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Cover
Varanus storri ocreatus, named in honour of Dr Glen Storr. Illustrated by Jill Ruse.

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OBITUARY

Glen Milton Storr

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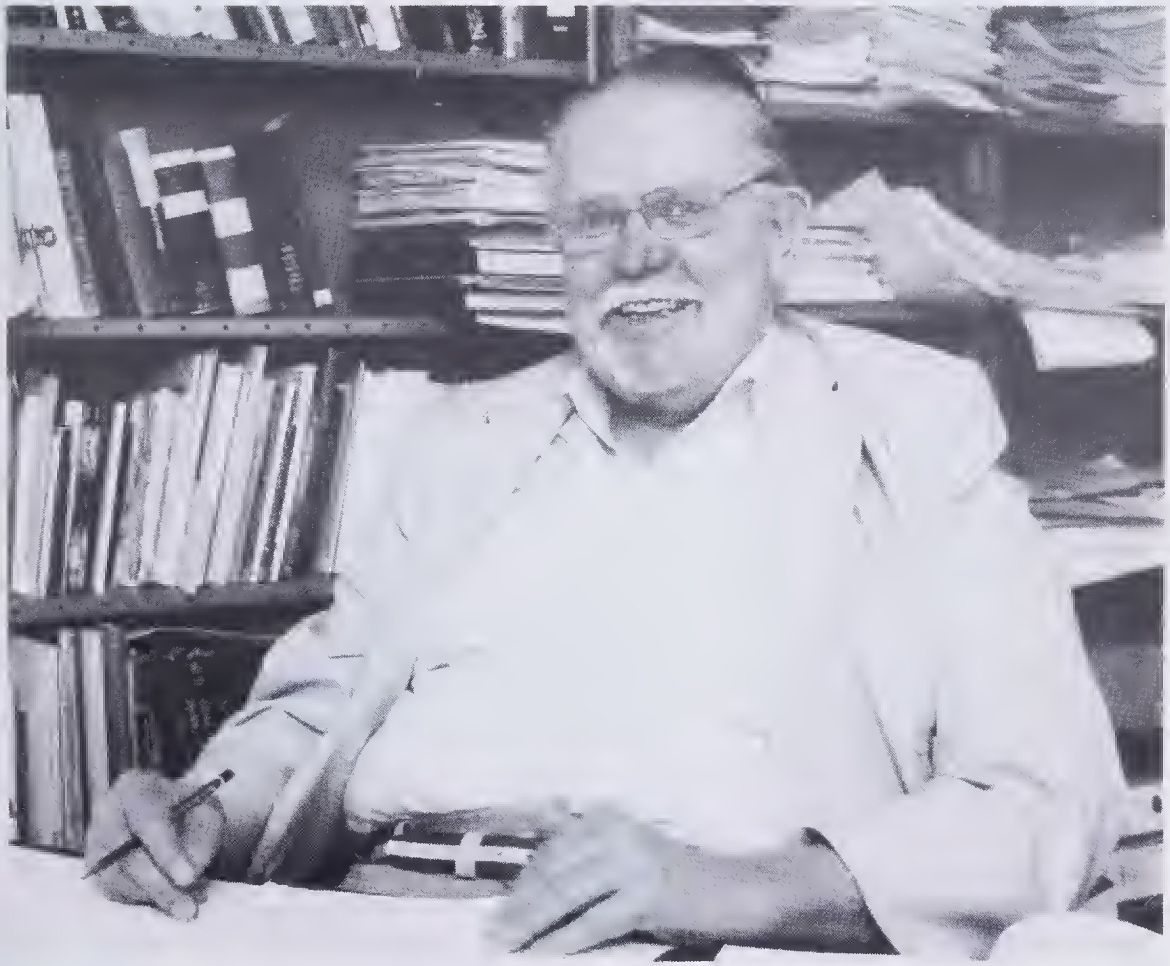

Glen Storr died at home early on the morning of 26 June 1990 while reading his newspaper. As usual he had assembled his work from the night before in readiness for the drive to the Museum. His retirement in 1986 had not changed his total dedication to his work and he still came in to the Museum three days a week.

Glen was born in Adelaide, South Australia, the eldest of three children. He grew up a city boy as his father was a master plumber and later a traffic inspector in Adelaide. It was probably his grandfather, a country blacksmith with an interest in wildlife who kindled Glen's boyhood interest in natural history. His sister Betty recalls him spending his pocket money on small bird books instead of lollies.

He attended the Cowandilla Public School and went on to Adelaide High School, obtaining his Leaving Certificate in 1938. In 1939 he joined the South Australian Lands

Department as a cadet and was articled to various Licenced Surveyors. In the course of his fieldwork his interest in natural history was further stimulated and he started to make notes, particularly on birds. In 1942 he enlisted in the Australian Imperial Forces and served from 1943-45 as an artilleryman with the Ninth Field Regiment in Queensland and New Guinea.

After returning from the war, Glen qualified as a Licenced Surveyor in 1946 and worked for the South Australian Lands Department until 1948. In August that year he arrived in Cooktown, northern Queensland for a two week holiday which finished up as a year-long stay. During this year Glen's life-long interest in documentation of Queensland birds began. In 1949 he returned to South Australia where he resumed surveying and met ornithologist Dominic Serventy through Herbert Condon, Curator of Birds at the South Australian Museum. After accompanying Dr Serventy to Bass Strait in 1952 to study the Short-tailed Shearwater, Glen decided to exchange surveying for a career in biology.

In 1953 he moved to Western Australia, where his sister had settled with her husband, and enrolled at the University of Western Australia. He graduated with a first class BSc (Hons.) degree in 1958 and in 1960 was awarded a PhD. His doctoral disseration, "Some field aspects of nutrition in Quokka *Setonix brachyurus*", was one of the pioneering ecological studies of Rottnest Island. Elegantly economical in style, it is regarded as a baseline study and is a testimony to the breadth of his biological skills (Glen was an excellent botanist). He continued with postdoctoral research on kangaroos in the Pilbara until appointed Assistant Curator (reptiles and amphibians) in the Department of Vertebrate Zoology of the Western Australian Museum in May 1962. He brought with him a collection of about 5000 reptiles, collected during his work with the University. On the resignation of G.F. Mees in 1963, Glen was appointed Curator (birds, fishes, reptiles and amphibians). In 1965 the fish collection was transferred from his care and he became Curator of Ornithology and Herpetology, the position he held until retirement in 1986. Glen never applied to become a Senior Curator; he believed that, as a bachelor, he was paid enough and as a matter of conscience he would not seek to be paid more. He was made an Honorary Associate of the Museum on retirement.

Why did Glen turn away from a promising career as an ecologist, where the breadth of his biological knowledge may have been more extensively used, and opt to dedicate his life to taxonomy? In 1959 and 1960 he visited the Houtman Abrolhos Islands to assess the possibility of undertaking comparative ecological studies of island and mainland reptile populations. His conclusion was that ecological work of this nature was not possible with the current inadequate state of reptile taxonomy and his first priority should be to sort out the alpha taxonomy of Western Australian reptiles.

Given that Western Australia covers about a third of the continent, the task was a daunting one, as Glen realised, observing "Gould knew more about Australia's birds in 1860 than we know of Australia's reptiles in 1960". He set about an active programme of field collecting until ill-health overtook him in 1970 (he was an inveterate chain-smoker). In 1971 he was hospitalized and nearly died, being left with impaired lung-function and unable to walk more than a short distance without becoming short of breath. Thereafter, Glen considered that he was living on borrowed time with every day a bonus, and this doubtless influenced how he approached achievement of his goals. He totally dedicated his life to work, tackling reptile taxonomy by day and bird distribution by night and at weekends. Paper after paper was churned out, each wonderfully concise to the point of being almost terse. He steadfastly refused to concede to pleas by colleagues, referees and editors to expand his papers to include fuller discussions and more biological information. The result, however, is his remarkable achievement of over 200 publications in which a similar number of taxa are described (see attached publications list). Glen's legacy to herpetology is a published taxonomy of the reptiles of Western Australia, unequalled in other Australian states, culminating in the series of handbooks coauthored with L.A. Smith and R.E. Johnstone. They had just completed a revision of the skink book before his death and the final, as yet unpublished, volume on turtles and crocodiles, will be completed and published by his coauthors.

Under Glen, the Museum's reptile collection increased from about 12,000 specimens in 1962 to about 100,000 in 1990. Its value lies not only in its comprehensiveness, but in the quality and accuracy of the data associated with each specimen. The register was fully computerized in 1984.

Glen's other major contribution was to Australian ornithology. Few people were aware that for most of his working life he undertook continuous searches of the literature and unpublished notes of fieldworkers. The result was the compilation of thousands of pages of meticulous notes on distribution, ecology, abundance, habitat, movements and taxonomy. This vast database was used in part for his publications "List of Queensland Birds", "Birds of the Northern Territory" and his eight regional avifaunas of Western Australia, publications which have been extensively drawn on by other authors. In his 1974 review of "List of Queensland Birds", Shane Parker (*S. Aust. Orn* **26**: 146-148) writes "Although this is ostensibly a list of the birds of a single State, it is to my mind one of the most important works ever published on the distribution of Australian birds. Its value as a basis to systematics and as a source of problems for further investigation is enormous". The culmination of Glen's work on birds will be a handbook of Western Australian birds, a project that was well advanced at the time of his death and which will be completed by R.E. Johnstone.

In enumerating Glen's remarkable achievements, recognition should be given to the vital rôle played by his two dedicated technical officers Laurie Smith and Ron Johnstone. As Glen was unable to go into the field after 1970 they continued his fieldwork programme and became his eyes and ears in the bush. Under his demanding tutorship, they became amongst the most professional and competent naturalists in the State. Apart from this they also ably supported him in the laboratory and did much to shield him from administrative duties and other diversions from research.

Glen was extremely generous with his time and knowledge. Well versed in Latin and Greek he was an expert on nomenclature (despite his noncompliance with some minor aspects of the "Code") and readily provided advice to those who sought it. He also inspired and encouraged a new generation of naturalists. In addition to his longstanding friend, W.H. Butler, they included J.R. Ford, A.S. George, J. Dell, M. Peterson, N.

Kolichis, P.J. Fuller, G. Harold, P. Griffin, B. Maryan, J. Smith, S. Wilson and D. Knowles.

