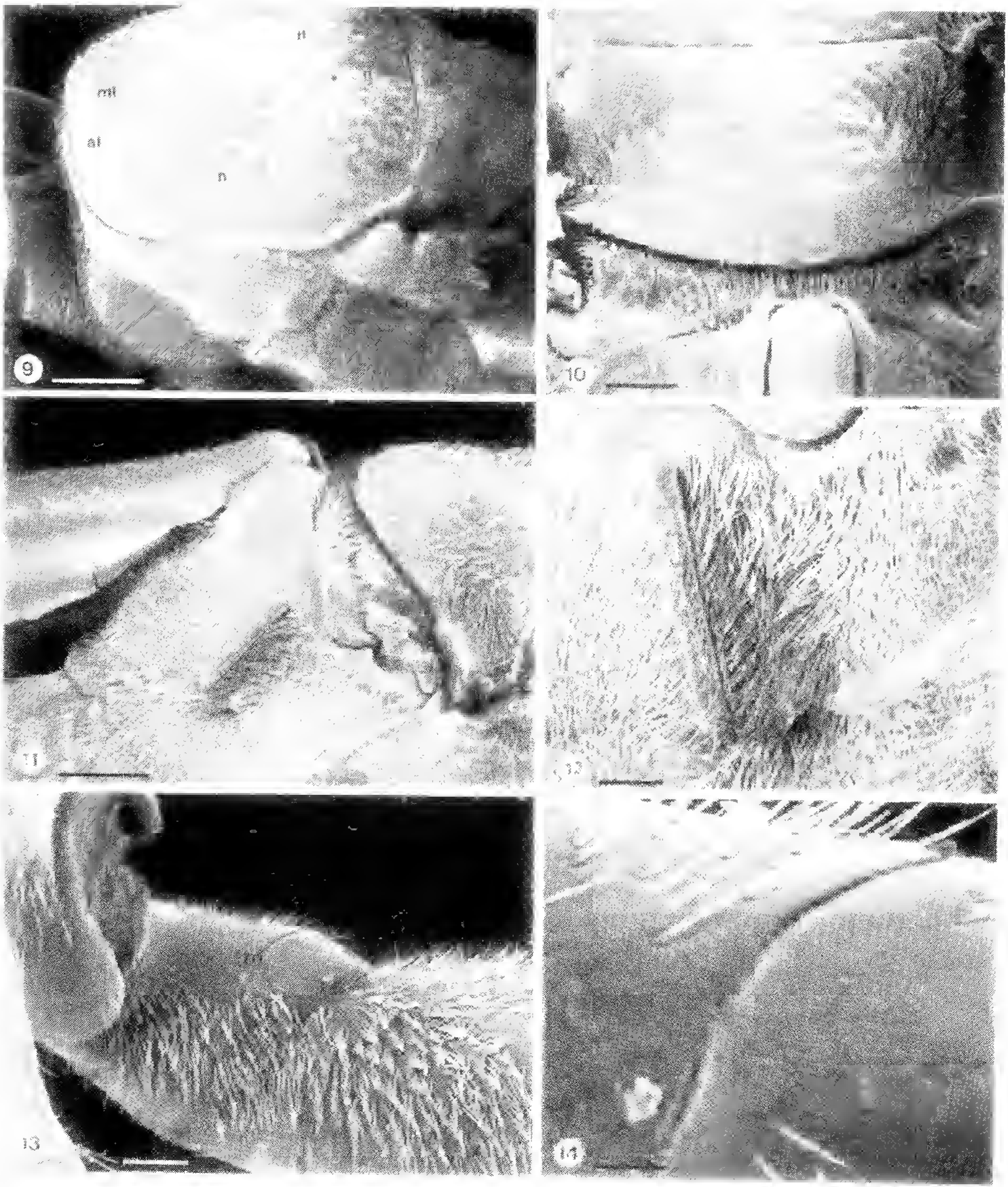
♀, "Western Australia, Swan River", no other data (BMNH).

Other Specimens Examined

Australia: Western Australia: 1 ♀, Roebourne, 1912–111 (BMNH); 1 ♂, 30 miles W. of Coolgardie, 29.xi.1958, E.F. Riek (ANIC); 1 ♂, Moore River National Park (31.10S, 115.40E), 31.xii.1989, T.F. Houston, on flowers of *Melaleuca* (WAMP). **Northern Territory:** 1 ♀, 33 km W.N.W. of Alice Springs (23.36S, 133.34E), 30.ix.1978, J.C. Cardale (ANIC); 1 ♀, 30 km N.W. by W. of Alice Springs (23.32S, 133.38E), 7.xi.1978, J.C. Cardale (ANIC).

Female

Head: 1.2 (1.1–1.3) x as wide as mesosoma; frons coarsely strigate to strigate-rugose, punctate-reticulate along lateral margins; distance from posterior ocellus to eye margin 0.8 (0.7 – 0.9) x distance between posterior ocellus and occipital carina; vertex longitudinally strigate medially, becoming very finely strigate-punctate towards occipital carina, finely rugulose laterally; occipital margin smooth or faintly crenulate; gena finely punctate-reticulate; malar space 0.4 x height of eye, 1.2 (1.0 – 1.4) x as long as scape; clypeus finely



Figures 9–14 *Crassifoenus houstoni*, ♀ paratype: (9) dorso-lateral view of mesosoma; (10) dorso-posterior view of scutellum; (11) lateral view of posterior mesosoma and T1 of metasoma; (12) propodeal spiracle; (13) base of hind leg showing suture between the trochanter and femur, and the trochanteral groove; (14) trochanteral groove on the hind trochanter. Scale lines: 1.0 mm (9, 11); 0.5 mm (10); 250 μm (12, 13); 50 μm (14). (al = admedian line, ax = axilla, ml = median line, n = notaulus, pl = parapsidal line, sc = dorsal scutellum, S = suture between the trochanter and femur, TG = trochanteral groove).

punctate-reticulate with a few large scattered punctures medially, smoother medially, almost glabrous, with scattered short hairs which become denser laterally; medial face finely rugulose, sometimes with scattered fine punctures in ventral part, lateral face finely punctate-reticulate, face virtually glabrous, with some hairs laterally and around antennal insertions; epistomal suture distinct, not impressed; first flagellomere 1.6 (1.3 – 1.8) x as long as scape, 3.9 (3.7 – 4.3) x as long as pedicel, second flagellomere 1.1 x as long as third flagellomere, terminal flagellomere 2.0 (1.8 – 2.2) x as long as broad; mandible strongly curved distally, with two prominent medial teeth (sometimes slightly worn and indicated by dull surface).

Mesosoma: Propleuron finely rugulose, with short dense setae, ventro-lateral carina expanded anteriorly into flange, not reaching to posterior margin of propleuron; lateral pronotum finely punctate-reticulate ventrally, rugose dorsally, with scattered short setae, oblique depression narrow, crenulate; mesoscutum almost as broad as long, median lobe coarsely transversely strigate-rugose, with scattered short hairs; admedian lines indistinct, faintly carinate, short, converging from anterior margin of median lobe; median line virtually absent, indicated by subtle change in sculpturing in anterior half of median lobe; notauli with faint punctate or scrobiculate sculpturing; parapsidal lines faintly carinate, almost reaching to notauli; lateral lobes of mesoscutum coarsely transversely strigate-rugose; axillae and dorsal scutellum transversely strigate-rugose, almost glabrous; lateral scutellum finely punctate; metanotum with dense pubescence; metanotal depression carinate; dorsal part of mesepisternum finely punctate-reticulate, with scattered short hairs, separated from ventral part by carinate depression, ventral part coarsely rugose, with short dense pilosity, grading to smooth and glabrous on ventral surface; mesepimeron deeply concave, scrobiculate in ventral part, transversely strigate above; epicnemium finely transversely strigate, sometimes almost smooth with fine rugose-punctate sculpturing at lateral margins; ventral part of metapleuron rugose to coarsely rugose, sometimes with striate margin, with, dorsal part strongly convex, the anterior half smooth and glabrous, posterior half with fine transverse striae and dense pilosity; propodeum rugose, with scattered short hairs, median longitudinal carina present in posterior one-third to one-quarter.

Legs: All tibiae and tarsi with short dense golden pilosity; mid tibial notch slight; outer surface of mid tibia with scattered stout spines; hind coxa finely punctate except for striate dorsal depression; hind femur short and broad, about 3 x as long as wide, equal in length to hind tibia, with short pilosity dorsally and scattered hairs ventrally; inner tibial spur about 1.5 x as long as outer spur; first tarsal segment with ventro-apical pecten of short teeth, second to fourth tarsal segments without ventro-apical pecten but with long stout setae; apical part of fifth hind tarsal segment almost as wide as preceding four segments, with dense mat of setae on ventral surface.

Wings: Fore wing with 1-Rs+M intersecting basal cell about 0.3 x distance from M+Cu; 2-Rs+M 4.8 x as long as m-cu; r 2.5 x as long as 2-Rs; hind wing with 5-7 hamuli.

Metasoma: 1.8 (1.8 – 2.0) x length of mesosoma; transversely strigate-rugose sculpturing on dorsal part of first tergum becoming rugose-punctate posteriorly; dorsal part of second tergum very finely imbricate-punctate; hypopygium in lateral view elongate and broadly pointed apically; lateral margins of ventral ovipositor valves dentate.

Colour: Body generally red-brown or yellow-brown, first metasomal tergum with broad black band; variable amount of black surrounding ocelli, on propleuron, mesopleuron, mesosternum, posterior half of mesoscutum, metapleuron, and base of hind coxae; tegula and wing bases yellow; vein C, M+Cu and stigma of fore wing yellow-brown, remaining veins brown to dark brown.

Length: 15.5 (12.5 – 20) mm.

Male

Similar to female except as follows: length 18.5 (17 – 20) mm; terminal flagellomere 2.5 (2.3 – 2.6) x as long as broad; dorsal part of lateral pronotum virtually smooth; body more extensively black, including frons to vertex, larger proportion of mesoscutum, axillae, lateral metanotum and posterior margin of propodeum.

Biology and Distribution

Adults of *C. grossitarsis* have been collected from *Melaleuca* sp. in Western Australia. The host is unknown. The species has so far been recorded from Mediterranean and arid parts of Western Australia and the Northern Territory (Figure 25).

Comments

This species is closely related to *C. macronyx* but can be readily separated from it by the characters given in the key. In addition to these, *C. grossitarsis* can be distinguished by having a slightly longer malar space, ventro-lateral carina on propleuron expanded anteriorly into a flange, narrow oblique depression on the lateral pronotum, and finely transversely strigate epicnemium.

Crassifoenus macronyx (Schletterer)

Figures 5, 6, 21, 25

Gasteruption macronyx Schletterer, 1889: 385, 463–4.

Hyptiogaster macronyx (Schletterer): Kieffer, 1903: 94; 1912: 195, 204; Tillyard, 1926: 268; Hedicke, 1939: 49.

Crassifoenus macronyx (Schletterer): Crosskey, 1953: 356–7; 1962: 399.

Holotype

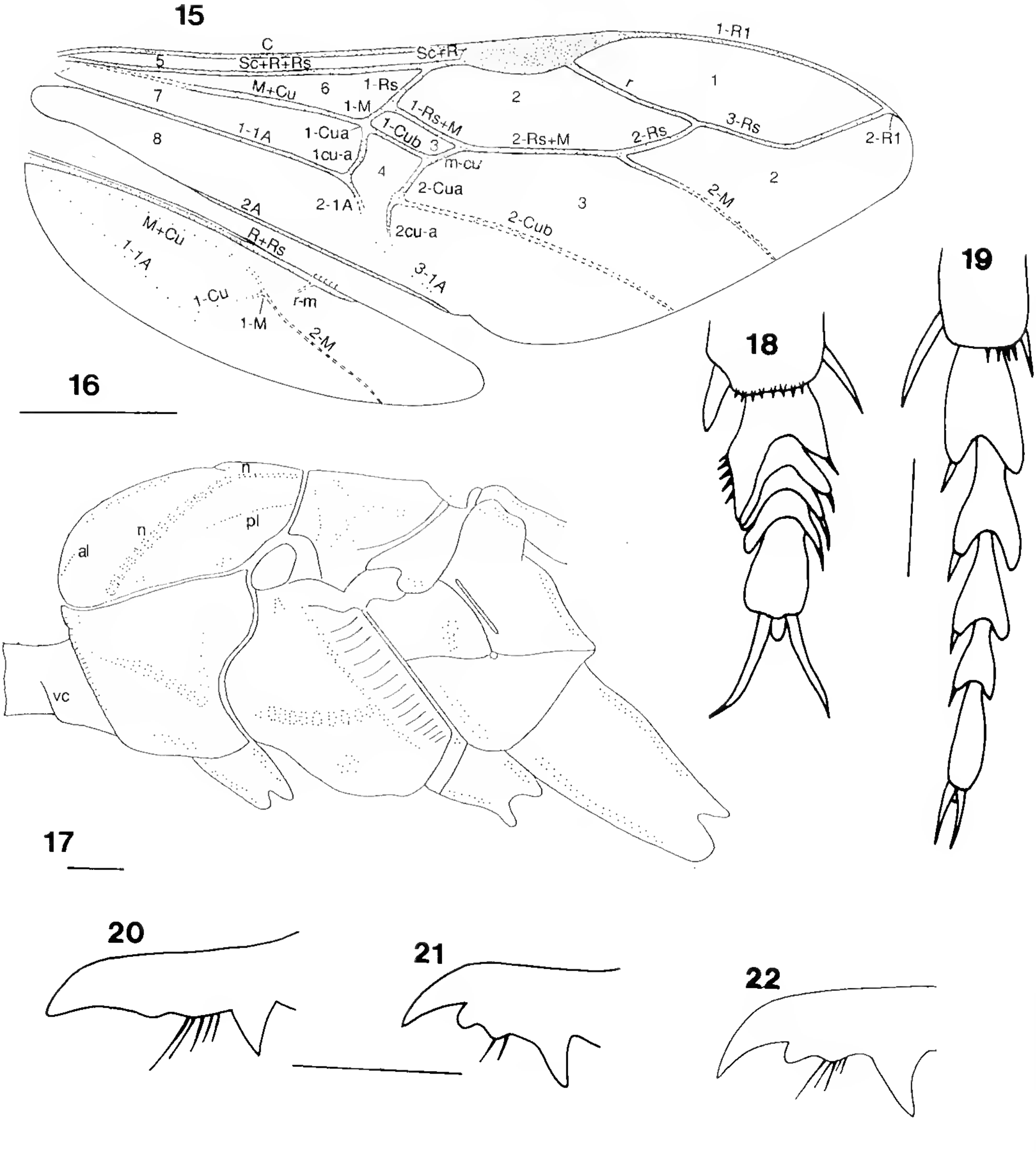
♂, "South Australia", no other data (MHNG).

Other Specimens Examined

Australia: Western Australia: 1 ♀, 1 km N. of Millstream (21.35S, 117.04E), 1.xi.1970, Upton & Feehan (ANIC). **South Australia:** 1 ♀, Blackhon (?), 20.xii.1893, Froggatt (ANIC); 1 ♀, Finniss Creek, W. of Marree, 2.i.1974, T.F. Houston, leaving nest of *Stenotritus* (WARI). **Queensland:** 2 ♀, 3 ♂, Brisbane, 4.xii.1911, H. Hacker (QMBA); 1 ♀, Brisbane, 4.xii.1911, H. Hacker (BMNH); 1 ♂, Enoggera, 3.xii.1913, H. Hacker (QMBA); 1 ♀, 3 ♂, Cunnamulla, Nov., N. Geary coll. (MCZC); 1 ♂, North Queensland (BMNH). **New South Wales:** 1 ♂, Fowlers Gap Res. Stn (31.05S, 141.42E), 29.xi.–2.xii.1981, J.C. Cardale, on flowers of *E. camaldulensis* (ANIC); 1 ♀, Fowlers Gap Res. Stn, 8–9.xii.1982, I.D. Naumann (ANIC); 3 ♂, Fowlers Gap Res. Stn, 8–9.xii.1982, I.D. Naumann & J.C. Cardale (ANIC, WARI). **Locality Unknown:** 1 ♀, 1.iii.[18]82, no collector (BMNH).