The intellectual contribution Glen made to the Division of Natural Science, and to the Museum as a whole, will be sadly missed. Particularly memorable are the lunchtime conversations over which he presided. These frequently left one aghast at the man's amazing memory and encyclopedic knowledge over a huge range of topics, of which biology was but one. These discussions also left one with the realisation that with his death a whole unique perspective on the ecology of Western Australia would be lost. He had in fact promised me that when he completed his current projects, he would produce zoogeographic syntheses. Unfortunately much of this information must now remain part of our memories of many lunchtime discussions.

Glen had a very cheerful disposition and also a great sense of humour. He claimed to have a recurring dream that he was a champion pole-vaulter — a marvellous image considering his 18 stone frame!

Despite his intelligence, Glen was not mechanically-minded. Ron Johnstone recalls "I once walked into his lab. to find he had pulled his entire microscope to pieces to replace a blown globe in the light source. On hearing my entry he looked up with a globe in his hand and exclaimed, 'Where does this bloody thing go?' He also confessed to me once that he never used the heater in his car because its operation remained largely a mystery. Even his old stapler, that required three independent actions to fill, always beat him hands down".

He was a lover of ballet and an avid and most knowledgeable follower of most sports, particularly football and cricket. He never normally took recreational leave and if he did not appear at work it was a sure sign that there was a cricket test on television, one of the few diversions he allowed himself. Remarkably, the official record shows that apart from 30 days absent from work in 1971 when he nearly died, Glen only took two days sick leave in his entire career, one in 1962 and one in 1982!

Sadly, in his lifetime Glen received little official recognition for his work. However, the legacy of his published contribution to herpetology and ornithology stands and as time goes on he will undoubtedly become recognised as one of Australia's great taxonomists.

P.F. BERRY

COMPLETE LIST OF PUBLICATIONS BY G.M. STORR

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A replacement name for *Buprestis scalaris* Gory & Laporte (Coleoptera: Buprestidae)

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Abstract

Diadoxus regius nomen novum is proposed as a replacement name for *Buprestis scalaris* Gory & Laporte, 1838 which is a junior primary homonym of *B. scalaris* Boisduval, 1835. *Buprestis scalaris* Gory & Laporte has its nomenclatural history discussed and is designated type species of the genus *Diadoxus* Saunders, 1868. *Diadoxus regius* is figured.

Gory & Laporte (1838:141) described and illustrated (Pl. 35, figure 193) *Buprestis scalaris* from an indeterminate number of specimens from "Nouvelle-Hollande," in the collection of Mr. Children ("Du cabinet de M. Children"). Horn & Kahle (1935:42) indicate the John George Children collection was auctioned by J.C. Stevens of London, but the present location of the syntype/s is unknown. Saunders (1868:4-5) transferred *B. scalaris* Gory & Laporte and *Stigmodera erythrura* White, 1846 to the genus *Diadoxus,* when he defined/diagnosed the latter through redescription of these two species. Since a type species for *Diadoxus* has not been formally designated, I take this opportunity to designate *Buprestis scalaris* Gory & Laporte, 1838 as type species of *Diadoxus* Saunders, 1868.

Apparently, Gory & Laporte (1838) forgot that Boisduval (1835: 89-90) had previously described a different Australian species as *Buprestis scalaris,* based on an indeterminate number of specimens from "Nouvelle-Hollande" in the collections of Messrs Dejean and Gory. The *B. scalaris* Boisduval female lectotype is located in the Museum National d'Histoire Naturelle, Paris, based on the holotype designation by Barker (1986:9). Boisduval certainly considered his description as a generic reassignment (and possibly as a redescription), since he clearly attributed the authorship of this taxon to Dejean (1833:79) by listing the latter's catalogue name, *Polychroma scalaris,* as a synonym. However, Dejean's name is a nomen nudum. *Buprestis scalaris* Boisduval was first transferred to *Stigmodera (Castiarina)* by Gory & Laporte (1837:40) who listed it as a synonym under the unavailable name *Stigmodera crucigera* Hope, [1836] even though the former species name would have had priority had the latter been validly described. Thus *B. scalaris* Boisduval has priority over *B. scalaris* Gory & Laporte.

The two known 'synonyms' of *B. scalaris* Gory & Laporte, that also must be considered as potential replacement names, are *Anthaxia erichsoni* Hope, [1836] and *Diadoxus scalaris* var. *blackburni* Obenberger, 1923. *Anthaxia erichsoni* Hope was 'described' in the pamphlet on Australian Buprestidae circulated by the Rev. F.W. Hope

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in 1836. Hemming & Noakes (1958) note that this pamphlet was declared unavailable for the purposes of nomenclature by the International Commission on Zoological Nomenclature, through publication of Opinion 234 in 1954. Thus *A. erichsoni* was first published as a junior synonym of *Diadoxus scalaris* (Gory & Laporte) by Saunders (1868) and is unavailable under the current International Code of Zoological Nomenclature (Article 11e). Obenberger (1923:72) described *D. scalaris* var. *blackburni* for some colour pattern variants from "Queensland", based on an indeterminate number of specimens ("some few specimens of my collection") now housed in the National Museum, Prague, Czechoslovakia. Under the current International Code of Zoological Nomenclature (Article 45g), the status of 'varietal' names, as the third name in a trinomen, is open to interpretation. Obenberger (1923) described subspecies as well as varieties, thus clearly differentiating the ranking of these terms. Subsequent citations by Obenberger and other authors did not find *D. scalaris* var. *blackburni* treated as a subspecies. Also, Obenberger did not state, in any of his numerous publications during his long career, that he considered the terms 'variety' and 'subspecies' interchangeable. Therefore, I consider '*blackburni* Obenberger' to be infrasubspecific, under Article 45g

Figure 1 Dorsal view of *Diadoxus regius* Peterson.

(ii, 1) of the International Code of Zoological Nomenclature, and unavailable for the purposes of nomenclature.

Since *B. scalaris* Gory & Laporte is a junior primary homonym of *B. scalaris* Boisduval, and none of the supposed synonyms of the former are available for the purposes of nomenclature, I propose the following replacement name: *Diadoxus regius* nomen novum for *Buprestis scalaris* Gory & Laporte, 1838.

Diadoxus regius (Figure 1) is named thus, for being the largest and most spectacular of the described *Diadoxus* taxa. This species occurs in all Australian mainland states.

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A new cave-dwelling cockroach from Western Australia (Blattaria: Nocticolidae)

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Abstract

A new cavernicolous cockroach, *Nocticola flabella* sp. nov. is described.

Introduction

Three species of *Nocticola,* namely *babindaensis* Roth, *australiensis* Roth, and one unnamed are found in Queensland, Australia (Roth 1988). In this paper I describe a new cavernicolous species of *Nocticola* from Western Australia. Most of the specimens were collected by Dr. W.F. Humphreys of the Western Australian Museum, Perth (WAMP) and sent to me by Dr. D.C.F. Rentz of CSIRO. I received one specimen from Dr. M.R. Gray of the Australian Museum, Sydney (AMSA).

In addition to describing the new taxon and providing a key to the Australian males of the genus, I am transferring *Paraloboptera rohini* Fernando to *Nocticola.*

Systematics

Nocticola flabella, sp. nov.

(Figures 1-8)

Holotype: ♂, Cape Range, Western Australia, Cave C118, 16.viii. 1988, Humphreys *et. al.,* Western Australian Museum, Reg. No. 88/2682.

Paratypes: Cape Range, Western Australia. WAMP: Cave C169, one ♀, 31.x.1987, R. Wood and M. East, W.A. Mus. Reg. No. 88/2683-4. The following were collected by Humphreys *et al.*: Cave C169, one nymph, 13.viii.1988, W.A. Reg. No. 88/2665; Cave C118, one nymph, 5.ix.1988, W.A. Mus. Reg. No. 88/2672; Cave C103, one ♀, 7.ix.1988, W.A. Mus. Reg. No. 88/2673-4, one ♀, 1 nymph (Area D), 15.viii.1988, W.A. Mus. Reg. No. 88/2667-8; Cave 167, one ♂, one ♀, 10.viii.1988, W.A. Mus. Reg. No. 88/2663-4. AMSA: Cave C126, one ♂, dark zone in litter soil floor, 19.ix.1988, S. Eberhard and M. Gray.

All specimens were originally preserved in alcohol and, except for the AMSA ♂, were cleared and mounted on slides in Permount. Figures 1-7 were drawn from slide mounted specimens.

The following information regarding the caves in which *N. flabella* was collected was kindly supplied by Dr. W.F. Humphreys:

C103 (Trionomo: 22°07′27″S 114°59′21″E). About 60 m deep with two vertical descents leading to some horizontal development where temperature was 23°C, 95% RH, and 38% soil water. Little litter in the caves and all contain many species of isopods and troglobitic millipedes.

C118 (not named: 22°09′21″S 113°59′27″E). A dry steam bed containing water-smoothed pebbles runs between mud-banks on cave floor before bifurcating to a lateral

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exit and two sump holes. Temperatures ranged from 17°C to 25.2°C with relative humidities varying from 63% to 100%. In addition to *N. flabella,* this cave contains large populations of earthworms, oniscoid isopods and white millipedes. At least 12 invertebrate species are present and small mammals have also been seen.

C167 (Spiral: 22°09'09"S 113°59'39"). Narrow pothole ends in a horizontal lead (walking height) which bifurcates. About 40 m deep and 30 m horizontal extent; at bottom 27°C, 100% RH, 0.5% CO_2. Troglobites are only found in the range at 12% soil water in mudbanks.

C169 (not named: 22°06'2"S 114°00'27"E). Narrow pothole perhaps 35 m deep opening into two chambers connected by a tiny hole into the chamber where *N. flabella* was found. Chamber was 28°C, 98% RH, soil moisture 26.8%, with almost no organic debris.

Diagnosis (see also key below)

Cavernicolous. Male: Eyes absent. Tegmina reduced, fan-shaped, hind wings absent. Anteroventral margin of front femur with a row of minute spines, terminal spines absent, pulvilli and arolia absent, tarsal claws symmetrical, minute. Abdominal terga unspecialized. Female: Eyes absent. Apterous.