Female

Head: 1.1 (1.0 – 1.2) x as wide as mesosoma; frons coarsely strigate-rugose in upper half, becoming more punctate laterally, lower half finely reticulate-punctate; distance between



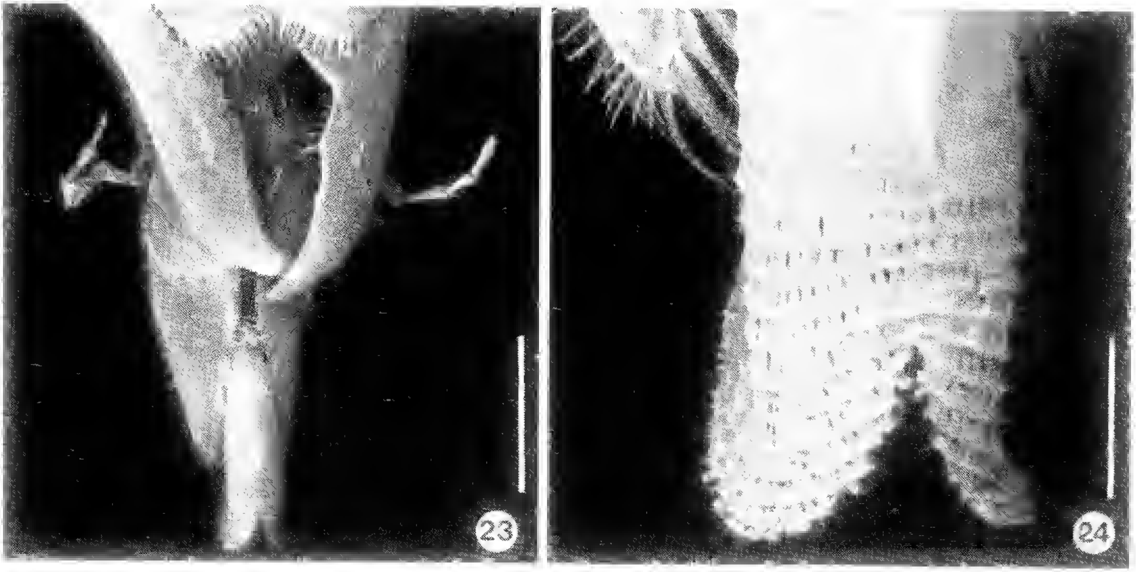
Figures 15–22 (15–20) *Crassifoenus houstoni*, paratypes: (15) ♂, fore wing; (16) ♂, hind wing; (17) ♀, lateral view of mesosoma; (18) ♀, dorsal view of hind tarsal segments; (19) ♂, dorsal view of hind tarsal segments; (20) *Crassifoenus houstoni*, ♀, lateral view of mandible; (21) *Crassifoenus macronyx*, ♀, lateral view of mandible; (22) *Crassifoenus grossitarsis*, ♀, lateral view of mandible. Scale lines: 1.0 mm. (al = admedian line, n = notaulus, pl = parapsidal line, vc = ventro-lateral carina; fore wing cells: 1 = marginal, 2 = submarginal, 3 =discal, 4 = subdiscal, 5 = costal, 6 = basal, 7 = subbasal, 8 = plical).

posterior ocellus and eye margin 0.6 (0.5 – 0.7) x distance between posterior ocellus and occipital carina; vertex very finely transversely substrigulate to imbricate with minute punctures, sometimes becoming papillate laterally, and sometimes with single row of large punctures directly behind ocelli; occipital margin smooth or faintly crenulate; malar space 0.35 x height of eye, 0.9 (0.8 – 1.1) x as long as scape; gena finely punctate-reticulate; clypeus finely punctate-reticulate laterally, smooth medially with a few scattered punctures, almost glabrous medially, with fine pilosity laterally; medial face finely punctate with short pilosity; lateral face punctate-reticulate with fine pilosity; epistomal suture distinct, not impressed; first flagellomere 1.6 (1.4 – 1.7) x as long as scape, 4.2 (3.7 – 4.4) x as long as pedicel, second flagellomere 1.2 (1.1 – 1.2) x as long as third flagellomere, terminal flagellomere 2.3 (2.2 – 2.7) x as long as broad; mandible strongly curved distally, with two prominent medial teeth (sometimes slightly worn and indicated by dull surface).

Mesosoma: Propleuron finely punctate-reticulate, with short pilosity, ventro-lateral carina even throughout, not expanded anteriorly into a flange, not reaching to posterior margin of propleuron; lateral pronotum finely punctate-reticulate ventrally, rugose-punctate dorsally, covered with short pilosity, oblique depression strongly arched, broad, coarsely scrobiculate; mesoscutum almost as broad as long, medial lobe coarsely transversely strigate-rugose, with scattered short hairs; admedian lines indistinct, faintly carinate, short, converging from anterior margin of median lobe, sometimes virtually absent or indicated only by change in sculpturing pattern; median line virtually absent, indicated by subtle change in sculpturing in anterior half of median lobe, sometimes also discernible in posterior half; notaular depression virtually unsculptured, sometimes with faint punctate or scrobiculate sculpturing; parapsidal lines faintly carinate, almost reaching to notauli; lateral lobes of mesoscutum coarsely transversely strigate-rugose; axillae and dorsal scutellum coarsely strigate-rugose; lateral scutellum finely punctate; metanotum with long hairs; metanotal depressions punctate-carinate; mesepisternum with dense pilosity partly obscuring underlying sculpturing, dorsal part rugulose, ventral part rugose grading to strigate, and then to smooth and glabrous on ventral surface, dorsal and ventral parts separated from dorsal part by a carinate depression; mesepimeron deeply concave, smooth beside scrobiculate margin; epicnemium smooth and glabrous; lower part of metapleuron rugulose, upper part strongly convex, rugose, both areas with dense pilosity; propodeum rugose to rugose-punctate, with scattered short hairs, median longitudinal carina virtually percurrent.

Legs: Tibiae and tarsi of fore and mid legs and inner surface of hind tibia and hind tarsi with short golden pilosity; mid tibial notch slight; outer surface of mid tibia with scattered stout spines; hind coxa variable, generally finely punctate-reticulate with covering of fine pilosity, dorsal depression smooth to finely transversely striate; hind femur short and broad, 3 x as long as wide, about as long as hind tibia, with fine scattered punctures and associated short hairs dorsally, laterally smooth and virtually glabrous; outer surface of hind tibia smooth, virtually glabrous except for scattered punctures and associated setae; inner tibial spur about 1.5 x as long as outer spur; first tarsal segment with ventro-apical pecten of short teeth, second to fourth tarsal segments without ventro-apical pecten but with long stout setae; apical part of fifth hind tarsal segment almost as wide as third and fourth segments, narrower than first and second segments, with dense mat of setae on ventral surface.

Wings: Fore wing with 1-Rs+M intersecting basal cell about 0.3 x distance from M+Cu; 2-Rs+M 4.3 x as long as m-cu; r 3.0 x as long as 2-Rs; hind wing with 5–7 hamuli.



Figures 23, 24 *Crassifoenus houstoni*, ♀ paratype: (23) mouthparts; (24) surface of distal glossae. Scale lines: 1.0 mm (23); 200 µm (24).

Metasoma: 2.1 (1.9 – 2.3) x as long as mesosoma; transversely strigate-rugose sculpturing on dorsal part of first tergum becoming rugulose to rugose-punctate posteriorly; dorsal part of second tergum very finely imbricate-punctate, with narrow smooth medial longitudinal band in anterior half; hypopygium in lateral view elongate and truncate apically; lateral margins of ventral ovipositor valves undulate.

Colour: Body red-brown to dark red brown, dorsal metasoma usually darker than rest of body, first metasomal tergum black dorsally, sometimes with area around ocelli or frons to vertex, medial mesoscutum, lower mesepisternum, posterior margin of propodeum, and segment 8 and ovipositor sheaths black; tegula and wing bases brown; vein M+Cu, distal veins and stigma of fore wing yellow-brown, remaining veins brown to dark brown.

Length: 17 (16 – 19) mm.

Male

Similar to female except as follow: length 18 (17 – 20) mm; terminal flagellomere more elongate; dorsal part of lateral pronotum smoother; margins of mesepisterum, metanotum, apico-dorsal coxae also black.

Biology and Distribution

This species has been collected from flowers of *Eucalyptus camaldulensis* in central New South Wales and has been observed leaving the nest of the stenotritine bee, *Stenotritus* sp. *C. macronyx* has been recorded from a range of habitats in a broad band across Western Australia, South Australia and Queensland (Figure 25).

Comments

In addition to the characters given in the key, *C. macronyx* can be distinguished from *C.*

grossitarsis by the ventro-lateral carina on propleuron lacking an anterior flange, broad oblique depression on the lateral pronotum, smooth epicnemium, and slightly denser pilosity on the lateral mesosoma.

Crassifoenus houstoni sp. nov.

Figures 1–4, 9–20, 23–29

Holotype

♀, "75 km E. of Hyden Western Australia 24–27 Oct 1985 T.F. Houston 629–22" "ex nest burrow of bee *Ctenocolletes smaragdinus* " (WAMP)

Paratypes

Australia: Western Australia: 1 ♀, Sandstone, 28.viii.1974, A.M. & M.J. Douglas (WAMP); 1 ♂, 15 km E. Mullewa (28.32S, 115.31E) 17.viii.1981, P.G. & G.W. Kendrick (WAMP); 7 ♀, 4 ♂, 28 km W. of Yalgoo, 1–2.ix.1981, G.A. Holloway (AMSA, WARI); 2 ♀, 3 ♂, 11 km E.N.E. of Anketell H. S. (28.02 S, 118.51 E), 4–6.ix.1981, T.F. Houston, near nest of *Ctenocolletes ordensis* (WAMP, WARI); 9 ♀, 1 ♂, 13 km S. of Wanoo

Figure 25 Distribution of *Crassifoenus* spp.: ■ = *C. grossitarsis*; ○ = *C. macronyx*, ● = *C. houstoni*.

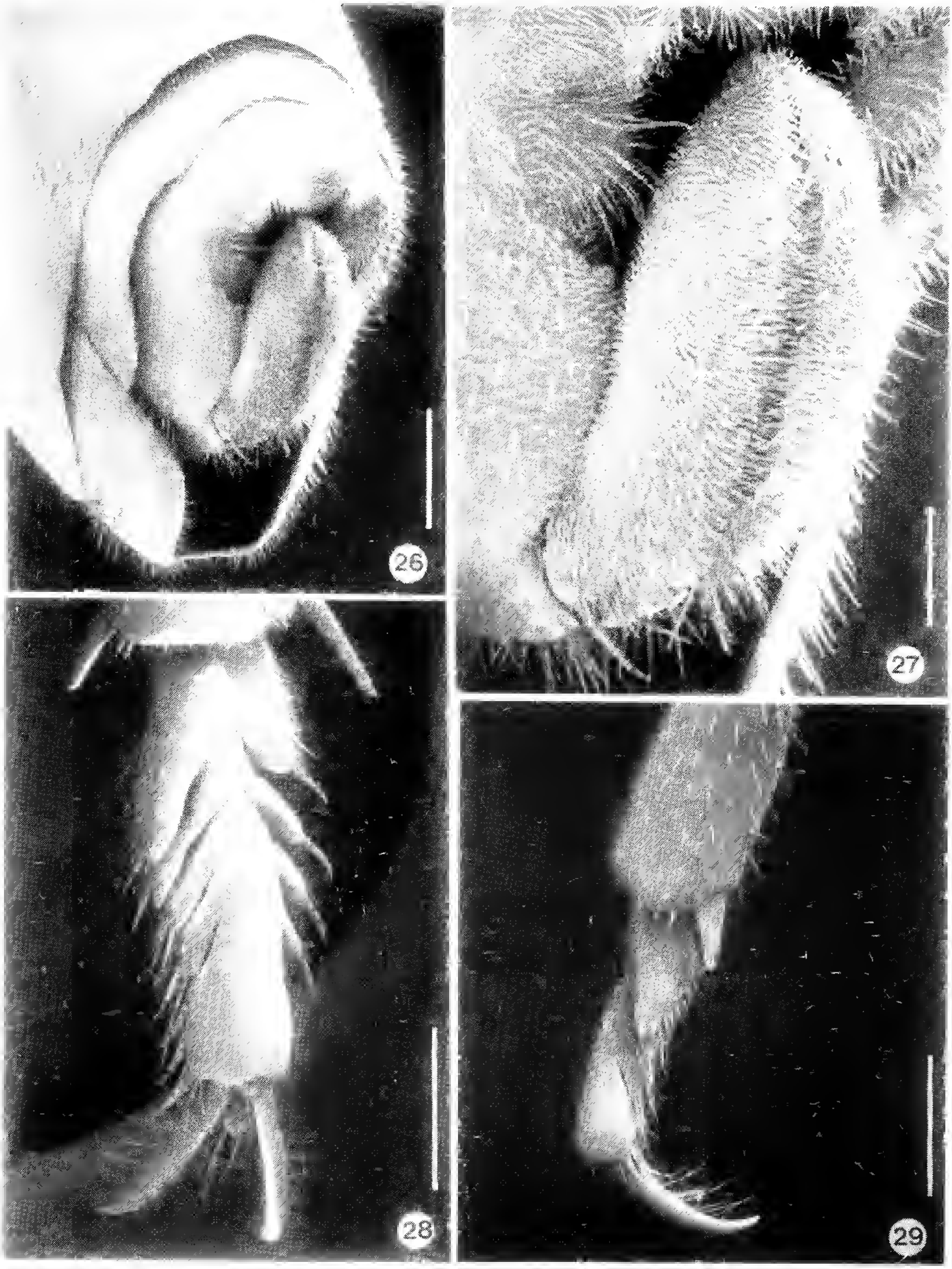
(26.49 S, 114.37 E), 24–28.viii.1984, T.F. Houston & B.P. Hanich, flying over nesting area of *Ctenocolletes nicholsoni* (WAMP, WARI); 1 ♀, East Yuna Reserve, 34 km W.N.W. of Mullewa, 13–16.ix.1984, T.F. Houston, flying over bare sandy ground (WAMP); 2 ♀, 75 km E. of Hyden, 24–27.xi.1985, T.F. Houston, ex nest of bee *Ctenocolletes smaragdinus* (WAMP).

Female

Head: 1.0 (0.9 – 1.0) x as wide as mesosoma; frons coarsely rugose in upper part, punctate laterally, antennal scrobes virtually smooth, with a few scattered fine punctures; distance between posterior ocellus and eye margin 0.8 (0.7 – 0.9) x distance between posterior ocellus and occipital carina; vertex coarsely scrobiculate to reticulate punctate, often smooth or finely reticulate-strigate towards occipital carina; occipital margin scrobiculate; malar space 0.35 x height of eye, 0.9 (0.7 – 1.1) x as long as scape; gena finely punctate-reticulate with a few scattered large punctures, covered with silver pilosity; clypeus finely punctulate-reticulate, with scattered larger punctures and fine white hairs; medial face coarsely punctate-reticulate, sometimes with fine punctate background sculpturing; epistomal suture distinct and slightly impressed; first flagellomere 1.4 (1.3 – 1.7) x as long as scape, 3.4 (3.1 – 3.9) x as long as pedicel, second flagellomere 1.2 (1.0 – 1.3) x as long as third flagellomere, terminal flagellomere 2.3 (2.1 – 2.5) x as long as broad; mandible weakly curved distally, with medial teeth indistinct to virtually absent.

Mesosoma: Propleuron strigate-punctate laterally, ventro-lateral carina robust, expanded anteriorly into a sharp flange, reaching almost to posterior margin of propleuron; lateral pronotum finely punctate ventrally, punctate to punctate-reticulate dorsally, with covering of short white hairs, oblique depression shallow, coarsely scrobiculate; mesoscutum as broad as long, surface coarsely punctate-rugose, with scattered minute hairs; admedian lines indistinct, faintly carinate, short, only slightly converging, area between admedian lines smoother than rest of median lobe; median line faintly carinate, about as long as admedian lines; notauli coarsely reticulate-punctate; parapsidal lines faintly carinate, reaching about half distance to notauli; axillae and dorsal scutellum coarsely punctate-rugose, virtually glabrous; lateral scutellum finely punctate, with scattered short hairs; metanotum with long silver pilosity; dorsal part of mesepisternum rugose with scattered white hairs, separated from ventral part by broad coarsely rugose depression with carina along lower margin; ventral part of mesepisternum rugose with dense silver pilosity, grading to smooth and glabrous with a few scattered large puncture on ventral surface; mesepimeron deeply concave, scrobiculate in ventral half, transversely strigate in dorsal half; epicnemium transversely strigate; metapleuron with covering of short silver pilosity, coarsely rugose dorsally above a smooth broad band, strigate ventrally; propodeum rugose-strigate, covered with dense silver pilosity, median longitudinal carina present and percurrent, sometimes indistinct medially due to confusion of surrounding sculpturing.