Description

Male. Head exposed, eyes absent (Figure 1). Pronotum elongate, relatively narrow (Figure 1). Tegmina greatly reduced, fan-shaped, coriaceous, veins absent, surface with some minute spicules; hind wings absent (Figure 1). Legs very long, femurs uniformly slender; anteroventral margin of front femur with a row of minute spinules, terminal spines absent (Type C_0); pulvilli and arolia absent, tarsal claws minute, symmetrical (Figure 7). Abdominal terga unspecialised. Supraanal plate broad, sides weakly angled, corners broadly rounded, medial region of hind margin indented; right and left paraprocts similar, lightly sclerotized plates (Figure 3). Subgenital plate asymmetrical with hind margin concavely excavated, styles absent (Figures 4, 5; in Figure 4 the hind margin of the plate is weakly concave and flattened; in Figure 5 the mounting medium was thicker with less distortion of the plate). Genitalia as in Figure 4: genital hook on left side, other phallomeres complex. Colorless except for pale amber around the mouthparts, and darker amber tegmina (Figure 8).

Female. Apterous. Eyeless (Figure 2). Supraanal plate convexly rounded (Figure 6). Subgenital plate valvular.

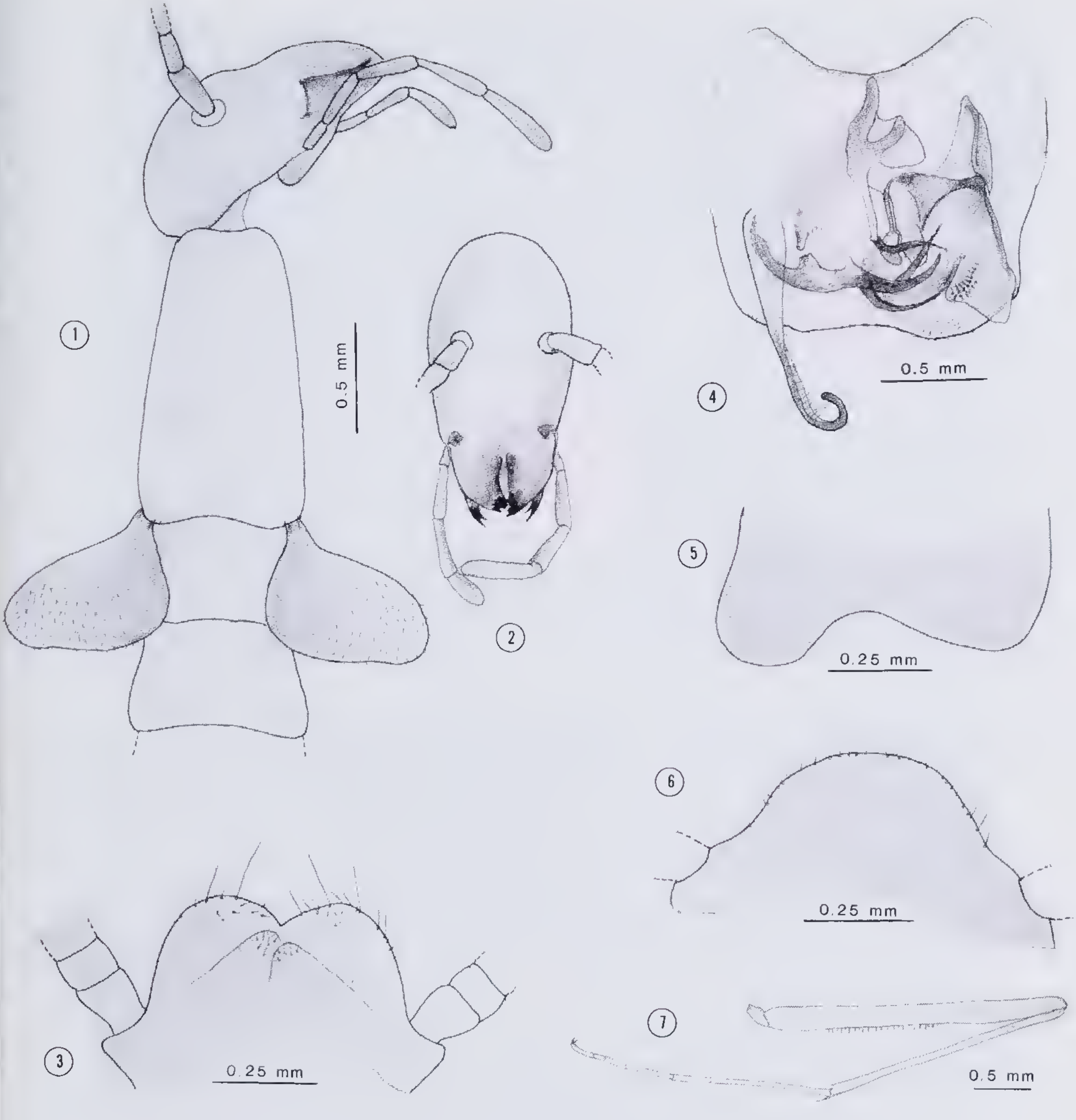
Measurements (mm) (♀ in parentheses). Length, 4.6-5.5 (4.1-5.7); pronotum length x width, 1.3 x 0.8 (0.9-1.2 x 1.0-1.4); tegmen length, 0.7-0.8.

Etymology

The specific name refers to the fan-shaped male tegmina.

Comments

Although males of *Nocticola* may have reduced tegmina, the fan-shape in *flabella* is unique for the known members of the genus. The absence of a male tergal gland places *flabella* in the *simoni*-species-group (Roth 1988).



Figures 1-7. *Nocticola flabella*, new species. 1, 5, ♂ holotype, 3, 4, ♂ paratype, 2, 6, 7, ♀ paratype. 1, Head (lateral view), thorax and tegmina (dorsal view); 2, Head (frontal view); 3, Supraanal plate and paraprocts (ventral view); 4, Subgenital plate and genitalia (dorsal view); 5, Distal part of subgenital plate (ventral view); 6, Supraanal plate (dorsal view); 7, Front leg (coxa not shown) (anterior view.)

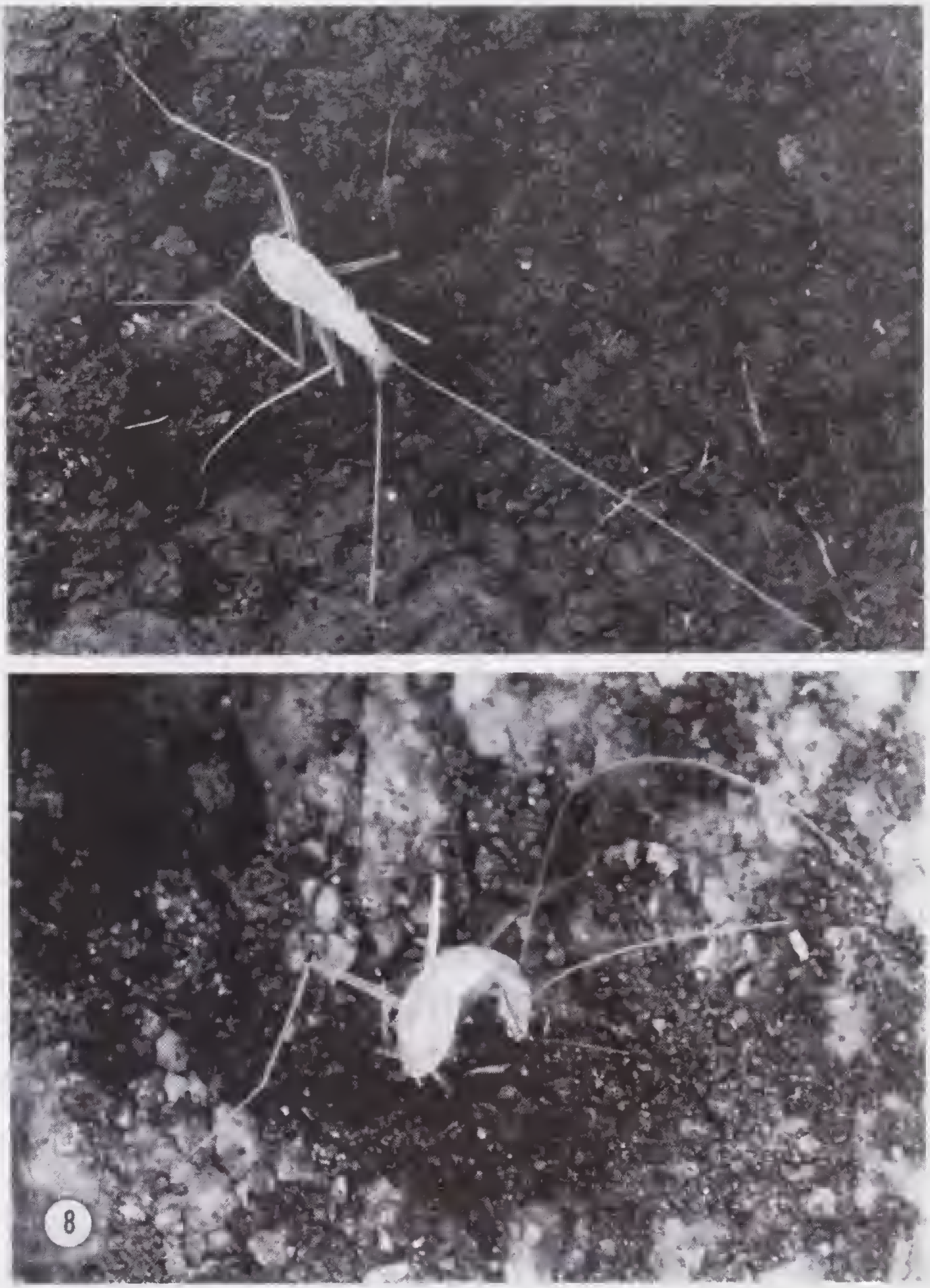


Figure 8. Two views of a living male *Nocticola flabella*, new species, the bottom figure shows the individual cleaning its leg. (Courtesy of Western Australian Museum, through Dr. W.F. Humphreys).