Legs: Femora mostly smooth, with a few scattered punctures and associated hairs; tibiae and tarsi of fore and mid legs with dense covering of light brown hairs; mid tibial notch deep; outer surface of mid tibia with small scattered spines which are not easily discernible from surrounding setae; hind coxa finely punctulate with dense silver hairs laterally, strigate dorsally with only scattered short white hairs; hind femur short and very broad, about 2.5 x as long as wide, slightly shorter than hind tibia; hind tibia with small scattered spines on outer surface among long setae; inner spur about 2.0 x as long as outer spur; first hind tarsal



Figures 26–29 *Crassifoenus houstoni*, ♀ paratype: (26) dorso-posterior view of posterior metasoma; (27) ovipositor sheaths; (28) dorsal view of hind tarsal segments; (29) lateral view of hind tarsal segments and distal tibia. Scale lines: 0.5 mm (26); 200 µm (27); 1.0 mm (28, 29).

segment with ventro-apical pecten of short teeth, second to fourth tarsal segments with very stout pecten-like ventro-apical setae; apical part of fifth hind tarsal segment almost as wide as third and fourth segments, narrower than first and second segments, ventrally surface almost glabrous, without dense mat of hairs.

Wings: Fore wing with 1-Rs+M intersecting basal cell about 0.25 x distance from M+Cu; 2-Rs+M 6.3 x as long as m-cu; r 1.9 x as long as 2-Rs; hind wings with 4 – 6 hamuli (N.B. 30% of specimens have different numbers on each wing).

Metasoma: 2.0 (1.5 – 2.3) x as long as mesosoma; transversely strigate-rugose sculpturing on dorsal part of first tergum sometimes only occupying anterior two-thirds of surface; dorsal part of second tergum reticulate-punctate, sometimes with narrow smooth medial longitudinal band in anterior half; hypopygium in lateral view moderately short and rounded apically; lateral margins of ventral ovipositor valves undulate.

Colour: Predominantly black, with two small dark red spots near margin of eye on vertex; variable amounts of dark red on clypeus, propleuron, mesoscutum, scutellum, pronotum, mesepisternum, mesepimeron and metanotum; tegula and wing bases black; venation and stigma black.

Length: 17 (15 – 23) mm.

Male

Similar to female except as follows: length 20 (18 – 23) mm; flagellomeres slightly longer.

Biology and Distribution

C. houstoni has been collected from the nests of the following stenotritine bees: *Ctenocolletes albomarginatus* Michener, *C. fulvescens* Houston, *C. nicholsoni* (Cockerell), and *C. smaragdinus* (Smith) (Houston 1987) and *C. ordensis* Michener (Houston 1984b and 1987). It has been recorded from Mediterranean and semi-arid regions of south-western Western Australia (Figure 25).

Comments

C. houstoni sp. nov. is strikingly different from the other two species. Apart from the characters given in the key, this is the largest and most robust species in the genus. It also has a larger ventro-lateral carina on the propleuron which almost reaches to the posterior margin, the mesoscutum more punctate-rugose, much denser pilosity on the lateral mesosoma and propodeum, transversely strigate epicnemium, much deeper mid tibial notch, longer 2-Rs+M vein compared with m-cu, much shorter r vein compared with 2-Rs, and substantially more robust hind legs and spinose hind tarsi.

This species has been named after Dr Terry Houston, Curator of Entomology at the Western Australian Museum.

ACKNOWLEDGEMENTS

We wish to thank the curators of the various collections listed above for their assistance in lending us specimens in their care; Mr S. McClure, CSIRO Division of Soils, Adelaide for assistance with the SEM work; Terry Houston for information on the biology of bees and their associated parasitoids; and Paul Dangerfield for advice on line drawings and his critical review of the manuscript.

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CYCLOPYGID TRILOBITES FROM THE ORDOVICIAN OF NORTHEASTERN TARIM, XINJIANG, NORTHWEST CHINA

Zhiyi Zhou*, Kenneth J. McNamara#, Wenwei Yuan* and Tairong Zhang**

ABSTRACT

Eight species of cyclopygid trilobites are described from the late early Tremadoc and late Llandeilo-early Caradoc of the Queerqueke-Yaerdang mountain area, northeastern Tarim, Xinjiang, China. Three of them are new: *Prospectatrix exquisita, Microparia (Heterocyclopyge) abunda* and *M. (Quadratapyge) curva.* The mesopelagic cyclopygids were mainly distributed along the marginal deep facies belt in Tarim, but only some of them were able to penetrate into shallow sites during the period of the great transgression. This indicates that different assemblages of cyclopygid genera may have lived at different depth levels in the water body. Morphological changes which took place during the ontogeny and phylogeny of cyclopygids were minimal, and only a few evolutionary lineages show local heterochronic evolution.

INTRODUCTION

The material on which this paper is based was mainly collected by the Regional Geological Surveying Team of Xinjiang during the last decade from the Queerqueke-Yaerdang Mountain area on the north bank of the Konqi River (Figure 1). The Ordovician lithostratigraphy in this area was erected by Norin (1937). Since then, however, more detailed information has been added (Zhou *et al.* in Zhou and Chen 1990; Zhong and Hao, 1990). Ordovician trilobites were partly described by Troedsson (1937) and Zhang (1981), but no cyclopygids had been reported from the vast northeastern area of Tarim until 1990, when a few specimens were recorded by Zhou (in Zhong and Hao 1990). In this paper eight species of cyclopygid trilobites in the genera and subgenera *Prospectatrix, Pricyclopyge, Cyclopyge, Microparia (Microparia), Microparia (Heterocyclopyge), Microparia (Quadratapyge), Degamella* and *Sagavia* are formally described, including three new species.

The terminology used in the ensuing taxonomic descriptions is essentially that defined by Harrington *et al.* (in Moore 1959: 117–126), except that the occipital ring is considered as part of the glabella, as no occipital ring is defined in any cyclopygids, even in the ellipsotaphrines (Fortey and Owens 1987: 188).

Specimens described in the following pages are all deposited at the Nanjing Institute of Geology and Palaeontology, Academia Sinica (NI).

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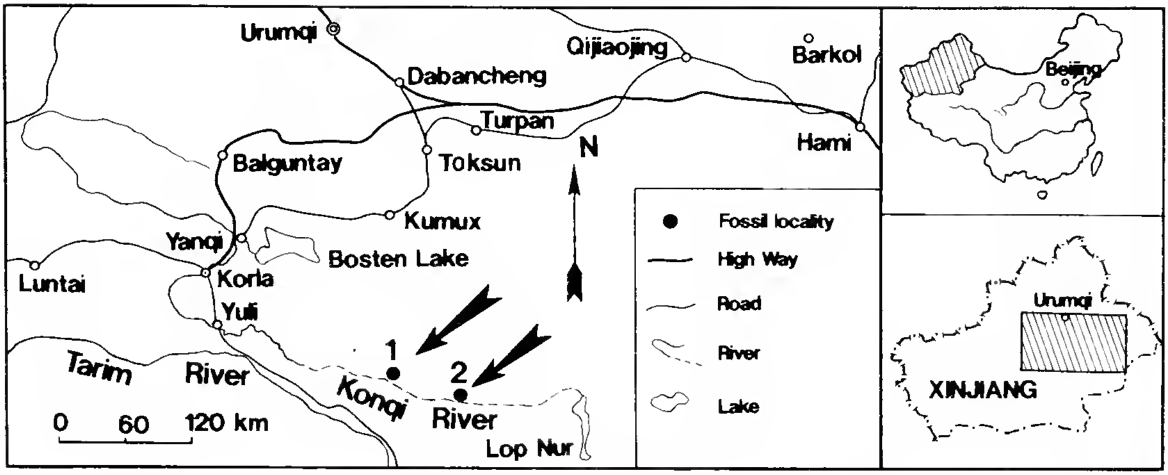


Figure 1 Sketch map showing the fossil localities. 1. Queerqueke; 2. southern Yaerdang.

Stratigraphy and age

All the cyclopygid trilobites described in this paper were collected from the measured section at Queerqueke (40°54'N, 88°18'E) (locality 1) except for a few additional specimens which were gathered from south Yaerdang (40°45'N, 89°02'E) (locality 2). They occur in three separate horizons and, according to Zhou *et al.* and Lin *et al.* (in Zhou and Chen 1990), the stratigraphic setting and other associated fossils are as follows:

1. The primitive cyclopygid *Prospectatrix exquisita* sp. nov. is the only form to appear at both localities, where it is found in a bed of greyish black thin-bedded argillaceous and nodular limestones of the upper part of the Torsuqtagh Group, which is 12m thick at Queerqueke and 23m thick at south Yaerdang. The other trilobites from this horizon include *Bienvillia cavernosa* Lisogor, *B. tetragonalis* (Harrington), *"Pseudoperonopsis" oblonga* Lu and Lin, *Dichelepyge sinensis* Lu and Lin, *Borthaspidella anderssoni* (Troedsson) and *Niobella preciosa* (Lu and Zhou), indicating the *Dichelepyge sinensis* Zone. Lu *et al.* (1984, Table 1), considered that the *D. sinensis* Zone can be roughly correlated to the *Adelograptus tenellus* graptolite Zone of the British standard zonation. The conodonts found in association with the trilobites are, *inter. al. Cordylodus angulatus* Pander, *C. rotundatus* Pander and *Drepanodus tenuis* Moskalenko, indicative of the *Cordylodus angulatus* Zone of late early Tremadoc age.

2. The most diverse cyclopygid assemblage in our collection makes its appearance at Queerqueke in the middle part of the Charchaq Group, a bed of rhythmic greyish green siltstones, shales and thin-bedded calcarenites, 400m in thickness; it comprises up to seven species: *Pricyclopyge* cf. *binodosa longicephala* Klouček, *Cyclopyge* cf. *recurva* Lu, *Microparia (Microparia)* sp., *M. (Heterocyclopyge) abunda* sp. nov., *M. (Quadratapyge) curva* sp. nov., *Degamella* cf. *princeps* (Barrande) and *Sagavia felix* Koroleva. Other trilobites found in the same bed were identified by the authors as *Dionide* sp., *Illaenopsis* sp. *Girvanopyge* sp., *Birmanites* sp. and *Lonchodomas* sp. The associated graptolites include, among others, *Nemagraptus gracilis* (Hall), *Corynoides pristinus* Ruedemann, *Dicranograptus brevicaulis* Elles and Wood, *Dicellograptus sextans exilis* Elles and Wood, *Cryptograptus tricornis* (Carruthers) and *Climacograptus brevis* Ellis and Wood, suggestive of the

Nemagraptus gracilis Zone, which is considered to be late Llandeilo to earliest Caradoc in age.

3. Two cyclopygids, that is, *Cyclopyge* cf. *recurva* Lu and *Microparia (Heterocyclopyge) abunda* sp. nov., extend upwards from the *Nemagraptus gracilis* Zone to an overlying bed of the Charchaq Group at Queerqueke, which is composed of variegated clastic sandstones and siltstones intercalated with calcareous shales, 350m in thickness. This has yielded graptolites, including *Climacograptus bicornis* (Hall), *C. minimus* (Carruthers), *Dicranograptus sinensis* Ge, *D. brevicaulis* Elles and Wood, *Pseudoclimacograptus scharenbergi* (Lapworth), *Dicellograptus sextans exilis* Elles and Wood, *D. pumilus* Lapworth and *Orthograptus calcaratus* Lapworth. All may belong to the *Climacograptus bicornis* Zone and indicate an early Caradoc age. One more cyclopygid has been found in this horizon by Zhong and Hao (1990: 120, pl.5, fig.13), and identified as *Ellipsotaphrus* sp. by one of the authors (Z.Z.).

Pattern of distribution

As pointed out by Zhou *et al.* (in Zhou and Chen 1990), during the Ordovician the vast expanse of the Tarim Block was a shallow-water carbonate platform with the water body gradually deepening northwards. The evidence from the lithofacies and biofacies demonstrates that a marginal basin (Tremadoc-early Arenig) or trough (middle Arenig-early Ashgill) existed along the present north margin of the block, and the Queerqueke-Yaerdang mountain area may have formed part of the exterior marginal belt.

According to Zhou *et al.* (in Zhou and Chen 1990), cyclopygids have hardly ever been found in the platform (for example, the Bachu area) or even in the shelf (for example, the Kalpin area) deposits in Tarim, except from late Llandeilo-Caradoc rocks when transgressive sedimentary regimes were progressively introduced worldwide (cf. Fortey 1984). During this great transgression a few cyclopygid forms penetrated over the former shallow shelf and became more widely distributed. In the period of the *Nemagraptus gracilis* Zone (Figure 2A) *Cyclopyge* cf. *recurva* Lu and *Microparia (Microparia) acuta* Zhang occur in a Nileid Association of shelf slope facies in association with *Nileus convergens* Lu, *Peraspis* sp., *Poronileus* sp., *Lonchodomas* sp., *Dividuagnostus* sp. and *Birmanites* sp., while *Cyclopyge* sp., *Microparia (Microparia)* sp., *M. (Quadratapyge) chedaoensis* Zhou and Dean and *M. (Q.)* sp. appear in the shelf-margin basin deposits together with various graptolites and other trilobites of a Shumardiid Biofacies, including *Lisogorites tarimensis* Zhang, *Dividuagnostus* sp., *Taklamakania xinjiangensis* Zhang, *Ampyx yohi* Lu, *Shumardia tarimuensis* Zhang, *Telephina angulata* (Yi), *Peraspis obscura* Zhou and Dean, *Birmanites* sp. and *Endymionia circularis* Zhang. In the interval of the *Climacograptus bicornis* Zone (Figure 2B) *Cyclopyge* cf. *recurva* Lu alone was found in a upper slope facies limestone bed in the Kalpin area; the other trilobites from this horizon include *Nileus convergens* Lu, *Birmanites kanlingensis* Zhang, *Stenopareia* sp., *Ampyx* sp., *Ovalocephalus* sp., *Dionide* sp. and *Corrugatagnostus* sp., suggestive of another Nileid Association. It is interesting to note that some cyclopygids, such as *Microparia (Heterocyclopyge)*, *Pricyclopyge*, *Sagavia* and *Ellipsotaphrus*, which flourished in the deeper water site never occurred in the shallower water site. *M. (Quadratapyge)* never spread into the shallower shelf.

The occurrence of *Prospectatrix* in late early Tremadoc in Tarim suggests that from their earliest occurrence the Cyclopygidae had a very wide distribution, extending from Europe across Asia. Kobayashi and Hamada (1970) considered that the earliest cyclopygids in Asia were Middle Ordovician in age. But the presence of *Prospectatrix* in Europe and Asia in the Tremadoc argues for a rapid radiation around much of marginal Gondwana.

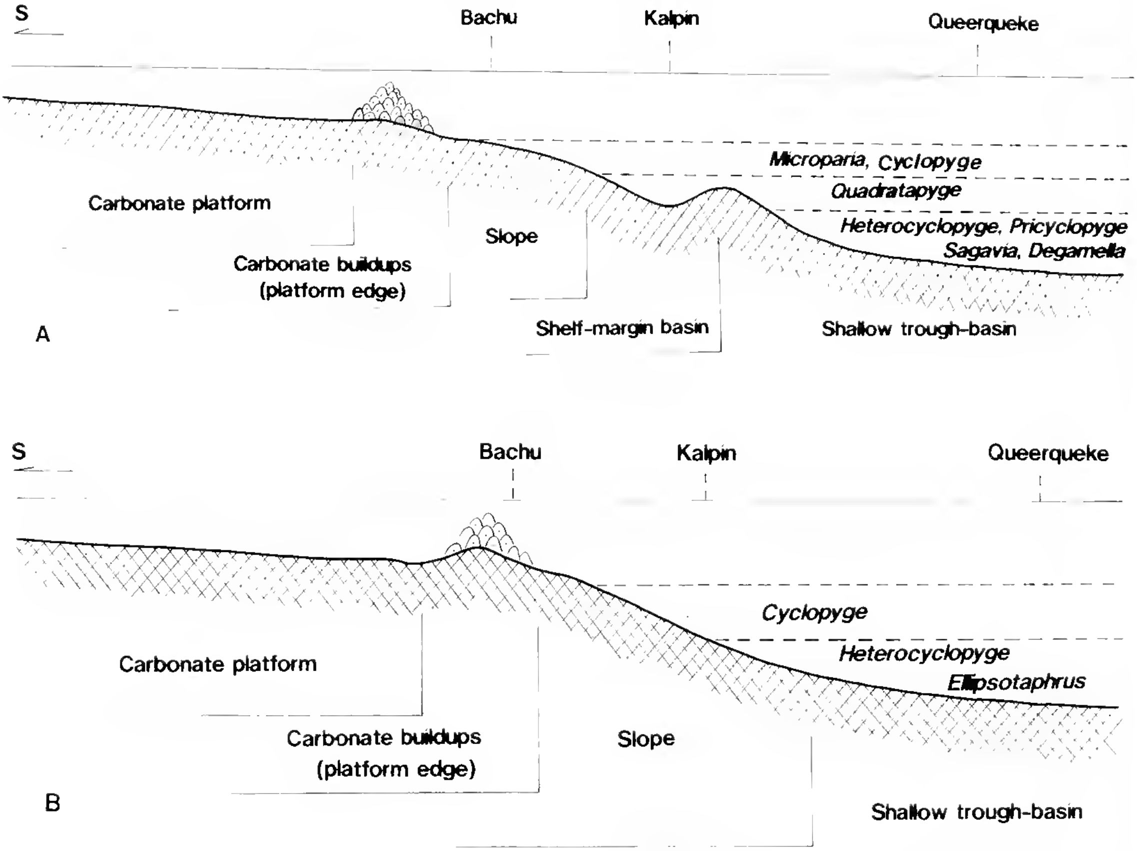


Figure 2 Palaeogeographic profiles across the Tarim Block (after Zhou *et al.* in Zhou and Chen 1990) showing the depth differentiation of the mesopelagic cyclopygids during the late Llandeilo-earliest Caradoc (A) and early Caradoc (B).