Key to males of known Australian *Nocticola* species

1. Abdominal terga unspecialised 2
   Fourth abdominal tergum specialised 3
2. Tegmina greatly reduced in length, fan-shaped, hind wings absent. Eyes absent (cavernicolous) .... *flabella*
   Tegmina and wings fully developed, Eyes normal. (epigean) .... *babindaensis*
3. Specialisation on T4 non-setose, inverted V-shaped on postero-medial hind margin (cavernicolous)........................ *australiensis*
   Specialisation on T4 a large transverse depression filled with dark, recumbent setae (epigean):................................... unnamed

Nocticola rohini (Fernando), new combination

Paraloboptera rohini Fernando, 1957, p.7, pl.1-6, figures 1-18; 1962, p. 90, figures 14, 15; Princis, 1969, 1014 (sp. *incertae sedis).*

Although I was unsuccessful in obtaining Fernando's types, his excellent description and illustrations leave no doubt that *Paraloboptera rohini* is a *Nocticola.*

The male's tegmina are small lateral lobes, and hind wings are absent. Eyes are represented by a few ommatidia. There is only one style. An inverted-V-shaped gland with a small setal tuft is on the fourth abdominal tergum placing the species in the *uenoi*-species-group (Roth 1988). The female is apterous, and segments two and three of its cercus have three strong ventral spines or hooks. These have been noted on two proximal cercal segments of females of *Nocticola australiensis,* and *N. termitophila* Silvestri. Fernando described the ootheca which was still attached in the vertical position to the female; there are only four eggs and the keel and respiratory tubules are more like those found in the Blattellidae than the Polyphagidae.

Nocticola rohini was first taken in the jungle of Uraniya (Uva Province) in Sri Lanka, and is widely distributed on the island where it lives under stones and fallen tree trunks (Fernando 1962). This is the first record of *Nocticola* in Sri Lanka. Another nocticolid, *Cardacus willeyi* (Shelford) is also found on that island (Roth 1988: Table 1).

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A new species of burrowing frog, *Neobatrachus* (Anura: Myobatrachidae), from the eastern wheatbelt of Western Australia.

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Abstract

A new species of *Neobatrachus* is described from the wheatbelt of Western Australia. This species has a diploid karyotype and can be distinguished from congeneric species by morphology and call.

Introduction

The delineation and identification of species of *Neobatrachus* has often proved difficult using morphological features alone. The analysis of chromosomes and mating call, however, have facilitated the resolution of species boundaries in this genus (Roberts 1978; Mahony and Robinson 1980; Mahony and Roberts 1986). Having defined species by call and/or karyotype it has often been possible to find consistent morphological differences between species (e.g. Mahony and Roberts 1986).

During field work in the eastern wheatbelt from 1983 to the present we have obtained, from several localities, specimens of a diploid *Neobatrachus* species which differs in call structure and appearance from *N. pelobatoides:* the only other diploid species we have observed in this area. These specimens are herein referred to a new species.

Materials and Methods

Frogs were collected and calls recorded during field work from 1983 to 1989. Call recording and analysis techniques and karyotype preparation follow Mahony & Roberts (1986). Genetic differentation of species was assessed using gel electrophoresis of soluble enzymes and proteins (Richardson *et al.* 1986); detailed methods follow Barendse (1984). Electrophoretic data were collected from five specimens of the new species (four from 20.5 km W Jerramungup; one from 4.2 km N Hopetoun) and, 31 specimens of *N. pelobatoides* (eight from 8.9 km SE of Beverley, 19 from 20.5 km W Jerramungup, and four from 4.2 km N Hopetoun). Because the new species is diploid, it was not necessary to include the tetraploid species *N. kunapalari* in the electrophoretic comparisons. Twenty-five presumptive gene loci were scored, including four non-enzymic general protein bands (Appendix 1).

Morphological differentiation was assessed by the same set of morphometric variables as reported by Mahony & Roberts (1986) with the addition of naris-snout (N-S, defined in Roberts, Wardell-Johnson and Barendse 1990), anterior interorbital

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distance (ant I-O, equivalent to inter-orbital distance of Roberts, Wardell-Johnson and Barendse 1990), posterior interorbital distance (post. I-O, distance between posterior corners of eyes) and width and height of tympanum (tymp. W and tymp. H, skin was not removed). Morphometric data were collected from 14-16 male specimens of each species as follows (all numbers refer to specimens in the W.A. Museum (WAM) collection, Perth. The letter prefixing registration numbers is an institutional identification): the new species, the type series; *N. pelobatoides*, R101156, R101158-59, R101162, R101164, R101166-67, R101170, R101177-78, R33365, R39535, R94426, R94428, R94429 and *N. kunapalarai*, R101187-88, R101197-99, R101201, R101204, R101207-8, R101210-11, R101213, R101214. Metric variables were analysed by one-way analysis of variance using Statview 512+ software on a Macintosh Plus personal computer.

Distribution data are based on WAM records and our own field recordings or observations of calling males.

Systematics

Neobatrachus albipes sp. nov.

Figures 1 - 3, 5.

Holotype

R101178, adult male, 37.2 mm SV, collected 4.2 km N Hopetoun, W.A., (33°54′S, 120°08′E) by J.D. Roberts and P. Kendrick, 3 May, 1988. Calls recorded as #3 on JDR Tapes 79 & 80. Tapes housed in the Department of Zoology, University of Western Australia.

Paratypes

Fourteen males: R36291, 41.6 km E Southern Cross, W.H. Butler, February 16, 1970; R39841, Greenshield Soak, near Lake Magenta, L.A. Smith *et al.* May 4, 1971; R49800, Dongolocking Nature Reserve, WAM Biological Survey, May 15, 1975; R52546 & R52550, Badjaling Nature Reserve, 11 km E Quairading, WAM Survey, May 6, 1975; R65144, 0.6 km W Lake Cronin, WAM Biological Survey, September 19, 1978; R93378, Junana Rock, Cape Arid National Park, L.A. Smith & R.A. Johnstone, November 3, 1985; R94796, Lake Magenta Nature Reserve, M.S. Graham, July 23, 1986; R96779, Fitzgerald River National Park, B. Maryan *et al.*, July 23, 1986; R101179, 20.5 km E Jerramungup, J.D. Roberts & P. Kendrick, May 2, 1988; R101185, same site as R101179, C.M. Majors, May 24, 1989; R101183-84, turn off to Pallarup Rocks, 44.6 km NE of Ravensthorpe, J.D. Roberts & P. Kendrick, May 3, 1988; R101186, Yoting, rubbish dump at turn off to Kellerberrin on Quairading-Bruce Rock road, J.D. Roberts, C.M. Majors, A. Savage & B. Murray, May 12, 1988.

One female: WAMR101180, 20.5 km E Jerramungup, May 2, 1988, J.D. Roberts & P. Kendrick.

Diagnosis

Moderately sized frog (adult males 33.2 to 45.4 mm S-V; female 35.3 mm S-V), light brown or grey with diffuse darker markings. Mating call a series of 33 to 40 pulses with a very high pulse repetition rate. Karyotype diploid. Metatarsal tubercle unpigmented or lightly pigmented. Upper surface of foot white, distinct light bar between eyes.

Description of holotype

Head wider than long (HW/HL 1.18), slopes down from eye to naris. Snout rounded when viewed dorsally, almost flat in profile. Lines from eye to naris and from snout tip to naris intersect on prominent naris at angle of about 110° so snout appears almost square in profile. Nares directed upwards and slightly lateral. Eye large (EL/HL 0.463) and prominent. Tympanum higher than broad (TH/TW 1.23) and obvious despite being covered by skin. Fingers slender, short, unwebbed (3>1>2>4). Prominent subarticular tubercle at first joint on all fingers. Prominent tubercle between fingers 1-2 and 2-3 but not between 3-4. Large, rounded, flattened inner metacarpal tubercle, elongate outer metacarpal tubercle. Nuptial pads on first two fingers from base to distal joint. Maxillary teeth present, vomerine teeth in short medially separated series between choanae, medial gap about equal to gap between lateral end of vomerine tooth row and adjacent choana. Distinct parotoid glands from behind tympanum extending medially almost to middle of back. Toes webbed. Webbing extends to end on first, second and third toes, to second joint on fourth and similar on fifth on right foot. Left foot is abnormal with only four toes obvious. Prominent, white, shovel-shaped inner metatarsal tubercle. No outer metatarsal tubercle. Weakly developed, subarticular tubercles on toes three, four only. Limbs moderate (T/SV 0.37), foot long (FL/T 1.76). Toes slender, 4>3>5>2>1. Colour in preservative: dorsum brown with irregular darker markings with poorly defined edges. Broad, lighter "V" shaped mark with well defined posterior margin between and extending onto skin above eyes. Similar, broad, darker "V" shaped bar on posterior portion of head and extending onto skin above eyes. Ventral surface of body, legs and upper-arms creamy-white, similar colour on inner margin of feet, anterior side of fore-arms. Plantar and palmar areas dark brown. Anterior and lateral margins of

Figure 1. Holotype in life, photographed by S. Hopwood.

submandibular skin suffused with dark grey-brown. Upper surface of foot and toes white with the ankle skin clear making it appear dark brown from the underlying muscle. In life, colour varied with the colour of background. On dark backgrounds, colour similar to above. On light backgrounds, general colour was grey to a light green-yellow, particularly on the flanks and posterior half of body, with darker markings.

Measurements of holotype (mm): snout-vent 37.2, head width 15.4, head length 13.0, eye-naris 2.7, inter-naris 2.7, naris-snout 1.3, inter-orbital (anterior) 6.6, inter-orbital (posterior) 12.0, tibia 13.6, foot 24.0, tympanum width 3.2, tympanum height 4.0.

Figure 1 shows holotype in life.

Variation

Paratypes showed the following minor differences from holotype: R10118 has mid-dorsal stripe extending from level of tympanum to cloaca. Mid-dorsal stripe also present on R52550. Parotoid glands more obvious in some, lighter brown-yellow in preservative. Distinctness of light bar between eyes varies; no bar as such in R101184 but still a distinct light spot between eyes. In R52550, R65144 and R93378 metatarsal tubercle faintly edged with light brown. R49800 and R39481 have nuptial pad as a thin line on the third finger as well as on first and second fingers.

Mating call

Detailed data and an oscillograph are given for call of holotype (Table 1, Figure 2). Mating calls have been recorded at several sites (Figure 3) and detailed analyses are given in Table 1. Call is short, a series of 36 to 40 pulses (mean 36) rapidly repeated (32 pulses s^{-1} at 11.4^{0}C), with an average dominant frequency of 1028 Hz. Pulse repetition rate and call duration vary with temperature but other variables do not (Roberts, unpublished data). The difference between the dominant frequency for the call of the holotype (1266 Hz) and the frogs recorded near Bruce Rock (mean 1028) is attributed to body size differences. The lowest dominant frequency at Bruce Rock was from a frog with a S-V length 5mm longer than the holotype. Body size is negatively correlated with dominant frequency in *Neobatrachus pictus* (Roberts 1978).