Fortey (1985) and Fortey and Owens (1987) considered the cyclopygids to be mesopelagic trilobites living above the lower limit of the photic zone, or at a depth of 200–700m below the water surface. The distributional pattern of cyclopygids in Tarim reveals that most of them were only distributed along the continental margin at a water level of considerable depth. However, a few genera, such as *M. (Quadratapyge)*, may have lived at shallower, but sufficiently deep, water levels to have been able to invade onto the shelf basin, or even, in the case of *Cyclopyge* and *M. (Microparia)*, onto the interior shelf slope. It seems likely, therefore, that there may have been a depth-induced ecological differentiation between the morphologically similar cyclopygid genera.

ONTOGENY AND HETEROCHRONY

Ontogeny

Aspects of the ontogenetic development of cyclopygids have been mentioned by a number of authors. The ontogeny of *Cyclopyge* has been discussed by Marek (1961), Tripp *et al.* (1989) and Kielan (1959); *Microparia* and *Heterocyclopyge* by Marek (1961), who along with

Barrande (1872) and Whittard (1961) discussed features of the ontogeny of *Degamella*. The ontogeny of *Pricyclopyge* was also covered, in part, by Marek (1961) and Whittard (1961), along with Rushton and Hughes (1981). Six of the species descriptions provided herein are based on both meraspid and holaspid material. Consequently ontogenetic changes that occurred in these six species have been documented and are found to involve 11 different morphological features. In two species, *Cyclopyge* cf. *recurva* and *Degamella* cf. *princeps*, the glabella elongated and narrowed anteriorly, whereas in *Pricyclopyge* cf. *binodosa longicephala* it broadened during ontogeny. In the latter species there was also a narrowing of the fixigena. In *Cyclopyge* cf. *recurva* and *Microparia (Heterocyclopyge) abunda* the palpebral lobe narrowed and became convex during ontogeny. In *C.* cf. *recurva* the visual surface of the eye enlarged by an increase of longitudinal files of lenses.

Deepening of the pygidial border furrow is a common feature in the ontogeny of these cyclopygids and was often associated with a widening of the border, which became more well-defined in later meraspids and holaspids. This occured in *Pricyclopyge* cf. *binodosa longicephala*, *Cyclopyge* cf. *recurva*, *Microparia (Heterocyclopyge) abunda*, *Microparia (Quadratapyge) curva* and *Sagavia felix*. On the contrary, effacement of pygidial pleural and interpleural furrows occured in *Pricyclopyge* cf. *binodosa longicephala* and *Sagavia felix*. Other ontogenetic changes that occurred in the pygidium were, among others, the widening of the axial rings in *Cyclopyge* cf. *recurva*, and the deepening of the axial furrow and development of the postaxial groove in *Microparia (Quadratapyge) curva*. In addition, the true pygidium, semicircular in early growth stages, tended to become triangular in late stages in *Pricyclopyge* cf. *binodosa longicephala*.

Heterochrony

Variations in the extent of ontogenetic changes between cyclopygid species enables the role of heterochrony in the evolution of this group of trilobites to be evaluated. It is probably no surprise, given the relatively minor morphological changes that occurred during ontogeny in cyclopygids, that morphological differences between cyclopygid species are correspondingly relatively slight. Hence the observation of Fortey and Owens (1987:151) that "many cyclopygid genera .... are extraordinarily conservative". Whereas they ascribe this conservatism to the stable, offshore environment in which the cyclopygids lived, we believe that it is, to a large degree, a reflection of the small degree of ontogenetic change that took place during the ontogeny of species within this family. This is the opposite situation to the case in many Cambrian trilobites (McNamara 1986) wherein the large scale ontogenetic changes engendered a wide range of interspecific heterochronic morphotypes.

Whereas in Cambrian trilobites the incidence of progenesis, arising from premature sexual maturation, was a relatively common phenomenon (McNamara 1983), it was of only relatively minor importance in cyclopygids. Fortey (1981) and Fortey and Owens (1987) consider *Prospectatrix* to be the most primitive cyclopygid and to have been derived from a nileid-like ancestor, as suggested by the small eyes and retention of the broad fixigenal area and cephalic median suture. This proposed relationship is strengthened by the discovery of an elongate median glabella tubercle in *Prospectatrix exquisita* sp. nov. The presence of this feature was not recorded in the type species of *Prospectatrix* by Fortey (1981).

The type species of *Prospectatrix* possesses seven thoracic segments (although the new species described herein has only six), and in this regard is comparable with many nileids. Cyclopygid genera, such as *Microparia* and *Sagavia*, that possess only 5 thoracic segments, are therefore relatively paedomorphic and are likely to have arisen by progenesis, as indeed would have species such as *Prospectatrix exquisita* sp. nov.

Minor local heterochronic changes in cyclopygids have previously been recognised by Fortey and Owens (1987). Of relevance to the material described in this paper, they note that the gradual change in shape of the glabella through a number subspecies of *Pricyclopyge binodosa,* from *eurycephala-binodosa/prisca-longicephala,* involves heterochrony, although they did not specify, whether by paedomorphosis or peramorphosis. The ontogenetic changes documented herein in *P.* cf. *binodosa longicephala* (Figures 3E, 5A,E) may allow the polarity of these changes to be assessed. The earliest form *P. binodosa eurycephala,* as its name implies, has a very broad cranidium, with the maximum width posterior to the crandial mid-length. Although the glabella of *P.* cf. *binodosa longicephala* widened during ontogeny, it attained the maximum width much more anterior than in *P. binodosa eurycephala.* The shape of the late meraspid glabellar of *P.* cf. *binodosa longicephala* is, in turn, similar to that of the early meraspid juveniles of *P. binodosa binodosa* illustrated by Rushton and Hughes (1981, pl.2, figs 20, 22, 23). Consequently, it can be argued that the three subspecies in question can be regarded as forming a paedomorphocline in this character.

Pricyclopyge is morphologically close to the primitive cyclopygid *Prospectatrix,* from which it may have been derived. The larger eyes of *Pricyclopyge* suggest a peramorphic increase in lens number from *Prospectatrix.* The rounded holaspid pygidium of *Prospectatrix* (Figure 3A) is reminiscent of the juvenile pygidium in *Pricyclopyge,* before it becomes acuminate posteriorly. This change in pygidial shape in *Pricyclopyge* is therefore also a peramorphic feature.

The cyclopygid species described in this paper that shows most ontogenetic change is *Cyclopyge* cf. *recurva* Lu in Wang, 1962 (Figure 4). These include a lengthening of the glabella, which became more narrowly rounded anteriorly (Figure 4C,G–I); the palpebral lobe is narrow (tr.) and wire-like in adult, but more flattened and wider (tr.) in juvenile specimens (Figure 4C,I); the pygidial border is absent until degree 3 (Figure 4C), but then gradually became more markedly defined (Figure 4H) and wider (sag.); the visual surface of the eye was enlarged by the increase of longitudinal files of lenses; axial rings widened (tr.); and the length /width ratio was much reduced from the transitory to the holaspid pygidium.

In primitive species of *Cyclopyge,* such as *C. grandis grandis* (Salter, 1859) (Fortey and Owens 1987: 151) the pygidial axis is long and segmented, while the eyes are separated anteriorly. In later species, such as *C.* cf. *recurva* described herein (see also Zhou and Dean 1987) and also later Ordovician forms such as *C. rotundata* Lu (see Tripp *et al.* 1989); *C. mirabilis* (Forbes MS *in* Salter, 1853) (see Whittard 1952); *C. vigilans* (Cooper and Kindle, 1936); *C. marginata* Hawle and Corda, 1847 (=*C. quadrangularis* Kielan, 1959: 83), the pygidial axis is short, including only one ring in large specimens. This is therefore a paedomorphic character in these later species. The eyes, however, became fused anteriorly in later species as the number of lenses increased by peramorphosis. The broader pygidial border of these later species is another peramorphic character. Marek (1961) has shown how the pygidial border is not developed in meraspids of *C. marginata,* but is wider and more defined in holaspids of *C. rotundata* (see Tripp *et al.* 1989).

Species of *Degamella* show an appreciable variation in eye size. For example, Fortey and Owens (1987: 160) have noted that the Llanvirn – Llandeilo *D. princeps* (described herein) has a surprisingly small eye for a cyclopygid, being smaller than in the late Arenig form *D. evansi* Fortey and Owens, 1987. Eyes in the Ashgill species *D. gigatea* (Barrande) (Marek

1961: 49, pl. 5, figs 1–3) are even smaller than *D. princeps*. Such eye reduction is likely to have occurred by paedomorphosis, and is somewhat at variance with the general trend for peramorphic increase in eye size in cyclopygids as a whole.

It has been suggested (Marek 1961; Fortey and Owens 1987) that *Degamella* and *Microparia* are closely related. The meraspid *Degamella* has a much wider glabella than the holaspid, and in this regard resembles the holaspids of *Microparia*. Fortey and Owens (1987: 172) have observed the similarity of the cranidium of a degree 5 meraspid of *D. nuda* (Whittard, 1961), and the holaspis of *M. teretis* Fortey and Owens, 1987. If *Degamella* is considered to have evolved from *Microparia*, then the narrowing of the glabella through ontogeny in *Degamella* would be a peramorphic feature.

Fortey and Owens (1987: 177) considered that the similarity in structure of the pygidial axis of *Sagavia*, *Microparia* and *Degamella* indicated a common ancestry. The increase in axial length and definition during the ontogeny of *Sagavia* (see herein Figure 8A–J), compared with the effacement that occured during ontogeny in some species of *Microparia*, suggests that the evolution of the pygidial axis in *Sagavia* occurred by peramorphosis.

Ecological significance of heterochronic morphological changes

Many of the morphological changes that occurred in cyclopygids by heterochrony can be explained in terms of selection for particular morphologies that were particularly suited to a pelagic existence. The specific morphological features that so typify cyclopygid trilobites, notably the broad axis, including the glabella, and the greatly enlarged eyes, arose by local peramorphic changes to growth allometries and rates of lens production. The massive eyes that were so produced greatly improved the visual area and were of strong selective advantage to pelagic trilobites. Those cyclopygids, such as *Degamella* and *Cyclopyge*, that underwent peramorphic elongation of the glabella, probably reflect selection for more active swimming morphologies (Fortey 1985).

The subsequent changes to these characters within particular lineages were relatively small and occurred over long time periods. Thus the generic assemblage of cyclopygid trilobites is very similar from the Arenig to the Ashgill. This morphological conservatism derives both from the stable environment that they inhabited, but also from the relatively small allometric changes that occurred during ontogeny, restricting the capacity for the evolution of heterochronic morphotypes.

SYSTEMATIC PALAEONTOLOGY

Family Cyclopygidae Raymond, 1925

Genus *Prospectatrix* Fortey, 1981

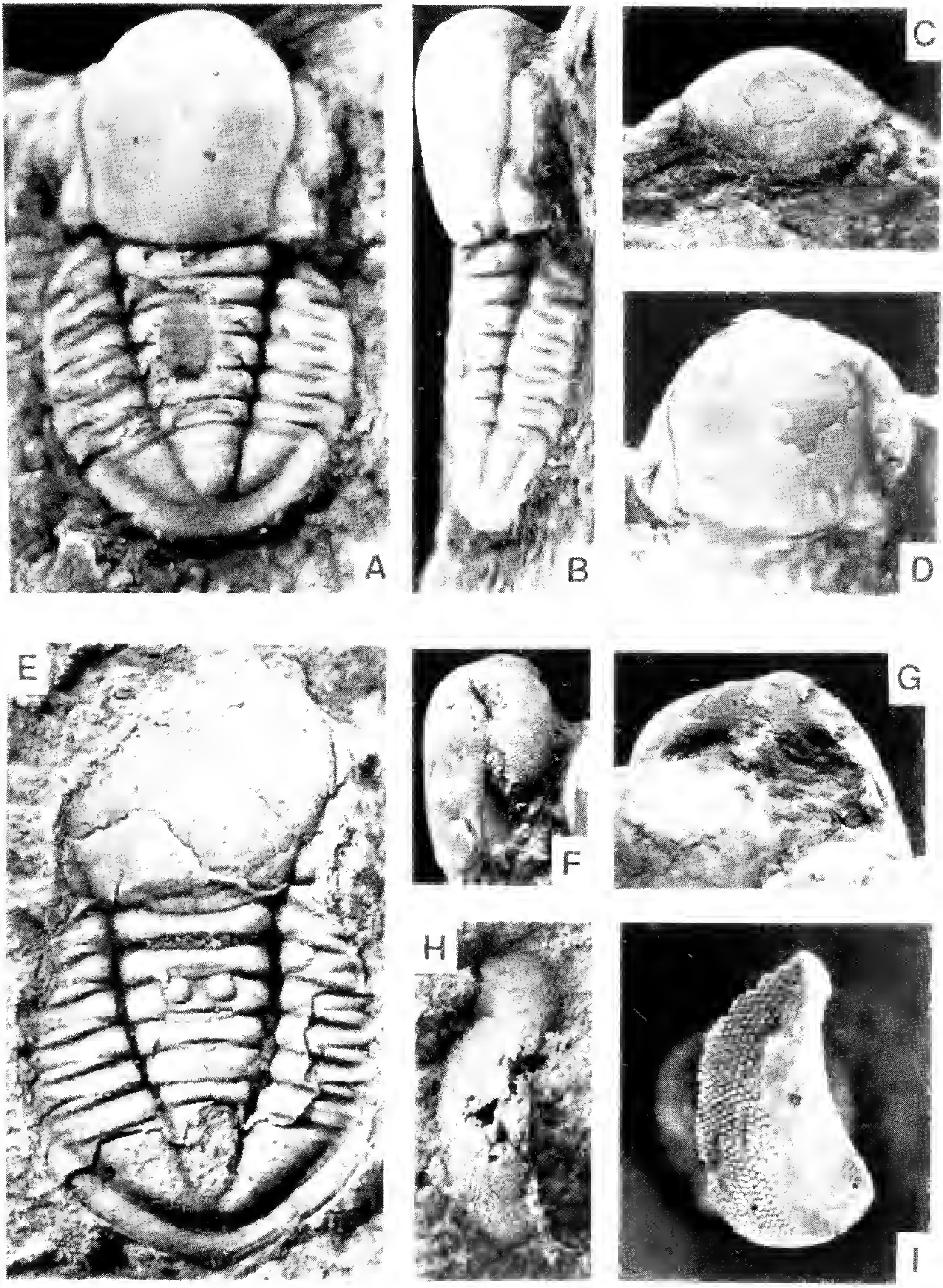
Type species

Cyclopyge genatenta Stubblefield in Stubblefield and Bulman 1927, from the *Shumardia (Conophrys) salopiensis* Zone of the Shineton Shales (upper Tremadoc), Shineton, Shropshire, England.

Prospectatrix exquisita sp. nov.

Figure 3A–D, F–I

Prospectatrix sp., Zhou in Zhong and Hao, 1990: 118, pl. 5, figs14, 15.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Etymology

Latin *exquisitus, a, um*, excellent, referring to the well preserved type specimens.

Holotype

Dorsal shield lacking librigenae, NI 120569 (Figure 3A–C), from the *Dichelepyge sinensis* Zone of the upper part of the Torsuqtagh Group, locality 1.

Paratypes

One incomplete cephalon (NI 120570) and one left eye (NI 120572) (locality 2), and one right librigena (NI 120571) (locality 1), all from the *Dichelepyge sinensis* Zone of the upper part of the Torsuqtagh Group.

Diagnosis

A species of *Prospectatrix* with six thoracic segments. Palpebral area of fixigena 14% width and 50% length of glabella; posterior area about 20% basal width of glabella. Pygidial axis with two rings defined by shallow ring furrows. Pygidial border furrow distinct.

Description

Dorsal shield oval in outline, 60% as wide as long; cephalon 45%, thorax 33%, and pygidium 22% the exoskeletal length. Cranidium wider than long. Glabella large, strongly convex, 90% as wide as long, broadly rounded and overhanging preglabellar furrow anteriorly, slightly constricted opposite the posterior pair of glabellar depressions, from where it expands forward to a maximum width at 44% glabellar length from front, nearly at the level of the median tubercle; three pairs of faint isolated oval depressions present on the flanks, successively becoming smaller anteriorly; only posterior lateral glabellar furrow well defined in some specimens, being eyebrow-shaped, extending along the anterior margin of the posterior depression; median tubercle elongate, shown only on testaceous surface, but absent in exfoliated specimens. Axial furrow sigmoid, deeply incised. Fixigena narrow (tr.), low, gently convex, turning downwards abaxially; palpebral area of fixigena 14% width of the glabella in plan; palpebral lobe strip-like, convexly curved abaxially, about 50% the glabellar length, alongside axial furrow anteriorly; palpebral furrow absent; posterior area of fixigena small, triangular, more than 20% the basal width of the glabella; posterior border short (exsag.), well demarcated by shallow border furrow. Posterior sections of facial sutures diverge backwards; anterior sections extending along axial furrows and meeting at sagittal line in front of the glabella. Librigena mainly composed of large eyes, which are recurved, strongly convex, with lenses hexagonally arranged, reducing in size ventrally; anterior to eye genal field narrowing forwards; median part of doublure crescentic in outline, rounded anteriorly, separated by median suture, covered with about 10 terrace lines roughly parallel to the

◀**Figure 3** A–D, F–I, *Prospectatrix exquisita* sp. nov., from the *Dichelepyge sinensis* Zone of the upper part of the Torsuqtagh Group; A–C, dorsal shield lacking librigenae, holotype, dorsal, lateral, anterior views, NI 120569, x5, Loc.1; D, F, G, cephalon, paratype, dorsal, lateral, ventral views, NI 120570, x5, Loc.2; H, right librigena, paratype, latex cast from external mould, NI 120571, x15, Loc.1, I, left eye, paratype, NI 120572, x10, Loc.2. E, *Pricyclopyge* cf. *binodosa longicephala* Kloucek, 1916, incomplete dorsal shield of degree 5, NI 120573, x10, from the *Nemagraptus gracilis* Zone of the middle part of the Charchaq Group, Loc.1.

posterior and lateral margins, tapering sharply backwards into narrow bands that extend along ventral margins of eyes.

Thorax of six segments. Axis convex (tr.), well defined by deep and broad axial furrows, tapering backwards; articulating half ring widely rounded anteriorly, more than 35% length of ring; articulating furrow deep and wide. Pleurae broadly rounded laterally, first pleura shortest, about 40% the axial width, progressively widening posteriorly to the fourth segment and similar width thereafter, including a horizontal proximal part adaxial to fulcra and a downwardly bent faceted distal part abaxial to fulcra; fulcrum of sixth segment placed at 40% its pleural width from axial furrow, becoming slightly successively closer to the axial furrow in preceeding segments; pleural furrow deeply incised, narrowing abaxially, dying out before reaching lateral margin; pleura uniform in width with truncated extremity except the first segment which is triangular in form and ends in a short point; facet triangular, wide (tr.).

Pygidium 50% as long as wide, semicircular in shape. Axis strongly convex, 32% the anterior width and 65% the length of the pygidium, narrowing steadly backwards, narrowly rounded posteriorly, including two rings defined by shallow ring furrows, and a terminal piece in addition to an articulating half ring; postaxial ridge short, extending from the rear end into the pygidial border. Pleural lobe gently convex; anterior half pleura narrowing adaxially, faceted anterolaterally, well delimited by deep pleural furrow. Border wide (sag.), uniform in width, low, flat. Border furrow well defined by change of convexity from pleural lobe to border.

Surface of cranidium, thorax and pygidium covered with fine anastomosing raised lines, mainly transversely extended but subparallel to the nearest exoskeletal margins peripherally. Similar lines are absent from the central glabellar part round the median tubercle, the lateral glabellar depressions, the posterior area of the fixigena and the palpebral lobe.

Discussion

Except for the type species, other forms referred to the genus *Prospectatrix* have been described from the late Tremadoc of the western Lake District, England (Rushton 1988), the early Arenig of the Taurus Mountains of Turkey (Dean 1973), and the Fennian (late Arenig) of South Wales (Fortey and Owens 1987). Additionally, a cranidium illustrated by Apollonov *et al.* (1984, pl.23, fig.11) from the Malyi Karatau Range, Kazakhstan may also referable to this primitive cyclopygid genus, as indicated by Rushton (1988: 694).

The new species closely resembles the type species *P. genatenta* (Stubblefield) (Stubblefield and Bulman 1927: 138, pl.4, figs 9–11; Fortey 1981: 611, pl.1, figs a–j), but differs in having six instead of seven thoracic segments, in the narrower posterior area of fixigena (20% vs. 30% the basal width of the glabella), in the longer palpebral lobe (50% vs. 36% the glabellar length) and in the shallower ring furrows but more distinct border furrow of the pygidium. It also differs in possessing an elongate median glabellar tubercle. These diagnostic features of the present species are in turn compatible with those of *P. superciliata* (Dean 1973: 314, pl.6, figs 2, 4, 6, 8, 9, 14), but the Turkish species displays a glabella steadily expanded forwards with no constriction opposite the 1p glabellar depressions, and its palpebral area of fixigena is slightly narrower (tr.) (11% vs. 14% the glabellar width in plan).

A juvenile pygidium described as Cyclopygid? gen. and sp. undet. by Dean (1973: 316, pl.6, fig.3) from the late Arenig of the Taurus Mountains, Turkey seems assignable to *Prospectatrix*; it is comparable with that of *P. exquisita*, especially in the deep pygidial border furrow, although it is longer. *P. brevior* Rushton (1988: 694, pl.68, figs 1–3) has a wider posterior area of fixigena that is similar in size to that of the type species, a very narrow (tr.) but shorter (exsag.) palpebral area of fixigena and a longer pygidium showing three axial rings; otherwise it is close to the new species.

Prospectatrix sp. (Zhong and Hao 1990) was recorded from the same locality and horizon as the holotype of this species. The characteristic features coincide well with each other, and we consider both as conspecific.

Genus *Pricyclopyge* Richter and Richter, 1954

Type species

Aeglina prisca Barrande, 1872, from the Šárka Beds (Llanvirn), Bohemia.

Pricyclopyge cf. *binodosa longicephala* Klouček, 1916

Figures 3E, 5A,E

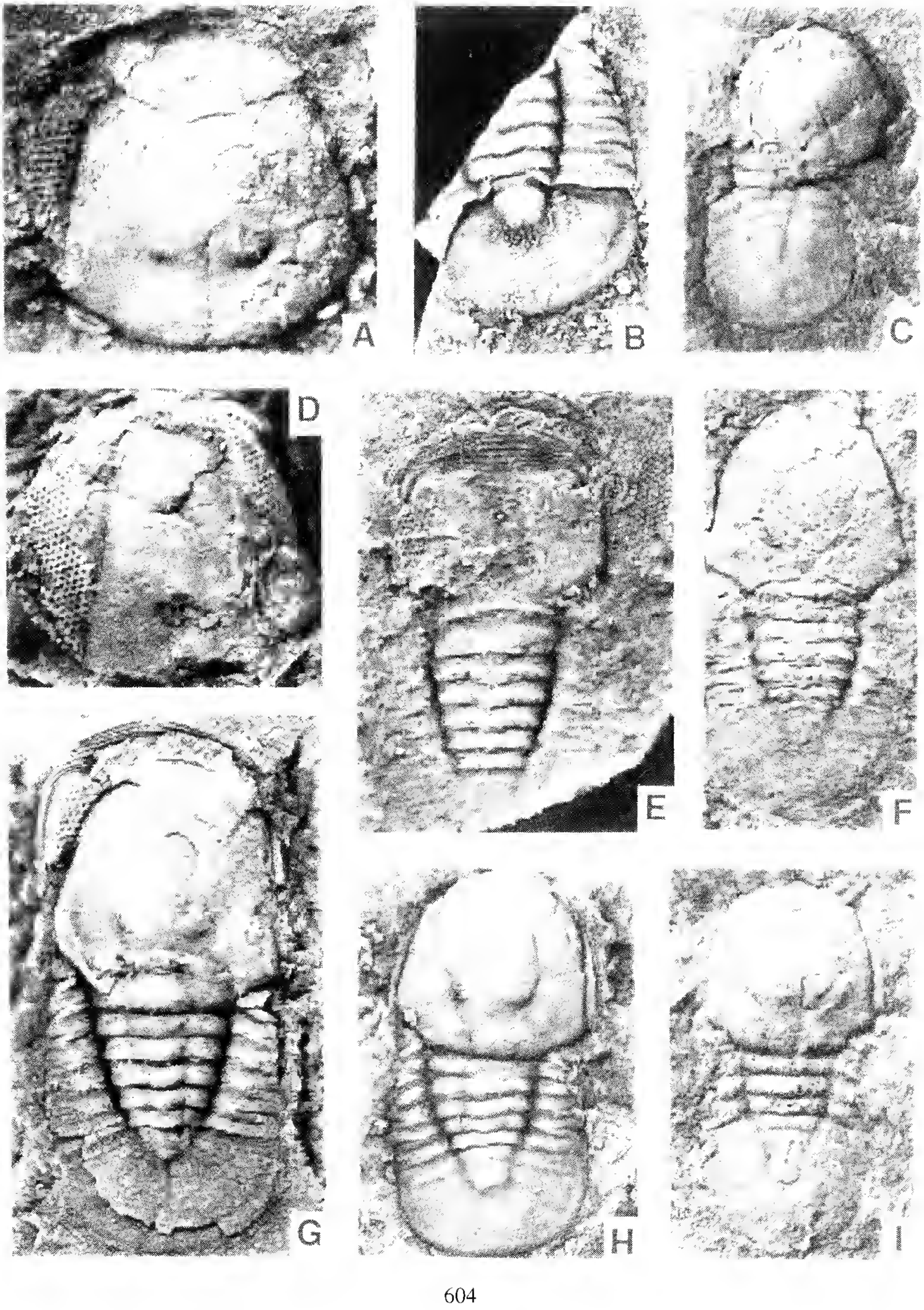
Figured specimens

Three dorsal shields (lacking librigenae) of degrees 5 (NI 120573), 2 (NI 120575) and 1 (NI 120574), all from the *Nemagraptus gracilis* Zone of the middle part of the Charchaq Group, locality 1.

Discussion

No mature specimens have been found in our collection, but the incomplete carapace of degree 5, 8mm in length, bears a great resemblance to the lectotype of *P. binodosa longicephala* Klouček, 1916 (see Marek 1961: 34, pl.1, fig.21) from the Dobrotivá Beds (Llandeilo), Malé Přilepy, near Beroun, Bohemia: the glabella is slightly shorter, but, as noted by Marek (1961: 34), the length/width proportion may vary in the subspeces of *P. binodosa*, especially if specimens are preserved in shales and more or less compressed. Judging from the anterior glabella margin which is gently forwardly convergent and a pair of slender spines shown on the anterior unliberated segment (future sixth thoracic segment), the present material may probably be referred to *P. binodosa longicephala*, but further adult specimens are required before we make a definite conclusion. With regard to the shape of the glabella and pygidium, this form is also comparable with *P. compesteris* Koroleva, 1967 (see also Koroleva 1982: 124, pl.25, fig.12) from the Llandeilo of northern Kazakhstan, but the terminal spines of the sixth thoracic segment seems slightly thicker in the latter. Fortey and Owens (1987: 184) have implied that the Kazakhstan species may be synonymous with the contemporaneous Bohemian species.

The degree 2 dorsal shield is about 4mm long. The glabella is pear-shaped, 80% as long as wide, with greatest width at 66% the glabellar length from the posterior margin. The fixigena is triangular, about half the basal glabellar width, and tapers forwards. The palpebral lobe is long, narrow and rim-like, and posteriorly extends just to the anterior margin of the posterior area of the fixigena. The transitory pygidium, about 85% as long as wide, shows slightly forwardly convergent lateral margins, but is broadly rounded posteriorly. The true pygidium has faintly furrowed pleural lobes but no well defined border furrow. The degree 1 dorsal shield, 3mm long, is similar to that of degree 2, but the transitory pygidium is longer (as long as wide). A pair of hollow nodes which is well defined on the axial ring of the third thoracic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segment is not seen on the axis of the degree 1 and 2 transitory pygidia. This is obviously owing to the poor preservation of these specimens.

According to the present incomplete growth series, the morphological changes during the meraspid period of this form may comprise the narrowing of the fixigenae, the deepening of the pygidial border furrow, the effacement of the pygidial pleural and interpleural furrows, and the broadening of the glabella and transitory pygidium. Furthermore, the shape of the true pygidium is triangular in degree 5 but semicircular in smaller specimens.

Similar morphological changes are also exhibited in the size series of *P. binodosa binodosa* (Salter in Murchison 1859), as described by Whittard (1940, 1961) and Rushton and Hughes (1981). Specimens of degree 1 in this European species (Rushton and Hughes 1981: 633, pl.2, figs 20, 23, 24), as compared with those at the same stage in the present form, display a slightly wider (tr.) palpebral area of fixigena. The dorsal shield shown by Rushton and Hughes (1981, pl.2, fig.22) may probably represent that of a degree 2 specimen, which differs in the broader glabella and better defined pygidial border furrow. The deeply incised pygidial border furrow and the more narrow anteriorly rounded glabella seen in holaspids of *P. binodosa binodosa* (Whittard 1961, pl.23, fig.16) appeared between meraspid degrees 2 and 3.

Genus *Cyclopyge* Hawle and Corda, 1847

Type species

Egle rediviva Barrande, 1846, from the Černin Beds (Caradoc) of Trubin, near Beroun, Bohemia.

Cyclopyge cf. *recurva* Lu in Wang, 1962

Figure 4A–I

Cyclopyge cf. *recurva* Lu, Zhou *in* Zhong and Hao, 1990: 119, pl. 5, fig. 12.

Figured specimens

One cephalon (NI 120576), three incomplete dorsal shields (NI 120580, 120581, 120582), one incomplete pygidium with attached thorax (NI 120577), one degree 2 dorsal shield (NI 120578) and one degree 5 dorsal shield (lacking librigenae) (NI 120583) from the *Climacograptus bicornis* Zone, and one cephalon (NI 120579) and one degree 3 dorsal shield (lacking librigenae) (NI 120584) from the *Nemagraptus gracilis* Zone, of the middle part of the Charchaq Group, locality 1.

Description

Holaspid stage

Dorsal shield elliptical in outline, about 6–7.5 mm long in the collection; cranidium 46%, thorax 28% and pygidium 26% the exoskeletal length. Glabella convex, tapering forwards,

◀ **Figure 4** A–I, *Cyclopyge* cf. *recurva* Lu in Wang, 1962, A–C, E–H, from the *Climacograptus bicornis* Zone, D, I, from the *Nemagraptus gracilis* Zone, of the middle part of the Charchaq Group, Loc.1; A, cephalon, NI 120576, x10; B, pygidium attached with incomplete thorax, NI 120577, x10; C, dorsal shield of degree 2, NI 120578, x15; D, cephalon, NI 120579, x10; E, incomplete dorsal shield, NI 120580, x8; F, dorsal shield lacking librigenae, NI 120581, x10; G, dorsal shield, NI 120582, x10; H, dorsal shield lacking librigenae, degree 5, NI 120583, x10; I, dorsal shield lacking librigenae, degree 3, latex cast from external mould, NI 120584, x15.

rounded anteriorly, almost as long as wide. 1p glabella furrow elongated, pit-like, abaxial extremity placed at 30% of glabella length from posterior margin, from there it extends inwards and backwards. A pair of circular swellings situated just posterior to the glabellar furrows. Median tubercle in line with anterior margin of 1p furrows. Palpebral lobe narrow, convex, wire-like, extending along glabella, well defined by deep and wide axial furrow. Posterior area of fixigena triangular, tiny. Librigenae united; eye reaches cephalic mid-line anteriorly, including at least 12 longitudinal files of hexagonal lenses; doublure widest (sag.) mesially, narrowing posteriorly, broadly embayed in posterior outline, covered with ten closely spaced raised terrace ridges subparallel to nearest margins.