Table 1. Call structures in *Neobatrachus* from Western Australia. Values given are means ± standard error. Variables are: sample size (n), pulse number, pulse rate (pulses s^{-1}), pulse duration (ms), call duration (s), dominant frequency (Hz), pulse rise time as a % of pulse duration and water temperature (^{0}C).

Species	n	Pulse number	Pulse rate	Pulse duration	Call duration	Dominant freq.	Rise time	Water temp.
N. albipes - holotype	1	39.0	52.5	9.4	0.74	1266	27.1	18.4
N. albipes[1]	6	35.6±1.0	31.8±.4	8.8±.5	1.11±.05	1028±17	29.1±1.5	11.4±.6
N. kunapalari[1]	8	19.9±1.4	12.4±.8	18.8±.8	1.59±.15	1101±31	19.3±1.2	11.7±.5
N. pelobatoides[2]	3	59.8±7.6	18.9±1.6	11.2±.9	3.23±.32	816±28	48.3±3.8	12.3±.2

[1] 4.3 km NW of Bruce Rock, on Doodlakine Road, 24 and 26, May, 1989

[2] Data from Table 2 of Mahony & Roberts 1986

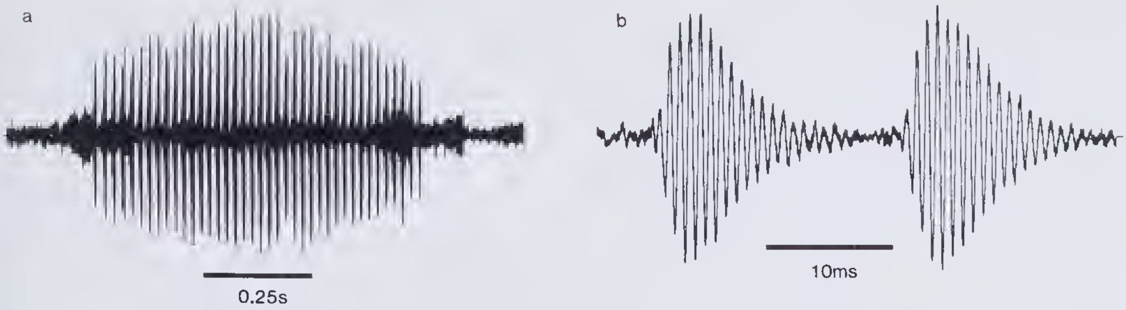

Figure 2. Oscillographs of call of the holotype: a) complete call b) detail of pulse structure showing two complete pulses.

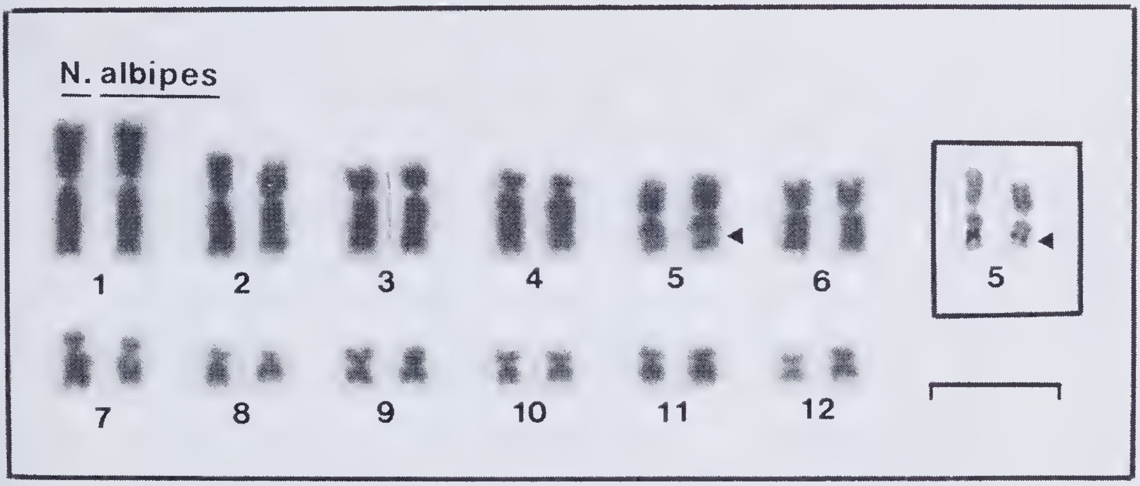

Figure 3. Karyotype of *N. albipes.* Inset: silver stained NOR. Scale bar 10μm.

Breeding biology

Males have been heard calling after summer rains (January 25, 1982, Narembeen, Kondinin), but most activity has been observed after autumn rains (May 1, 1988, W of Coolgardie; May 2-3, 1988 Jerramungup, Hopetoun area; May 12, 1988, Yoting; May 24-26 1989, Bruce Rock, Jerramungup, Ongerup, Lake Cronin) and early winter rain (12-16 June, 1989 Corabbin, Bodallin, Moorine Rock). Calls have also been recorded by A. Chapman at Ravensthorpe after a thunderstorm on March 3, 1983 and by D. Cale on the Chester Pass Road, 28 km east of Mount Barker, October 15, 1985. Breeding is typical of *Neobatrachus:* explosive activity for one or two nights after heavy rain. Males generally call from covered sites, under bushes or other flooded vegetation, and often in deep water (30-50 cm deep or more at sites near Hopetoun and at Bodallin). Males do not seem to move about as much as observed in choruses of *N. pictus* (Roberts 1978) and *N. kunapalari* (Mahony & Roberts 1986) but this has not been quantified. Amplexus is inguinal but egg deposition has not been observed. Males have been heard calling at water temperatures from 9.8°C to 19.8°C.

Karyotype

Neobatrachus albipes is diploid (2n = 24, Figure 3). As such it is readily distinguished from tetraploid congeners: *N. kunapalari, N. centralis* and *N. aquilonius.* The relative lengths and centromere positions of the chromosomes are very similar to those of both diploid and tetraploid species of this genus (see Mahony and Robinson 1980; Mahony and Roberts 1986). *Neobatrachus albipes* cannot be readily distinguished from diploid congeners with the exception of *N. fulvus* which has the nucleolar organiser region (NOR) terminal on pair five (Mahony and Roberts 1986). The NOR is medial on the long arm of chromosome five in *N. albipes* (Figure 3).

Genetic differentiation

Details of allele frequencies at individual loci are available on request from the senior author. There were fixed differences at two loci (LDH3 and MDH), with only a single allele in each species. No heterozygotes were detected confirming the reproductive isolation of *N. albipes* and *N. pelobatoides.* Nei's (1978) genetic distance between the two species (all populations combined for each) was 0.168 — a level consistent with species level differentiation in other organisms (Thorpe 1982; Richardson *et al.* 1986).

Distribution

Figure 4 shows the known distribution of *N. albipes.* The species occurs in the eastern and south-eastern wheat-belt, extending into adjacent western goldfields. There are no records west of a line running south from Quairading, and despite extensive field work in the Merredin area over the last six years, we have never observed this species north of

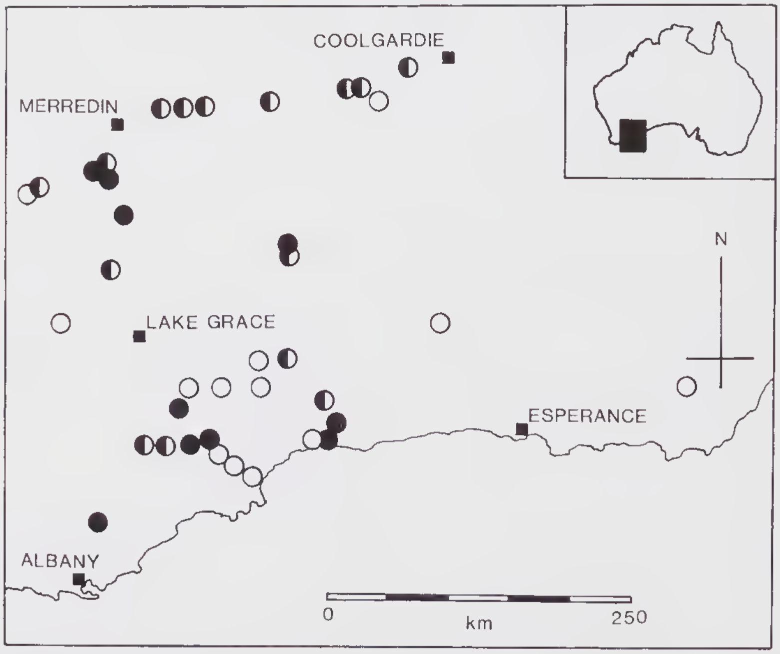

Figure 4. Distribution of *N. albipes:* closed circles, call recordings; half open circles, calls heard; open circles, specimen records.

Narembeen. *Neobatrachus albipes* is sympatric with *N. pelobatoides* and *N. kunapalari* throughout most of this range, but *N. kunapalari* does not occur in the area near the Stirling Range.

Comparisons with other species

Distinguished from all other species except *N. pelobatoides,* by the colour of the metatarsal tubercle: black in other species, unpigmented or edged with light brown in *N. pelobatoides* and *N. albipes.* Distinguished in life from *N. pelobatoides* by presence of white pigment in skin on upper surface of foot. Upper foot skin lacks pigment in *N. pelobatoides* making foot the colour of the underlying flesh in life (see Figure 5). This difference is not apparent in preserved material. Also distinguished by male call: *N. albipes* has a lower pulse number but higher pulse rate and dominant frequency than *N. pelobatoides.*

Figure 5. The upper surface of the foot in (a) *N. pelobatoides* (WAM R101178) and (b) *N. albipes* (WAM R101185) showing the difference in pigmentation. Photograph is of freshly killed material before preservation.

The combination of karyotype, electrophoretic and call structure data leave us in no doubt of the specific distinction of *N. albipes* from the broadly sympatric *N. pelobatoides* and *N. kunapalari.* Morphologically, however, these species are not markedly different and caution should be exercised in the allocation of preserved material. The following comparative notes may help with the correct identification of preserved specimens.