Thorax of six segments, subparallel-sided. Axis narrowing backwards, width of sixth ring about half that of the first one. Pleurae correspondingly widening backwards; turned downwards from fulcra, which are arranged roughly parallel to axial furrow; facet triangular, about two-thirds the pleural width in the sixth segment, slightly narrowing (tr.) forwards; pleural furrows deep and wide, narrowing abaxially and extending nearly to truncated distal tips.

Pygidium weakly convex, subparallel-sided, gently arched posteriorly, 57% as long as wide. Axis short (sag.), including one ring and a broadly rounded terminal piece. Postaxial field crossed by sagittal groove which fades out before reaching border furrow. Pleural lobe faceted anterolaterally; indications of anterior three pleurae present in some specimens. Border about 15% pygidial length (sag.), narrowing gently forwards from posterolateral corner. Border furrow shallow.

Meraspid stage

Degree 2 dorsal shield 3.2mm long. Glabella broadly rounded anteriorly. Palpebral lobe flattened, about 7% of the cranidial width (tr.). Eye extends along side of the glabella, reaching cephalic midline anteriorly, including 6 longitudinal files of hexagonal lenses. Thorax of two segments. Transitory pygidium as long as wide. Axis convex, funnel-shaped, with five rings and a terminal piece. Pleural lobe gently downsloping abaxially, with five pleurae which become successively weakly defined posteriorly. Border indistinct.

Degree 3 dorsal shield 3.6mm long. Cranidium broadly rounded anteriorly, gently tapering forwards. Palpebral lobe moderately convex, about 6% the cranidial width (tr.), slightly narrowing forwards. Thorax of three segments. Transitory pygidium 80% as long as wide. Axis funnel-shaped, convex, with four rings and a terminus. Pleural lobe slightly abaxially inclined, with four pairs of furrowed pleurae succeedingly becoming better defined anteriorly. Border obscure.

Degree 5 dorsal shield 5.5mm long. Glabella as in holaspids. Thorax of five segments. Transitory pygidium 60% as long as wide. Axis convex, broadly rounded posteriorly, with two rings in addition to a terminal piece. Pleural lobe slightly vaulted adaxial to border, with four pleurae indicated by interpleural ridges. Border narrow (sag.), faintly defined.

Discussion

The morphological changes from meraspids to holaspids in the present species are as follows:

1. The glabella becomes longer and more narrowly rounded anteriorly;
2. The palpebral lobe is narrow (tr.) and wire-like in adult, but more flattened and wider (tr.) in juvenile specimens;

3. The pygidial border is absent until degree 3, but then appears and gradually becomes more markedly defined and wider (sag.);
4. The visual surface of the eye is enlarged by the increase of longitudinal files of lenses;
5. Axial rings grow wider (tr.);
6. The length /width ratio is much reduced from the transitory to the holaspid pygidium.

The adult specimens of this form agree well with those of *Cyclopyge binodosa* Zhang (1981: 191, pl.72, figs1–3) from the lower part of the Qilang Formation (Caradoc) of Kanling, Kalpin, northwestern Tarim, Xinjiang, and of *C.* cf. *recurva* Lu (Zhou and Dean 1986: 758, pl.61, figs 2–5, 7–9, 14) from the upper part (Caradoc) of the Chedao Formation of Chedao, Huanxian, Gansu, northwest China. They are probably conspecific. All of them seem in turn indistinguishable from *C. recurva* Lu in Wang (1962: 53, pl.20, figs 5, 6, 9; 1964: 47, pl.13, figs 14–16; Lu *et al.* 1965: 542, pl.113, figs 8–10; Lu 1975:173, pl.30, figs 8–12) from the Pagoda Formation (Caradoc) of southern Shaanxi. However, the original specimens of *C. recurva* including the cranidium and transitory pygidia are poorly preserved. In this paper, we follow Zhou and Dean (1986) in referring this form to *C. recurva* with reservation pending a more complete knowledge of the latter. Several species of *Cyclopyge* recently established from the Middle–Upper Ordovician of Uzbekstan (Abdullaev in Abdullaev and Khaletskaya 1970), Turkestan Ridges of southern Tien-Shan (Petrunina in Repina *et al.* 1975) and northern Kazakhstan (Koroleva 1967; 1982) are also closely related to the present form. They include *C. ocula* Abdullaev, *C: abdullaevi* Petrunina, *C. alia* Koroleva, *C. festa* Koroleva, *C. sola* Koroleva, *C. tereki* Koroleva and *C. timida* Koroleva. The tiny likely differences between those central Asian species and the present form might be accounted for in the different preservation and size.

As noted by Zhou and Dean (1986: 760), *C.* cf. *recurva* is characterized by the anteriorly narrower eyes, a feature distinct from that of the lectotype of *C. mirabilis* (Forbes MS in Salter, 1853) (see Whittard 1952, pl.32, figs 6–8) from the Portrane Limestone (Ashgill) of Ireland. It also bears a superficial resemblance to the Canadian Ashgill species *C. vigilans* (Cooper and Kindle, 1936: 367, pl.52, figs 36, 39, 41–51) from the Whitehead Formation of Percé, Quebec, but differs in the more elongated glabella and narrower (sag.) pygidial border.

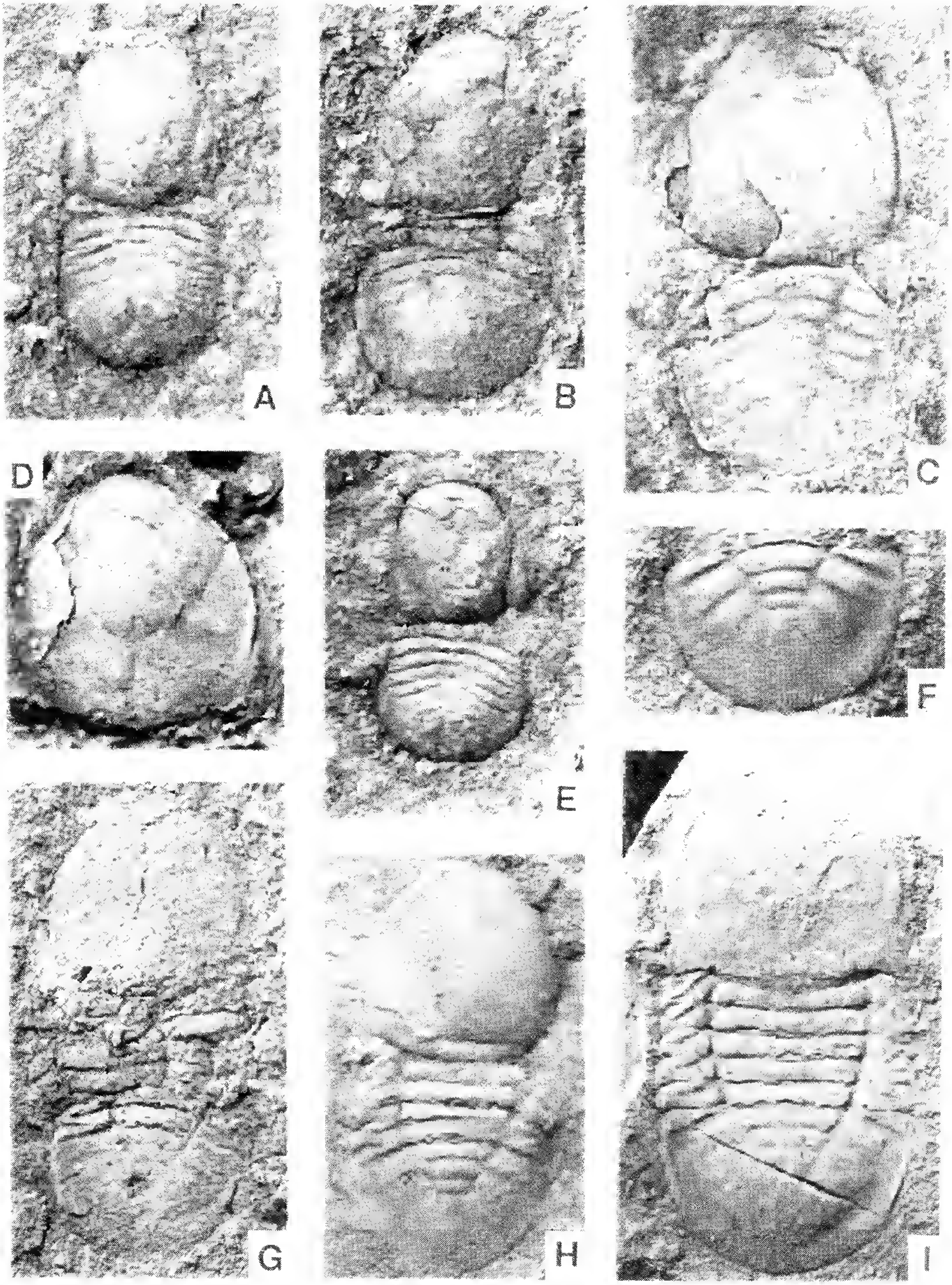
Genus *Microparia* Hawle and Corda, 1847

Type species

Microparia speciosa Hawle and Corda, 1847, from the Králův Dvůr Beds (Ashgill), Králův Dvůr, Bohemia.

Discussion

We follow Fortey and Owens (1987: 164) in regarding *Heterocyclopyge* Marek, 1961 as a subgenus of *Microparia*. Fortey and Owens also implied that *Microparia* (*Quadratapyge*) Zhou in Zhou *et al.* 1977 might be considered as an independent genus, being characterized by its rectangular pygidium provided with a well defined short pygidial axis and very wide flattened border. The pygidium of the new species *M. (Q.) curva* as described below is typical of *Quadratapyge*, but displays a broadly rounded instead of straight posterior margin. It is therefore closely similar to that of *Heterocyclopyge*, such as the type species *M. (H.) pachycephala* (Hawle and Corda) (Marek 1961: 27, pl.5, figs 9, 10), *M. (H.) nigra* Hörbinger and Vaněk (1985: 60, pl.1, figs 6, 7, pl.2, fig.4) and *M. (H.) abunda* sp. nov. (see below). It differs in the wider (sag.) pygidial border and the more distinct border furrow. The latter feature is, however, shared with *M. (H.) shelvensis* Whittard (1961: 177, pl.24, figs 3) only as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suggested by Fortey and Owens (1987: 167). The wide pygidial border alone is not thought sufficient to warrant separation at the generic level. Therefore, the subgeneric status of *Quadratapyge* is retained in this paper.

Subgenus *Microparia* Hawle and Corda, 1847

Microparia (Microparia) sp.

Figure 5B

Figured specimen

One dorsal shield (lacking librigenae) of degree 2 (NI 120585) from the *Nemagraptus gracilis* Zone of the middle part of the Charchaq Group, locality 1.

Discussion

The juvenile incomplete dorsal shield of degee 2, 5.2mm long and 2.7mm wide across the base of the cranidium, shows a well vaulted transitory pygidium with ill-defined border and axis. The cranidium is as long as wide and narrowly rounded anteriorly. It tapers forwards in a parabolic curve. The cranidial outline suggests that the present form is closely allied to *M. (M.) klouceki* (Richter and Richter) (Marek 1961: 42, pl.3, figs 17, 18; also see Whittard 1952: 113, pl.32, fig. 9) and *M. (M.) plasi* Marek (1961: 44, pl.3, figs 22, 23), both from the Dobrotivá Beds (Llandeilo), Bohemia. Judging from the description and illustration given by Marek (1961), the eyes of *M. (M.) klouceki* abut each other, while those of *M. (M.) plasi* may be separated. As librigenae are not known in this form, it seems difficult for the time being to assign it to either of these two species.

Subgenus *Heterocyclopyge* Marek, 1961

Type species

Cyclopyge pachycephala Hawle and Corda, 1847, from the Černin Beds (Caradoc), Turbin, Bohemia.

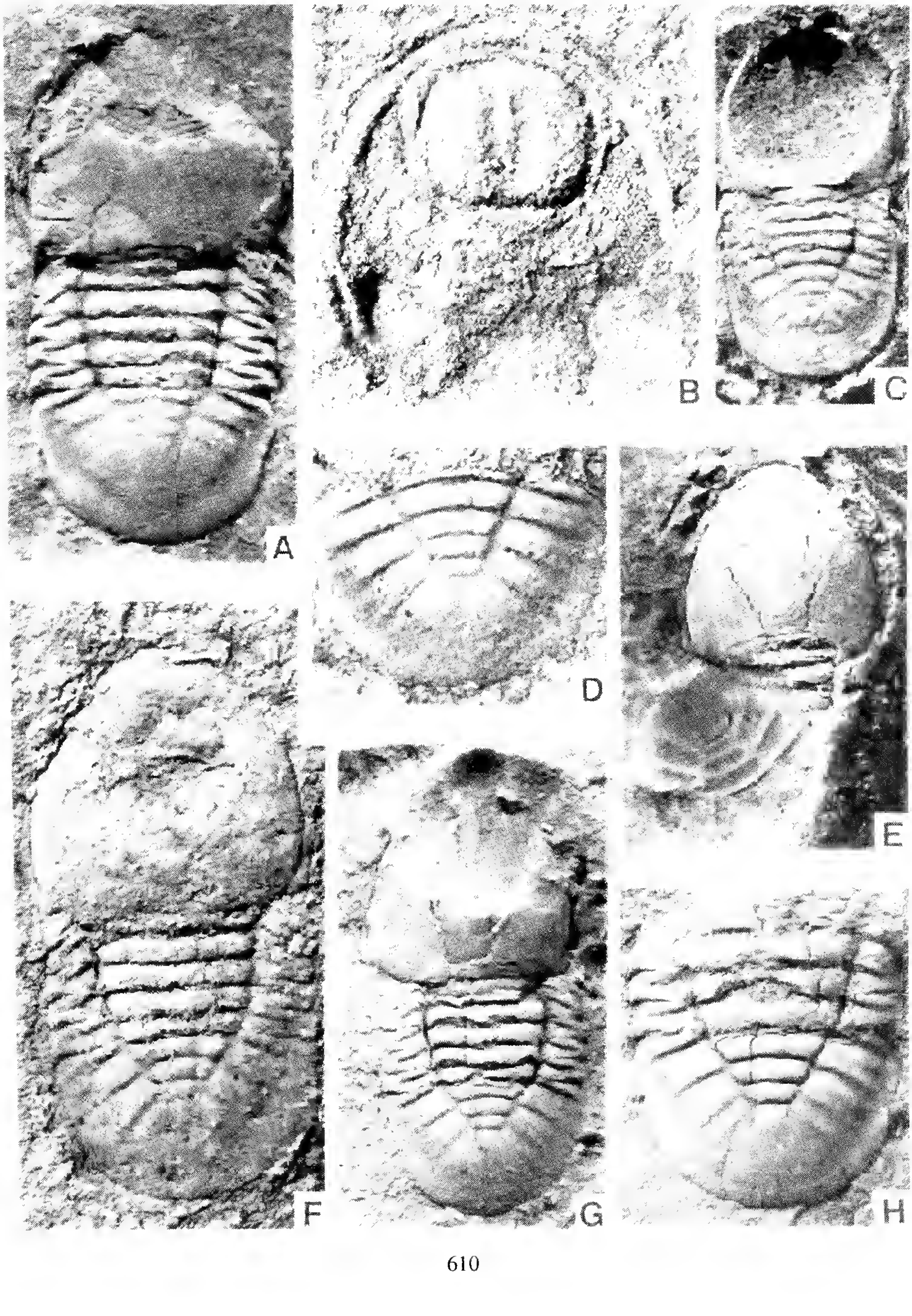
Microparia (Heterocyclopyge) abunda sp. nov.

Figures 5C, D, F–I, 6A–H, 7A, C, E, H

Etymology

Latin *abundus, a, um*, abundant, referring to the specimens of this new species which outnumber those of other cyclopygids in our collection.

◀ **Figure 5** A, E, *Pricyclopyge* cf. *binodosa longicephala* Klouček, 1916, from the *Nemagraptus gracilis* Zone of the middle part of the Charchaq Group, Loc.1; A, dorsal shield lacking librigenae, degree 1, latex cast, NI 120574, x15; E, dorsal shield lacking librigenae, degree 2, latex cast, NI 120575, x10. B, *Microparia (Microparia)* sp., from the *Nemagraptus gracilis* Zone of the middle part of the Charchaq Group, Loc.1, dorsal shield lacking librigenae, degree 2, NI 120585, x10. C, D, F–I, *Microparia (Heterocyclopyge) abunda* sp. nov., all from the *Nemagraptus gracilis* Zone, except G from the *Climacograptus bicornis* Zone, of the middle part of the Charchaq Group, Loc.1; C, dorsal shield lacking librigenae, degree 1, paratype, NI 120586, x15; D, cranidium, paratype, NI 120587, x10; F, pygidium, paratype, NI 120588, x10; G, dorsal shield lacking librigenae, paratype, NI 120589, x6; H, dorsal shield lacking librigenae, paratype, latex cast, NI 120590, x6; I, incomplete dorsal shield, paratype, NI 120591, x4.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Holotype

Incomplete dorsal shield, NI 120592 (Figure 6A), from the *Nemagraptus gracilis* Zone of the middle part of the Charchaq Group, locality 1.