General morphology

Colour of metatarsal tubercle generally distinguishes *N. albipes* (13 of 16 unpigmented, three edged with brown), N. pelobatoides (13 of 15 edged with brown, two unpigmented), and *N. kunapalari* (10 black, four edged with black or dark brown). Mid-dorsal stripe generally present in *N. pelobatoides* (11 complete, two partial, two absent), generally absent in *N. albipes* (one present, one partial, 14 absent) but variable in *N. kunapalari* (one present, one partial, 14 absent). Light "V", or a derivative of this marking, between eyes always clear in *N. albipes* but never so obvious in *N. pelobatoides* and not present in *N. kunapalari.* Darker markings on the dorsum usually larger with clearly defined edges in *N. pelobatoides:* edges of markings diffuse in *N. albipes.* Darker markings on dorsum of *N. kunapalari* smaller than in *N. albipes* and also have a diffuse edge. In frogs where the black pigmentation of the nuptial pads was obvious on the first two fingers, we scored the presence of a nuptial pad on the third finger: *N. albipes,* two present, 11 absent; *N. pelobatoides,* 10 present, one absent; and *N. kunapalari,* seven present and five absent.

Morphometrics

Anova on all measured variables indicate significant differences in several variables, with *N. albipes* and *N. pelobatoides* similar but smaller than *N. kunapalari* (SV, HL, EL, T, F, EN, IN: Table 2, Fisher's multiple comparison test). For the three variables showing significant differences between all three species (HW, AIO, PIO; Table 2), *N. albipes* was intermediate between *N. kunapalari* and *N. pelobatoides. N. pelobatoides* has a longer snout but smaller tympanum than both *N. kunapalari* and *N. albipes* (NS, TW, TH; Table 2).

Table 2. One way analyses of variance for 13 metric variables amongst three species: *N. albipes, N. kunapalari* and *N. pelobatoides.* Superscripts (^{1}, ^{2}, ^{3}) indicate means that do not differ significantly using Fisher's multiple comparison test. All analyses have 2,42 degrees of freedom. Asterisks indicate probabilities: *, $p<0.05$, **, $p<0.01$, ***, $p<0.001$,

Variable	F value	*N. kuna.*	*N. pelo.*	*N. albipes*
S-V	44.9***	52.0^1	39.6^2	39.4^2
HW	100.9***	21.9^1	15.6^2	16.9^3
HL	81.5***	17.7^1	13.6^2	14.0^2
EL	27.3***	7.9^1	6.1^2	6.4^2
ant. I-O	30.1***	8.4^1	6.2^2	7.1^3
post. I-O	57.9***	15.9^1	11.5^2	13.2^3
E-N	38.9***	3.7^1	2.7^2	2.6^2
I-N	20.7***	3.1^1	2.5^2	2.6^2
N-S	3.3*	1.6^1	1.9^2	1.6^1
tymp. H	7.6**	4.4^1	3.6^2	4.0^1
tymp. W	13.5***	3.6^1	2.8^2	3.4^1
T	9.1***	16.9^1	14.8^2	14.1^2
F	36.2***	32.0^1	25.3^2	24.9^2

In summary, *N. albipes* has a shorter snout, larger tympanum and broader head than *N. pelobatoides* of comparable size. *N. kunapalari* is generally larger than both other species.

Discussion

The discovery of another species of *Neobatrachus* from south-western Australia takes the number of species in this genus to 10: four tetraploid forms, *N. sudelli, N. centralis, N. kunapalari* and *N. aquilonius;* and six diploid forms, *N. pelobatoides, N. pictus, N. sutor, N. wilsmorei, N. fulvus* and *N. albipes.* Although each of these forms is readily distinguished from sympatric congeners using a combination of karyotype and call only *N. wilsmorei* is easily distinguished by external morphology. This, coupled with compex patterns of sympatry and parapatry has often made identification difficult. The holistic approach to species recognition adopted here, combining data from call, karyotype and allozyme electrophoresis allows unambiguous delineation of species boundaries. Importantly it also facilitates the recognition of consistent, albeit slight, morphological differences between species, thereby allowing easier identification of field and museum specimens.

Acknowledgements

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Appendix 1. Presumptive gene loci surveyed for electrophoretic variation in *N. albipes* and *N. pelobatoides.* Enzymes are numbered in order of their relative cathodal migration. Buffers are described in Richardson, Baverstock and Adams (1986).

Presumptive gene locus	Buffer	Tissue
Enzymic loci		
Acid phosphatase	TEB	liver
Creatine kinase	TEB	muscle
Esterase	TEB	muscle
Glutamate dehyrodgenase	TEB	muscle
Glutamate-oxaloacetate transaminase	TEB	muscle
Isocitrate dehydrogenase 1, 2	TM	liver
Lactate dehydrogenase 1, 2, 3	TM	liver
Leucyl amino peptidase	TC8	liver
Leucyl glysine peptidase	TEB	muscle
Leucyl tyrosine peptidase	TEB	muscle
Malic enzyme	TEB	muscle
Malate dehydrogenase	TM	muscle
Mannose-6-phosphate isomerase	TEB	muscle
6-phosphoglucose dehydrogenase	TM	liver
Phosphoglucomutase	TEB	muscle
Phosphoglucose isomerase	TC6	muscle
Super oxide dismutase 1, 2	TM	muscle
Non-enzymic loci		
General protein 1-4	TEB	muscle

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Freshwater fishes of the genus *Craterocephalus* (Artherinidae) from the southern drainages of Papua New Guinea and Irian Jaya with reference to *C.s. stercusmuscarum* from Australia.

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Abstract

A new species, *Craterocephalus pimatuae,* from tributaries of the Purari River (Papua New Guinea), is described. It differs from all other Papua New Guinea hardyheads osteologically (shape of premaxilla) as well as morphologically (midlateral and transverse scale counts, gill raker number in first lower gill arch). *C. nouhuysi, C. lacustris* and *C. randi* the other Papua New Guinea/Irian Jaya species are redescribed and distinguished on the basis of their external morphology, osteology and electrophoresis. *C. randi* is compared with the redescribed Australian species, *C. stercusmuscarum stercusmuscarum* since these species have often been confused in the past. *C. annator* on the basis of osteology, external morphology and electrophoresis is placed into the synonymy of *C. randi.* The relationships of *C. s. stercusmuscarum* with hardyheads from the southern drainages is examined with reference to the geologic history of the region.

Introduction

The systematics and relationships of the Papua New Guinea species of hardyheads have never been examined. The descriptions of each of the species by their authors were clear and unequivocal. However, Whitley in 1938, did compare specimens from Fly River with *C. nouhuysi* and *C. randi* and concluded that his new species, *Craterocephalus annator* was different on the basis of measurements, counts, colour and pattern. In subsequent years, *C. randi* and *C. stercusmuscarum* were confused because of similarity of colour and marking (e.g. Allen and Hoese, 1980). The status of *C. lacustris* has never been questioned. The new species, *Craterocephalus pimatuae,* appears to be most similar to *C. randi* and is a typical member of the *stercusmuscarum* group (Ivantsoff *et al.,* 1987a). The northern drainage of Papua New Guinea is almost devoid of hardyheads with *C. kailolae* (Ivantsoff *et al.,* 1987a) being the only exception.

The southern half of the island of Papua New Guinea/Irian Jaya is regarded as part of the Australian plate (Pigram and Davies, 1987) and its history appears to be inextricably associated with it. Papua New Guinea and Australia were connected in Tertiary and Quaternary during periods of low sea level. This resulted in common radiation of freshwater fishes with some 35 species belonging to 16 families (Munro, 1964). It could be assumed that radiation of hardyheads would have followed a similar pattern, with species in common to both sides of Torres Strait. Electrophoretic evidence, however,

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suggests that periodic geographic isolation was sufficient to initiate speciation but with none of the extant species of hardyheads from Papua New Guinea found living in Australia.

Material and Methods

Methods for morphological proportions and meristic counts follow those of Ivantsoff *et al.* (1987a). Specimens for osteology were stained following the methods of Taylor (1967). Cluster analysis (Figure 8a) of the species examined was made by using 57 osteological characters (represented by binary notation — 1/0 to indicate presence or absence; large or small etc.). The procedure was based on an algorithm modified from Sneath and Sokal (1973) by Dr. George McKay of Macquarie University. Electrophoresis, following the methods of Richardson *et al.* (1986), was used to assess the genetic differences of all species except *C. pimatuae* of which only 5 specimens are known. Six specimens from each of the populations of *C. randi* and *C. s. stercusmuscarum* were assayed, with 10 specimens of each of the other species *(C. lacustris* and *C. nouhuysi)* being used. Nineteen enzymes (21 loci) were examined. Genetic distances were calculated using Rogers' (1972) R formula where R = Distance. The R values were used in a cluster analysis programme (Figure 8b) based on an algorithm of Sneath and Sokal (1973) modified by Dr. George McKay of Macquarie University.

Areas of collection for specimens used in electrophoresis:

C. lacustris: Lake Kutubu (PNG).

C. nouhuysi: Tabubil, creek south of Ok Tedi on Kiunga Road; Sawmill Creek, Ok Tedi; South Sawmill Creek, about 10 km along Kiunga Road, all in PNG.

C. randi: Samongas, 5 km from Kiunga; Ok Mac, small creek 1 km south Kiunga; Rupi Creek, Kiunga (tributaries of Fly River near d'Albertis Junction, type locality of *C. annator* Whitley (1938). Kubuna River, Kubuna (type locality), all in PNG.

C. s. stercusmuscarum: Edith River, Northern Territory; Roper River, Mataranka Thermal Spring Road, 6 km from Stuart Highway, N.T.; Mulgrave River, Qld; Rollingstone Creek, 51 km north of Townsville; River Dee, 1/2 km west of Dululu, Qld, all in Australia.

Enzymes assayed: ADA; ADH; AK; ALD; CK; FDP; FUM; GAPD; GLDH; αGPD; GPI (2 loci); GOT (2 loci); IDH; LDH; MDH; ME; MPI; PGM; XDH. (for methods and stains, see Richardson *et al.*, 1986).

Material from the following institutions was examined: American Museum of Natural History, New York (AMNH); The Australian Museum, Sydney (AMS); British Museum of Natural History, London (BMNH); Commonwealth Scientific and Industrial Research Organization, Hobart, Tasmania (CSIRO); Kanudi Fisheries Research Station, Kanudi, Papua New Guinea (KFRS); Macquarie University, North Ryde (MQU); Late Dr. D.E. Rosen, personal collection (DR); Western Australian Museum, Perth (WAM); Zoologisch Museum, Amsterdam (ZMA).

Key to the Hardyheads of the Southern Drainages of Papua New Guinea

1a. Gill rakers in first lower gill arch never less than 10 (10-13); narrow interorbital, 3.2 (2.9-3.6) in head for this species. Lower lip protruding in adults. Anal plate short; interdorsal pterygiophores lacking well developed ventral processes. *PGM*^{a} allele present . . . . *C. lacustris*

1b. Gill rakers in first lower gill arch 6-11, rarely more than 10, interorbital 2.4-3.2 in head, for all species following. Lower lip never protrusive. Anal plate elongate; interdorsal pterygiophores with well developed ventral processes. *PGM*^{a} allele never present. 2

2a. Dorsal process of premaxilla in eye never more than 1.6; midlateral scale count never less than 35; pectoral rays 12-15; ventral wings of 5th ceratobranchial always lateral; basihyal cartilage either as long as basihyal bone or almost rudimentary 3

2b. Dorsal process of premaxilla in eye 1.6 (1.2-2.0); midlateral scale count 34.4 (32-37), usually less than 35; pectoral rays 11-13; ventral wings of 5th ceratobranchial medial; basihyal cartilage about half length of basihyal bone . . . . *C. randi*

3a. Transverse scale count 8.1 (8-8.5). Dorsal process of premaxilla robust, 1.5 (1.4-1.6) in eye; snout in eye 1.1 (1.1-1.3). 5th ceratobranchials incompletely fused; basihyal bone and cartilage about equal in length; sensory canals never enclosed . . . *C. pimatuae*

3b. Transverse scale count always 7. Dorsal process of premaxilla long and slender, 1.1 (1.1-1.3) in eye; snout in eye 1.0 (0.9-1.1). 5th ceratobranchials completely fused; basihyal bone long; basihyal cartilage rudimentary; sensory canals of nasal and post-temporal bones enclosed or nearly so . . . . *C. nouhuysi*

Systematics

Craterocephalus pimatuae sp. nov.

Figure 1

Holotype

WAM P26971-004 25.4 mm SL. Small seine, Junction of Pima and Tua Rivers, 6°25′S 144°49.5′E. Papua New Guinea. Collected by G.R. Allen, September 1980.

Paratypes

WAM P26971-004 (3), data as for holotype; WAM P26971-004, prepared alizarin specimen, data as for holotype. Size range 24-35 mm SL.

Diagnosis

A freshwater species of hardyhead belonging to *C. stercusmuscarum* group (see Ivantsoff *et al.*, 1987a) and superficially similar to all Papua New Guinea members of this genus. Distinguished from those species by its robust dorsal process of premaxilla

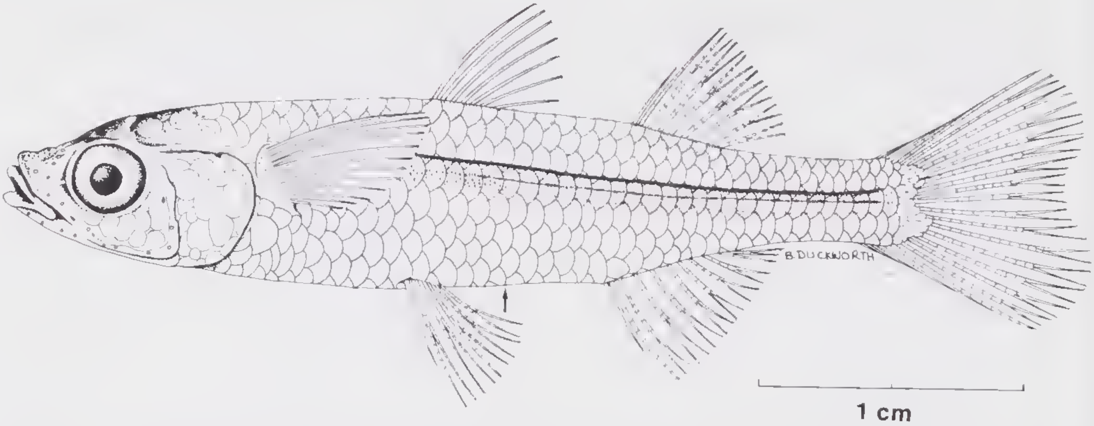

Figure 1. Holotype of *Craterocephalus pimatuae* WAM P.26971-004, 25.4 mm SL., Junction of Pima and Tua Rivers, Papua New Guinea.

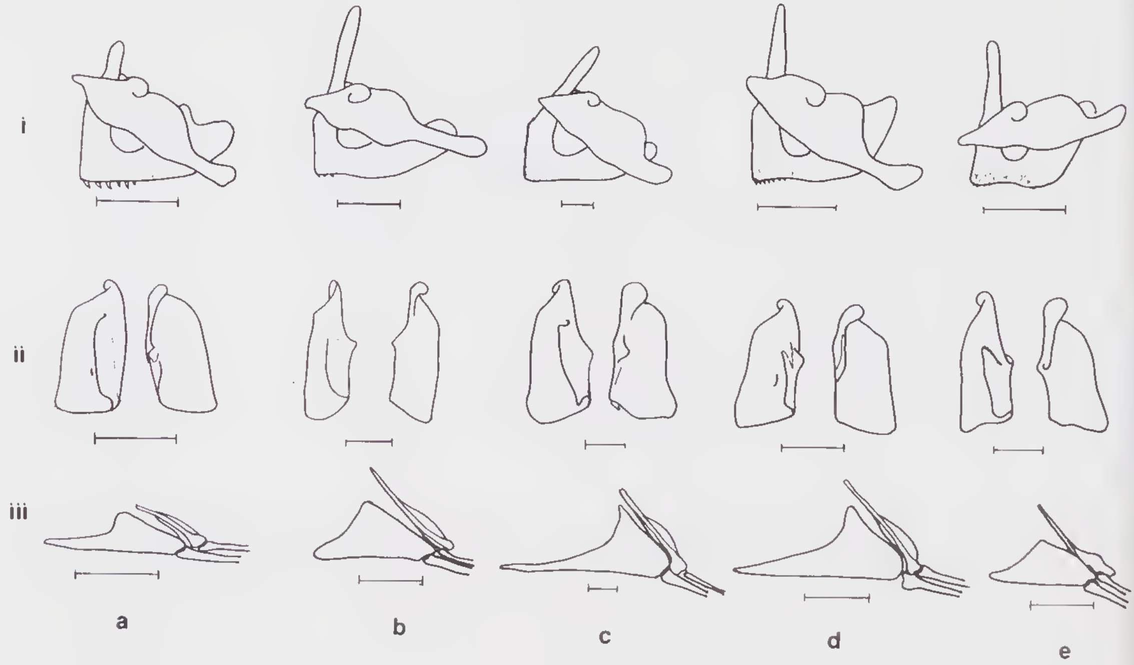

Figure 2. i) Premaxilla and maxilla, ii) dorsal and ventral aspects of nasal bone and iii) anal plate of: a. *Craterocephalus pimatuae;* b. *C. lacustris;* c. *C. nouhuysi;* d. *C. randi;* e. *C. s. stercusmuscarum.* Bar represents 1 mm.

Table 1. Morphometrics and meristics for the holotype and four paratypes of *Craterocephalus pimatuae* also morphometrics and meristics for three other species of hardyheads from the southern drainages of Papua New Guinea. Data expressed as mean, range and standard deviation.