Paratypes

Five incomplete dorsal shields (NI 120590, 120591, 120597, 120598, 120601), two cranidia (NI 120587, 120602), one cranidium and pygidium (NI 120596), one pygidium (NI 120588), two pygidia with attached thoracic segments (NI 120599, 120603), two incomplete meraspid dorsal shields of degree 1 (NI 120586) and degree 4 (NI 120594), and one degree 4 transitory pygidium (NI 120595) from the *Nemagraptus gracilis* Zone, and one incomplete dorsal shield (NI 120589), one cephalic doublure attached with hypostoma (NI 120593), and one pygidium and thorax (NI 120600) from the *Climacograptus bicornis* Zone, of the middle part of the Charchaq Group, locality 1.

Diagnosis

A species of *M. (Heterocyclopyge)* with straight-sided pygidium. Pygidial axis 51–55% the length (sag.) of pygidium, with three well defined rings and a triangular weakly delimited terminal piece. Pleural lobes with three pairs of furrowed pleurae.

Description

Holaspid specimens

Adult dorsal shield 8–18mm long in the collection; cranidium 46–48%, thorax 20–24% and pygidium 29% the exoskeletal length. Cranidium about as long as wide. Glabella convex, parabolic in outline, narrowly rounded anteriorly (Figure 6F), slightly convex backwards posteriorly, with maximum width attained at 38% the glabellar length in front of the posterior margin; a tiny median tubercle situated slightly posterior to the mid-length (Figure 7E). Palpebral lobe rim-like, probably meeting in front of the glabella. Posterior area of fixigena tiny, elongated-triangular. Librigenae united; cephalic doublure narrows backwards gently, surface covered with raised terrace lines subparallel to its margin; eyes poorly preserved, but indications (Figure 5G) suggest that they may probably closely approach the mid-line in front. Hypostoma (Figure 6B) trapezoid-shaped, broadly rounded anteriorly, about 80% as long as wide; middle body moderately convex, with a median ridge well defined by deep and broad longitudinal furrows on either side; anterior wing small, triangular; border furrow deep and wide; border convex, almost even in width.

Thorax of five segments, subparallel-sided (Figure 5I). Axis wide (tr.), gently convexly curved laterally, tapering moderately backwards over posterior three rings, occupying 60% the thoracic width anteriorly and 50% posteriorly; articulating half ring short (sag.), ridge-like. Axial furrow deeply incised (Figure 6A,F,H). Pleurae slightly widens backwards over the

◀ **Figure 6** A–H, *Microparia (Heterocyclopyge) abunda* sp. nov., all from the *Nemagraptus gracilis* Zone, except B from the *Climacograptus bicornis* Zone, of the middle part of the Charchaq Group, Loc.1: A, incomplete dorsal shield, holotype, NI 120592, x6; B, cephalic doublure with attached hypostoma, paratype, latex cast, NI 120593, x10; C, incomplete dorsal shield, degree 4, paratype, NI 120594, x8; D, transitory pygidium, degree 4, paratype, NI 120595, x15; E, cranidium and external mould of pygidium, paratype, NI 120596, x8; F, dorsal shield lacking librigenae, paratype, latex cast, NI 120597, x10; G, dorsal shield lacking librigenae, paratype, NI 120598, x10; H, pygidium and attached three thoracic segments, paratype, NI 120599, x7.

posterior three segments. Each pleura bluntly pointed distally (Figure 5I); fulcrum fairly close to the axial furrow; facet triangular, wide (tr.); pleural furrow deep and wide, widening adaxially.

Adult pygidium 3.3–9mm in width and 2.3–6mm in length, semicircular in outline (Figure 6H), straight-sided laterally, 63–70% as long as wide. Axis occupying 51–55% pygidial length and 40–50% pygidial width at anterior margin, slightly convex, funnel-shaped, entire, with three well defined rings and a faintly shown triangular terminal piece. Pleural lobes moderately declined towards border furrow abaxially, with three pairs of pleurae weakly outlined by shallow interpleural furrows, which successively become weaker posteriorly; pleural furrows broad and distinct, but only the first pair being deeply incised, delimiting a widely faceted anterior half pleura. Border slightly adaxially declined laterally, feebly bent down mesially, 10–20% pygidial length (sag.), sharply narrowing forwards from posterolateral pygidial corners. Border furrow shallow and broad, more faintly defined sagittally. Doublure broad (Figure 6A), up to 30% the pygidial length (sag.), narrowing forwards laterally, covered with fine terrace lines subparallel to the border furrow.

Meraspid specimens

Degree 1 dorsal shield (lacking librigenae) (Figure 5C) 4.5mm long and 2.3mm wide. Cranidium shows a proportionally slightly wider (tr.) palpebral lobe than in adult. Transitory pygidium as long as wide, parallel-sided, broadly rounded posteriorly. Axis funnel-shaped, divided into seven rings and a terminal piece. Axial furrow shallow, becoming shallower backwards. Pleural lobes include seven pairs of furrowed pleurae; the posterior three pairs of interpleural furrows very weak. Border ill-difined.

Degree 4 dorsal shield (lacking librigenae) (Figure 6C) 6.3mm in length and 3.1mm in width. Cranidium almost indistinguishable from the adult. Thorax of four segments, parallel-sided; axis wide (tr.), well defined by deep and broad axial furrows, which are gently curved laterally. Transitory pygidium 75% as long as wide, straight-sided laterally, broadly rounded posteriorly. Axis with four well defined rings and a weakly outlined terminal piece in addition to a ridge-like anterior half ring. Pleural lobe slightly vaulted, provided with four pleurae; pleural furrows distinct; interpleural furrows weak; anterior half pleura convex, broadly faceted. Border 10% the pygidial length sagittally, narrowing forwards, defined by shallow and broad furrow, which becomes fainter mesially.

Discussion

The new species bears a great resemblance to the type species *M. (H.) pachycephala*, and *M. (H.) nigra* from the Dobrotivá Beds (Llandeilo), Praha-Libeň, Bohemia, in many respects, especially in the shape of the pygidium. The type species differs in the longer pygidium (length/width ratio 74–89% vs. 63–70%), the longer axis (50% vs. 51–55% pygidial length) with more weakly incised ring furrows but better defined and posteriorly more rounded terminal piece, and the effaced pleural lobe. *M. (H.) nigra* is closely related to *M. (H.) pachycephala* with regard to the characters of the pygidal axis and pleural lobe. According to Hörbinger and Vaněk (1985: 60) the length/breadth index of the pygidium is 74%, but judging from the dimensions of the holotype given in the same paper, the figure should be greater than 75%. In this regard, therefore, the diagnostic feature of *M. (H.) nigra* appears to fall within the range of variation of the type species, indicating that both the Bohemian species might be synonymous.

The pygidium of *M. (H.) shelvensis* Whittard from the Stapeley Volcanic Group, Linley, Shropshire, England has three well marked axial rings, a weakly demarcated triangular terminal piece, three pairs of pleurae and a wide (sag.) doublure (less than 30% the pygidial length in the holotype according to Rushton and Hughes 1981: 634) as in that of the new species, but it is proportionally slightly short (60% as long as wide) with more rounded lateral margins (cf. straight-sided). The cephalon of the English species recalls that of *M. (H.) abunda* sp. nov., but possesses a glabella more bluntly rounded anteriorly, and, as pointed out by Whittard (1961: 178), its eyes reach only almost to the level of the glabellar front.

The featureless cranidium, the holotype of *Cyclopyge angustata* Cooper and Kindle (1936: 367, pl.53, figs 26, 34), from the Whitehead Formation, Percé, Quebec, Canada, is similar to the present species in outline, but the presence of its glabellar anterior tongue suggests that the eyes may well be separated in front of the glabella. As no pygidium has been referred to that Ashgill form, its generic assignment is still in doubt. However, a small pygidium identified as *Cyclopyge* sp. (Cooper and Kindle 1936: 367, pl.52, fig.14) might belong to *C. angustata* as suggested by the authors. If this were the case, *C. angustata* would be referable to *M. (Heterocyclopyge)* as the pygidium is almost identical with that of this species.

The incomplete size series as described above indicates that the morphological changes of the new species from the meraspids to the holaspids may include the deepening of the pygidial border furrow, the broadening of the pygidium, and the narrowing of the palpebral lobe. During the holaspid stage, the pygidial border gradually becomes wider and better defined, but the axial and ring furrows seem to become shallower.

Subgenus *Quadratapyge* Zhou in Zhou *et al.*, 1977

Type species

Microparia (Quadratapyge) latilimbata Zhou in Zhou *et al.*, 1977, from the Modaoxi Formation (Caradoc), Modaoxi, Taojiang, Hunan, S China.

Microparia (Quadratapyge) curva sp. nov.

Figure 7D, F,I

Etymology

Latin *curvus, a, um,* curved, referring to the backwardly arched posterior margin of the pygidium.

Holotype

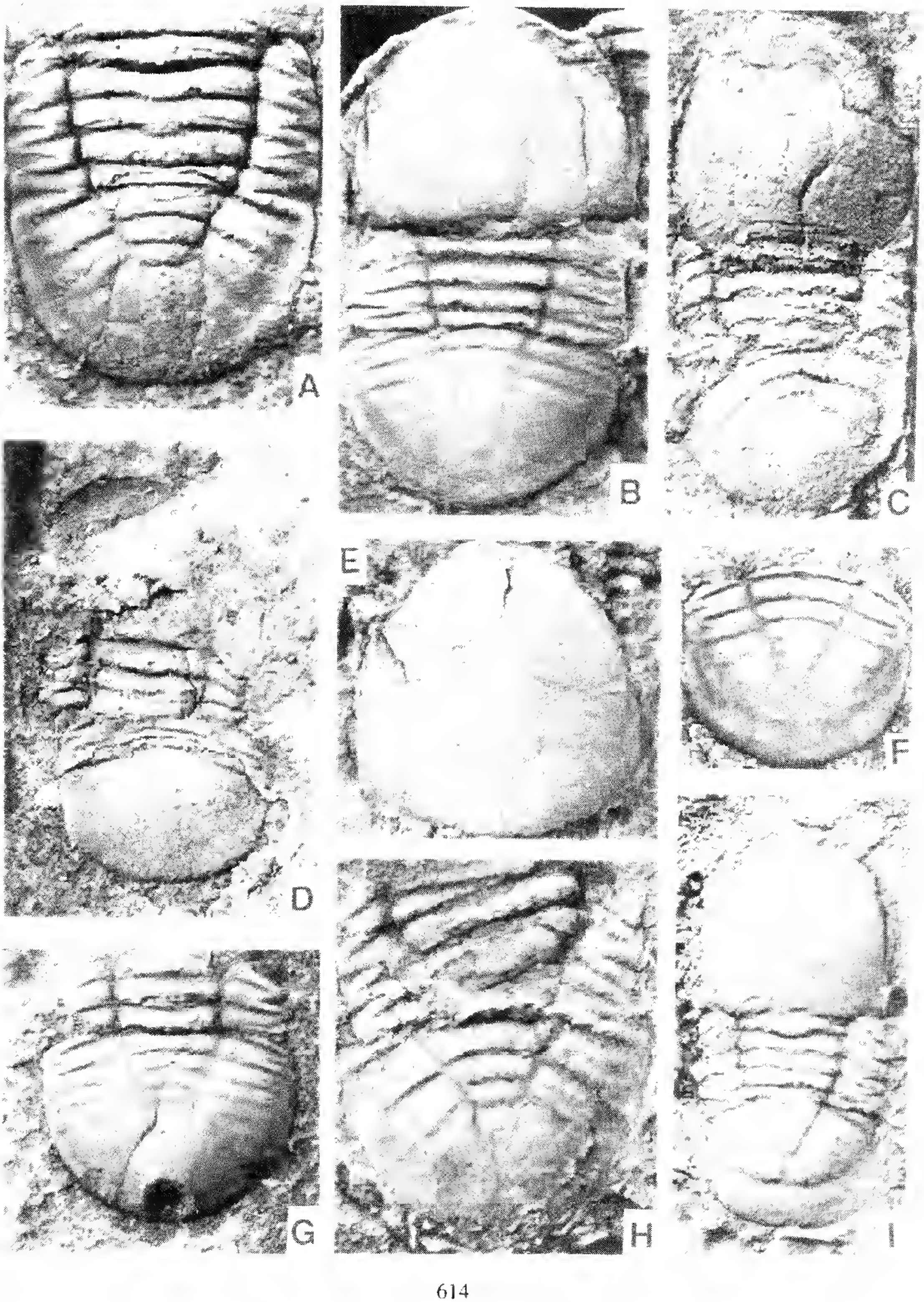
Dorsal shield lacking librigenae, NI120608 (Figure 7I), from the *Nemagraptus gracilis* Zone of the middle part of the Charchaq Group, locality 1.

Paratypes

One transitory pygidium of degree 3 with attached thorax and cephalic doublure (NI 120606) and one transitory pygidium of degree 3 (NI 120607), from the same horizon and locality as the holotype.

Diagnosis

A species of *M. (Quadratapyge)* with pygidium broadly rounded posteriorly. Axis conical in outline. Postaxial groove extending sagittally and reaching border furrow.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Description

Holaspid specimens

Dorsal shield elliptical in form, cranidium 48%, thorax 20% and pygidium 32% of the exoskeletal length. Glabella convex, parabolic, widely arcuate anteriorly, slightly longer than wide, with a tiny median tubercle located at 40% the glabellar length from rear. Axial furrow deeply incised adaxial to palpebral lobe, shallower posteriorly adaxial to the small triangular posterior area of fixigena. Palpebral lobe narrow (tr.), strip-like, gently narrowing forwards.

Thorax of five segments, parallel-sided. Axis wide (tr.), convex, tapering backwards moderately from first to third but more rapidly from third to fifth rings, occupying 55% thoracic width (tr.) anteriorly and 40% posteriorly. Pleurae narrowing forwards; pleural furrows wide and deep, widening adaxially; fulcra much closer to the axial furrows; each pleura bluntly pointed distally, with broad (tr.) triangular facet.

Pygidium subrectangular in outline, broadly rounded posteriorly, 68% as long as wide. Axis moderately convex, conical in shape, occupying 47% sagittal length and 32% anterior width of pygidium, well defined by distinct axial furrows, with three faintly defined rings and a terminal piece in addition to a ridge-like articulating half ring. Postaxial groove extending from axial tip to border furrow. Pleural lobe slightly vaulted; anterior half pleura raised, narrowing adaxially, facet occupying 70% the anterior pleural width; first pair of pleural furrows deep, other two very faint though traceable. Border crescentic in shape, straight-sided, 33% pygidial length sagittally, narrowing slowly abaxially to posterolateral pygidial corner, from there then sharply tapering forwards, well defined by distinct semicircular-extended border furrow.

Meraspid specimens

Cephalic doublure, as exhibited in an incomplete dorsal shield of degree 3 (Figure 7D), broadly rounded anteriorly, widest at sagittal line, narrowing backwards, covered with raised terrace lines subparallel to its posterior margin. Transitory pygidium of degree 3, 2.9–3.2mm wide and 2.4–2.9mm long, parallel-sided, broadly rounded posteriorly. Axis conical, including five rings which successively become faintly defined posteriorly, a tiny terminus and a ridge-like anterior half ring. Pleural lobe faceted anterolaterally, with five pairs of pleural and interpleural furrows, of which the posterior two are only weakly developed. Border 25% length (sag.) of the transitory pygidium, narrowing anteriorly. Border furrow very shallow or poorly defined. Doublure slightly wider than, or of almost equal width as, the border.

◀ **Figure 7** A, C, E, H, *Microparia (Heterocyclopyge) abunda* sp. nov., A from the *Climacograptus bicornis* Zone, C, E, H from the *Nemagraptus gracilis* Zone, of the middle part of the Charchaq Group, Loc.1; A, pygidium and thorax, paratype, NI 120600, x10; C, dorsal shield, paratype, NI 120601, x10; E, cranidium, paratype, NI 120602, x6; H, pygidium and thorax, paratype, NI 120603, x8. B, G, *Degamella* cf. *princeps* (Barrande, 1872), from the *Nemagraptus gracilis* Zone of the middle part of the Charchaq Group, Loc.1; B, dorsal shield lacking librigenae, degree 4, NI 120604, x8; G, transitory pygidium and attached thorax, degree 2, NI 120605, x10. D, F, I, *Microparia (Quadratapyge) curva* sp. nov., from the *Nemagraptus gracilis* Zone of the middle part of the Charchaq Group, Loc,1; D, transitory pygidium attached with thorax and cephalic doublure, degree 3, paratype, NI 120606, x10; F, transitory pygidium of degree 3, paratype, NI 120607; x10; I, dorsal shield lacking librigenae, holotype, NI 120608, x8.

Discussion

Only two species have been assigned to *M. (Quadratapyge)*, the type species *M. (Q.) latilimbata* Zhou (in Zhou *et al.* 1977: 230, pl. 69, figs 14–16), and *M. (Q.) chedaoensis* Zhou and Dean (1986: 761, pl. 61, figs 6, 10, 11, 13, 16) from the lower part (late Llandeilo-basal Caradoc) of the Chedao Formation, Chedao, Huanxian, Gansu, northwest China. Both differ from the new species in the straight posterior pygidial margin, the broadly rounded posterior end of axis and the absence of a postaxial groove. Furthermore, the pygidial axis is much wider (40–50% the pygidial width anteriorly) and the median glabellar tubercle is more forwardly placed (in front of the glabellar centre) in the type species. The pygidial axis occupies 33% the pygidial width anteriorly in *M. (Q.) chedaoensis*, a feature shared with the present species, but its pygidial border is narrower (sag.) (20% the pygidial length) and the median tubercle is situated in the centre of the glabella. The pygidial border furrow is much more faintly defined, the axial furrow is shallower, and the postaxial groove is absent in the transitory pygidium of this new species as compared with the adult specimens.

Genus *Degamella* Marek, 1961

Type species

Aeglina princeps Barrande, 1872, from the Dobrotivá Beds (Llandeilo), Svatá Dobrotivá, Bohemia.

Degamella cf. *princeps* (Barrande, 1872)

Figure 7B, G

Figured specimens

One dorsal shield (lacking librigenae) of degree 4 (NI 120604), and one degree 2 transitory pygidium and thorax (NI 120605), from the *Nemagraptus gracilis* Zone of the middle part of the Charchaq Group, locality 1.

Description

Meraspid specimens

Dorsal shield of degree 4, 8.8mm long, oval in outline. Glabella gently convex, subcircular in form, wider than long, extremely broad-rounded anteriorly, with an elongated median tubercle situated at 60% the sagittal length from the posterior margin. Axial furrow shallow posteriorly, deep adjacent to palpebral lobe. Palpebral lobe band-like, narrowing forwards, posteriorly placed, about 40% the glabellar length. Posterior area of fixigena tiny, triangular. Thorax of four segments, subparallel-sided. Axis convex, half the thoracic width (tr.) anteriorly, tapering backwards. Axial furrows deep. Pleurae broadly faceted abaxially, distal ends bluntly pointed. Pleural furrows deep and wide. Transitory pygidium weakly vaulted, 64% as long as wide, semicircular in outline. Axis flatly convex, conical, 76% the length and 22% the anterior width of the pygidium, entire, divided into six rings and a narrowly rounded terminal piece, of which only anterior two are well defined. Pleural lobes including three pairs of feebly marked pleurae in addition to two well demarcated anterior future thoracic segments. Border flattened. Border furrow shallow and wide. Doublure about 19% the length of the transitory pygidium sagittally, narrowing gently abaxially, covered with subparallel and closely spaced terrace lines, anterior margin convexly arched forwards along the sagittal line and almost reaching the terminal end of the axis.

Degree 2 transitory pygidium 2.7mm long, 77% as long as wide. It is more vaulted, with an axis funnel- rather than cone-shaped, and the axial, border, and pleural furrows are more weakly defined on the true pygidium than in degree 4.

Discussion

D. princeps (Barrande) was described in detail by Marek (1961: 46, pl.4, figs 1–7), but no ontogenetic series has been established except a specimen of degree 3 (Marek, 1961:48), which has been recorded by Barrande (1872, pl.14, figs 6, 7). It shows an oval dorsal shield with a subcircular, anteriorly very widely rounded glabella, and an indistinctly segmented pygidium, in contrast to an elliptical carapace with an elongated, anteriorly narrowing rounded glabella and almost smooth pygidium both in axis and pleural lobe in mature specimens, but almost identical with the present degree 4 specimen. Moreover, both forms share a very distinctive character in cyclopygids – the mesially upcurved pygidial doublure. We therefore consider the present specimens either referable or at least very close to the type species of *Degamella*. Marek (1961) separated the type species into two subspecies, that is, *D. princeps princeps* and *D. princeps praecedens* (Klouček 1916), but the latter, though from an earlier horizon (the Llanvirn Šárka Beds) in Bohemia, is in fact no different from the former, as indicated by Fortey and Owens (1987: 160).

The meraspid degree 3 and 5 and young holaspid dorsal shields of *D. nuda* (Whittard, 1961: 180, pl.24, figs 5–10) have been well described and figured from the Llanvirn of Shropshire, England. It is interesting to note that the immature specimens also exhibit a shorter carapace and a broader glabella as in the type species and the present form, suggesting that the elongation of the exoskeleton and glabella may be the most prominent morphological change which took place during the ontogeny of the known species of *Degamella*.

Genus *Sagavia* Koroleva, 1967

Type species

Sagavia felix Koroleva, 1967, from the Llandeilo of northern Kazakhstan.

Sagavia felix Koroleva, 1967

Figure 8A–J

Sagavia felixa Koroleva, 1967: 82, pl. 10, figs 2–4.

Sagavia felixa Koroleva, Abdullaev, 1972: 107, pl. 46, fig. 9.

Sagavia felixa Koroleva, 1982: 127, pl. 26, fig. 7.

Sagavia sp.1, Koroleva, 1982: 130, pl. 26, fig. 7 (as pl. 10, fig. 3 of Koroleva, 1967)

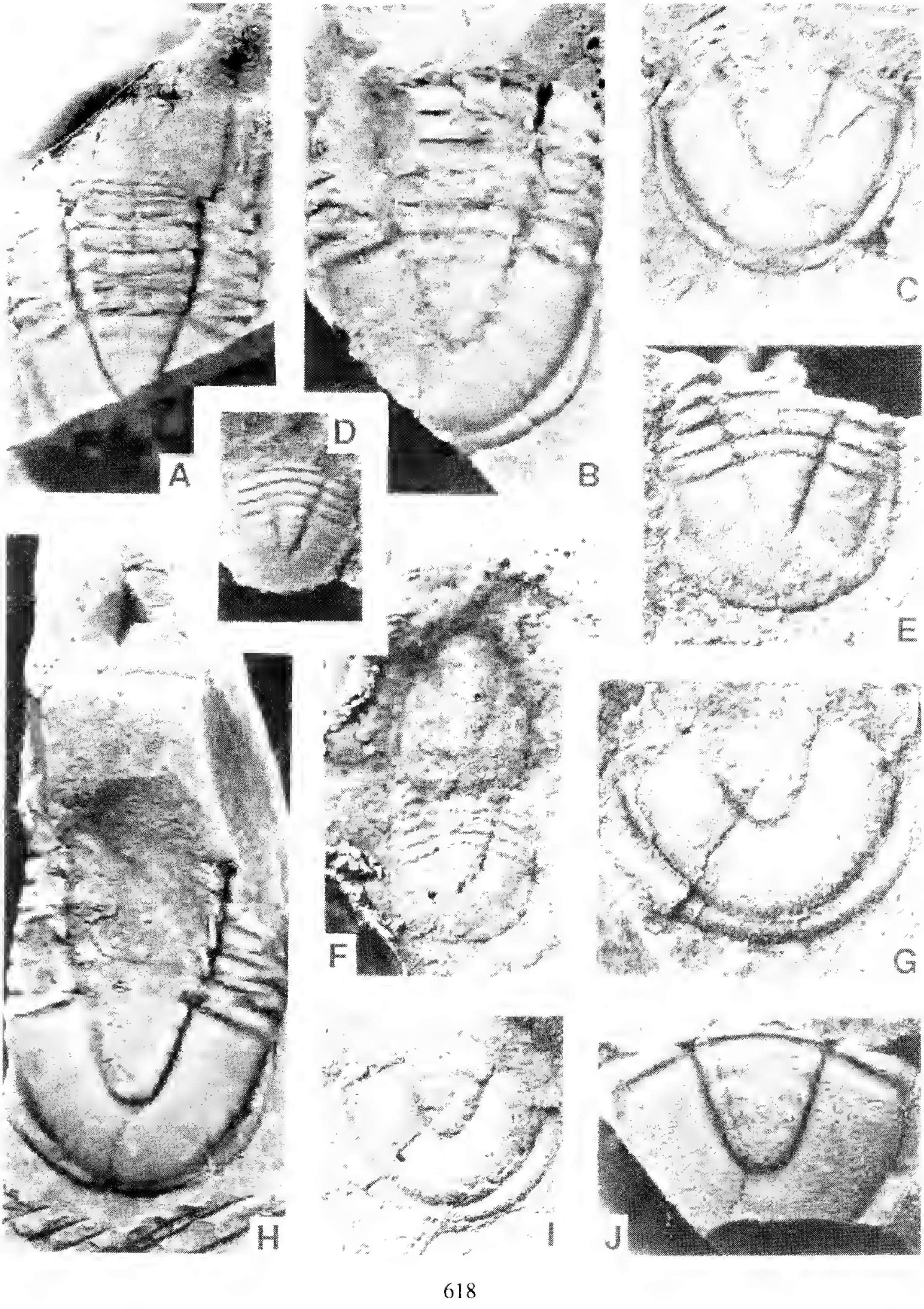
Sagavia felix Koroleva, Fortey and Owens, 1987: 177.

Holotype

Incomplete dorsal shield, K–98–2, figured Koroleva (1967, pl.10, fig.2; 1982, pl.26, fig.4), from the Tselinograd horizon (Llandeilo), right bank of the Sagi River, northern Kazakhstan.

Figured specimens

One fragmentary dorsal shield (NI 120609), one pygidium attached with incomplete thorax and cephalic doublure (NI 120616), one pygidium and thorax (NI 120610), four pygidia (NI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120611, 120615, 120617, 120618), one degree 1 dorsal shield (lacking librigena) (NI 120614) and two degree 1 transitory pygidia (NI 120612, 120613) from the *Nemagraptus gracilis* Zone of the middle part of the Charchaq Group, locality 1.

Description

Holaspid specimens

Cranidium incompletely preserved. Glabella broadly arcuate laterally, well defined by deep and broad axial furrows. Palpebral lobe long, narrow (tr.), strip-like. Posterior area of fixigena tiny, triangular. Librigena occupied mainly by large eyes; doublure wide (sag.), narrowing backwards, covered by subparallel fine terrace lines. Hypostoma fragmentary, but indicating an outline of reversed trapezoid; surface overspread with terrace lines subparallel to the nearest margin.

Thorax of five segments, broadly curved but almost parallel-sided laterally. Axis gently tapering backwards, 50% and 40% the thoracic width on the first and fifth segments respectively. Pleurae narrowing forwards; each pleura extending abaxially for about 30% its width to fulcrum, then curving gently downwards into a trucated distal extremity; pleural furrow wide and deep; facet wide (tr.), triangular.

Pygidium semioval in form, moderately vaulted, 51–81% as long as wide. Axis entire, tapering backwards, rounded posteriorly, 45–55% the length and 37–44% the width of pygidium, consisting of three rings, a rounded terminal piece and an articulating half ring; ring furrows shallow and wide. Axial furrow deep and broad. Pleural lobes decline gently towards the border furrow; anterior half pleura raised, widening abaxially, faceted anterolaterally, well defined by deep first pair of pleural furrows; faint indications of second and third pairs of pleural furrows present only on internal moulds. Border convex, widest at posterolateral corner, from where it narrows anteriorly and posteriorly. Border furrow broad and deeply incised.

Surface of testaceous thorax and pygidium covered with wide-spaced raised lines, which are transverse on axis, subparallel to lateral margin on thoracic pleurae, and curved convexly forwards on pleural lobe of pygidium.

Meraspid specimens

Degree 1 dorsal shield (Figure 8F) 4.9mm long. Glabella gently arcuate laterally, narrowly rounded anteriorly, 74% as long as wide. Palpebral lobe long, wire-like, slightly narrowing forwards. Thorax of one segment. Pleura faceted, shortly pointed abaxially, with deep and wide pleural furrow. Transitory pygidium 1.8–2mm in length, as wide as long, parallel-sided, broadly rounded posteriorly. Axis about 70% pygidial length, tapering backwards sharply, composed of four well marked and three faintly defined rings and a narrowly rounded terminus. Axial furrow becomes shallower posteriorly. Pleural lobe slightly vaulted, with seven pairs of pleural and six pairs of interpleural furrows; posterior two pairs of pleural and

◀ **Figure 8** A–J, *Sagavia felix* Koroleva, 1967, from the *Nemagraptus gracilis* Zone of the middle part of the Charchaq Group, Loc.1; A, incomplete dorsal shield, NI 120609, x4; B, pygidium and attached thorax, NI 120610, x5; C, pygidium, NI 120611, x4; D, E, transitory pygidia of degree 1, NI 120612, 120613, x10, x15; F, dorsal shield lacking librigenae, degree 1, NI 120614, x10; G, pygidium, NI 120615, x8; H, pygidium attached with incomplete thorax and cephalic doublure, NI 120616, x4; I, pygidium, NI 120617, x5; J, incomplete pygidium, NI 120618, x5.

interpleural furrows only faintly shown. Border defined by shallow furrow, narrow (sag.), widest posterolaterally, narrowing anteriorly to, and confluent with, anterior half pleura of fifth pleura.

Discussion

Since the type species *S. felix* was established by Koroleva (1967), a single pygidium has subsequently been referred to it by Abdullaev (1972) from the late Ordovician of the Bukantau Mts, Uzbekistan. The new material agrees well with the original specimens, and is also considered as referable to the species. The pygidium of the holotype is 77% as long as wide with the axis about 55% the pygidial length. The figures fall within the range of variation shown in our specimens.

Four other species from Central Asia have been assigned to the genus *Sagavia*: *S. modica* Koroleva (1967: 83, pl.10, figs 5, 6; 1982:129, pl.26, figs 5, 6), *S. novakellaformis* Koroleva (1982: 30, pl.26, fig.9) and *S. heterocyclopygeformis* Koroleva (1982: 32, pl.26, fig.10) from the Middle Ordovician (Llandeilo-Caradoc) of northern Kazakhstan, and *S. elongata* Petrunina (in Repina *et al.* 1975: 191, pl.33, figs17, 20–23) from *Kielanella-Tretaspis* beds of Ulugtay District, south Tien-Shan. All these species were separated largely on the basis of different proportions of the pygidial width to length and the pygidial axis to the pygidium, but, as noted by Fortey and Owens (1987: 179), they all have well defined pygidial axes and posterolaterally widening pygidial borders as in the type species. In specimens of these four species, the length/width ratio of the pygidium varies from 60% to 80%, and the length of the pygidial axis is 50–58% the pygidial length, almost comparable with the range of intraspecific variation in *S. felix* as indicated by the present material. It seems likely that these Central Asian species may be either a group of species closely related to, or even conspecific with, the type species.

Sagavia glans Fortey and Owens (1987: 177, Fig. 54a–c) from the Pontyfenni Formation (late Arenig), Pontyfenni, South Wales has been considered as a primitive form by the authors; it is characterised by the pygidial axis being poorly defined posteriorly and the pygidial border steadily widening posteriorly.

Judging from the present material, morphological changes that took place during the ontogeny of *S. felix* are minimal, including only the deepening of the border furrow and posterior axial furrow of the pygidium. Following the successive release of the anterior segments to the thorax, the transitory pygidium becomes proportionally shorter (sag.); it is 45% the exoskeletal length in the meraspid degree 1, but in the holaspid pygidium the corresponding figure is 36%.

ACKNOWLEDGEMENTS

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Guide to Authors

Subject Matter:

Reviews, observations and results of research into all branches of natural science and human studies will be considered for publication. However, emphasis is placed on studies pertaining to Western Australia. Longer papers will be considered for publication as a Supplement to the *Records of the Western Australian Museum.* Short communications should not normally exceed three typed pages and this category of paper is intended to accommodate observations, results or new records of *significance*, that otherwise might not get into the literature, or for which there is a particular urgency for publication. All material must be original and not have been published elsewhere.

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