Character/Species Morphometric proportions		*C. pimatuae*	*C. nouhuysi*	*C. lacustris*	*C. randi*	*C. s. stercusmuscarum*
Number of specimens	Holotype	4 paratypes	30	42	25	44
In SL						
Head	3.4	3.4 (3.3-3.5) 0.10	3.7 (3.4-4.2) 0.16	3.4 (3.2-3.8) 0.15	3.7 (3.4-4.1) 0.60	3.6 (3.2-3.9) 0.18
Pec Length	4.9	5.3 (4.9-5.7) 0.28	5.4 (4.8-6.1) 0.35	6.4 (5.1-9.4) 0.62	6.2 (5.3-7.3) 0.61	6.3 (5.2-9.2) 0.86
H. max	4.8	4.8 (4.7-4.8) 0.06	4.8 (4.1-5.7) 0.59	4.6 (3.5-6.0) 0.44	5.1 (4.5-5.7) 0.27	5.1 (3.5-5.7) 0.38
H. min	10.8	10.6 (10.4-10.9) 0.22	9.7 (7.6-13.0) 1.65	11.7 (10.6-12.9) 0.68	10.8 (9.8-12.5) 0.56	10.9 (9.1-12.6) 0.88
Pec/anus	3.2	3.2 (3.1-3.2) 0.06	3.3 (2.9-3.4) 0.14	3.4 (3.0-4.0) 0.22	3.5 (3.0-3.8) 0.19	3.4 (2.9-3.7) 0.16
SnOD1	2.0	2.0 -	2.1 (2.0-2.1) 0.05	2.1 (2.0-2.2) 0.06	2.1 (2.0-2.2) 0.05	2.0 (1.8-2.2) 0.07
SnOD2	1.4	1.4 -	1.4 -	1.4 (1.4-1.5) 0.04	1.4 (1.3-1.5) 0.05	1.4 (1.3-1.5) 0.04
SnOV	2.1	2.2 (2.1-2.2) 0.04	2.3 (2.2-2.5) 0.08	2.3 (2.2-2.4) 0.06	2.3 (2.2-2.6) 0.08	2.3 (2.1-2.4) 0.09
SnTV	1.6	1.6 -	1.7 (1.6-1.8) 0.06	1.7 (1.6-1.8) 0.05	1.7 (1.6-1.8) 0.05	1.7 (1.6-1.8) 0.06
SnOA	1.5	1.5 -	1.4 (1.4-1.5) 0.04	1.5 (1.4-1.6) 0.04	1.4 (1.4-1.6) 0.04	1.4 (1.4-1.5) 0.04
SnTA	1.2	1.3 (1.2-1.3) 0.06	1.2 (1.2-1.3) 0.09	1.2 (1.0-1.5) 0.07	1.2 (1.1-1.3) 0.05	1.2 (1.0-1.3) 0.05
In Head						
Eye	3.1	3.3 (3.1-3.5) 0.17	3.5 (3.0-3.8) 0.15	3.4 (2.9-5.0) 0.53	3.3 (2.7-3.9) 0.10	3.1 (2.6-3.7) 0.24
Interorb	2.9	2.8 (2.8-2.9) 0.04	2.8 (2.4-3.2) 0.24	3.2 (2.9-3.6) 0.22	2.7 (2.5-3.1) 0.70	2.9 (2.2-3.3) 0.24
Postorb	2.4	2.4 (2.3-2.4) 0.05	2.4 (2.2-2.7) 0.11	2.3 (2.0-2.7) 0.17	2.3 (2.0-2.5) 0.13	2.5 (2.1-2.8) 0.17
In Eye						
Sn	1.2	1.1 (1.1-1.2) 0.02	1.0 (0.9-1.1) 0.07	1.2 (0.7-1.5) 0.23	1.2 (0.9-1.5) 0.18	1.3 (1.0-1.7) 0.18
Pmax	1.1	1.1 (1.0-1.1) 0.06	1.1 (0.9-1.3) 0.12	1.1 (0.7-1.4) 0.17	1.3 (1.0-1.5) 0.11	1.4 (1.1-1.7) 0.17
PmaxP	1.6	1.5 (1.4-1.6) 0.10	1.1 (1.0-1.3) 0.09	1.3 (0.8-1.9) 0.26	1.5 (1.0-2.1) 0.29	1.6 (1.3-2.0) 0.21
Lips/Pmax	2.3	2.5 (2.2-2.8) 0.21	2.0 (1.7-2.2) 0.13	2.0 (1.5-2.4) 0.20	1.9 (1.4-2.4) 0.20	1.8 (1.5-2.2) 0.16
Meristic Counts						
Midlateral	37	36.0 (35-37) 0.82	36.9 (36-38) 0.83	34.3 (32-38) 1.31	34.4 (32-37) 1.20	32.9 (32-34) 0.76
Transverse	8	8.1 (8-8.5) 0.25	7.0 -	7.3 (6-8) 0.60	7.3 (6.5-8) 0.60	7.0 (6.5-7) 0.11
Interdorsal	7	7.5 (7-8) 0.58	8.0 (7-9) 0.69	7.4 (6-9) 0.72	7.8 (6-9) 1.00	7.2 (6-9) 0.59
Predorsal	16	16.4 (16-19) 1.00	15.8 (14-18) 1.12	13.8 (11-18) 1.96	15.4 (11-19) 2.08	16.1 (12-18) 1.40
Vertebrae	36	37.2 (36-38) 0.58	38.0 (37-38) 0.91	36.5 (35-39) 1.04	36.0 (34-39) 1.41	36.7 (35-38) 1.22
D1	5	6.5 (5-7) 0.58	6.9 (5-8) 0.76	7.1 (5-8) 0.77	6.6 (5-8) 0.76	6.6 (5-8) 0.62
D2	7	7.3 (7-8) 0.50	7.3 (6-8) 0.53	7.2 (6-8) 0.54	7.1 (6-8) 0.81	6.1 (4-7) 0.50
A	9	8.5 (8-9) 0.58	8.8 (7-10) 0.73	8.1 (7-9) 0.57	7.8 (6-10) 0.88	7.1 (6-8) 0.53
Pec	13	14.3 (13-15) 0.96	13.5 (12-15) 0.68	12.6 (11-15) 1.69	11.9 (11-13) 0.78	11.7 (10-13) 0.66
Gr	9	9.3 (9-10) 0.50	7.9 (6-10) 1.07	11.7 (10-13) 0.77	8.6 (7-11) 1.23	10.3 (9-12) 0.81
Posit A	F3	F2.0 (F1.5-3) 0.41	F2.0 (F1-2.5) 0.60	F1.0 (F0-2) 0.53	F1.2 (F0-2) 0.36	F1.2 (F0-2) 0.61
OD1-TV	F6	F5.8 (F5-6) 0.50	F4.1 (F3-6) 0.92	F5.2 (F3-7.5) 1.01	F4.5 (3-6) 0.95	F4.5 (F3-6) 0.56
OD1-Tpec	B0	B0.5 (B0.5-1.0) 0.41	B2.2 (B0-4) 1.00	B0.8 (F1-B3) 0.99	B1.6 (F0.5-B4) 1.18	B2.5 (B0-4) 1.00
Ov-Tpec	F0	F1.0 (F0-1.5) 0.29	F1.6 (F0-3) 0.86	F1.5 (F0-3) 0.70	F1.3 (B1-F4) 1.07	F0.7 (B1-F2) 0.67

and by basihyal bone and cartilage being about equal in length, with basibranchial bone longer than cartilage in all other species. Nasal bone rounded anteriorly, lateral margin not straight (see Figure 2). Also distinguished from *C. nouhuysi* and *C. lacustris* by gill raker count and by length of dorsal process of premaxilla.

No fresh material for genetic studies was available.

Description

Slender freshwater species of the genus, most closely related to *C. stercusmuscarum* species, but lacking completely fused 5th ceratobranchials common to other members of the group. Mouth small with gape restricted by labial ligament to about two thirds of length of premaxilla. Lips moderately thin; lower lip not protrusive as in *C. lacustris.* Premaxilla not reaching anterior margin of orbit; dorsal process of premaxilla robust, with very long medial symphysis; dorsal process barely reaching interorbital space. Teeth large, in two distinct rows in upper and lower jaws. Other bones in mouth edentulous. Wings of partially fused 5th ceratobranchial lateral, high and rounded anteriorly. Gill rakers about half diameter of eye, lacking spinules. Scales dorso-ventrally elongated, in even rows along sides of body.

For morphometric and meristic differences between species, see Table 1.

Colour:

Live specimens olive to light brown above midlateral stripe, whitish below; silver midlateral stripe from upper pectoral to hypural joint. Fins clear. Preserved specimens pale cream colour with faint brownish reticulate pattern on uppermost scales along sides of body; body below midlateral stripe pale cream to whitish with no markings; midlateral stripe brownish, solid above, remainder of stripe below formed by light speckling anteriorly, to about vertical through tips of ventral fins, then solid throughout to hypural joint. Midlateral stripe not extending to head. All fins pale with no markings. Eye silvery with dark blotch along top; dorsum of head and interorbital speckled brownish; snout speckled with two distinct dark blotches on either side of median line; single distinct dark blotch on upper lip; rest of upper and lower lips slightly speckled.

Etymology

pimatuae, refers to the locality from which the new species was collected, i.e. the junction of Pima and Tua Rivers.

Distribution

Known only from the Pima and Tua Rivers in Papua New Guinea, located directly south of Mount Hagen. These rivers are tributaries of the Purari River in the central Highlands of Papua New Guinea. The fish were collected in deep pools in quiet backwaters near the junction of these tributaries. Presently, the area is inaccessible except by helicopter.

Craterocephalus lacustris Trewavas

Figure 3

Craterocephalus lacustris Trewavas, 1940: 286, type locality: Lake Kutubu, Papua New Guinea, holotype in BMNH (1940: 3.11.7-8); paratype in BMNH (1940.3.11.7-8); Schultz, 1948:20; Munro, 1958:155, 1964:166, 1967:174; Ivantsoff, 1978: 272.

Material examined

BMNH 1940.3.11.7-8, Lake Kutubu, Papua New Guinea, holotype and paratype of *Craterocephalus lacustris;* AMS IA. 8087 (1); CSIRO C3174 (1); MQU 70-40c (156). 42 specimens measured and counted, size range 25-115 mm SL. Other material examined but not used for measurements and counts: WAM P.28159-002 (65); WAM P.28258-002 (72). Material examined for osteology WAM P28159-002 (1); MQU W170-40 (1); MQU W170-41(2), all of the above collected in Lake Kutubu.

Diagnosis

Lacustrine species of genus *Craterocephalus,* most closely related to other Papua New Guinea members of *C. stercusmuscarum* group. Distinguished from those species by possessing highest gill raker count (10-13 in lower gill arch), narrow interorbital space (2.9-3.6 in head) and from all other species of *Craterocephalus* by protruding lower lip, especially in adults. Interdorsal pterygiophores lacking ventral process. Anal plate not elongate. Anterior of nasal bone not rounded; lateral margin of nasal straight (see Figure 2). Uniquely different from all other Papua New Guinea species in possessing a PGM^a allele (see Table 2).

Description

Robust fish, deep bodied in large adults, smaller fish seemingly more slender (Figure 3a,b) but not supported by measurements (Figure 4). Lips very fleshy and fusing about half way along premaxilla. In adults lower lip very protrusive, about twice thickness of upper. Premaxilla robuts, its dorsal process reaching into interorbital space. Distinct secondary lateral process also present. Teeth in two rows in upper and lower jaws not large. Basihyal bone long; basihyal cartilage small. Urohyal with narrow shallow ventral pocket. 5th ceratobranchial fused; occasionally only partially fused in specimens <30 mm SL; ventral wings for attachment of *pharyngoclavicularis* muscle lateral, not markedly high or rounded anteriorly. Gill rakers moderately long with small spinules. Scales not thin; dorsoventrally elongated, in even rows along sides of body. Preopercles and opercles scaled.

For morphometric and meristic differences between species see Table 1; for genetic differences see Tables 2 and 3.

Colour

Live specimens silvery golden colour; midlateral band dark and iridescent; opercles and abdomen silvery; dorsum of head darker than lower part of head. Some spots apparent along sides of body above and below midlateral band. Preserved specimens pale creamy anteriorly to light tan posteriorly. Reticulate marking of scales not apparent, with light speckling of melanophores present on scales above midlateral band. Midlateral band, dark, of even width from upper origin of pectoral fin to caudal peduncle. Dorsum of head with very dark, H shaped marking. Double row of spots apparent below midlateral band and single row above. Abdomen without melanophores. Snout very dark to above upper lip. Lips and chin unpigmented. Eye dark.

Table 2. Table of genetic frequencies for Papua New Guinea *Craterocephalus* together with *C. s. stercusauscarus*. Only loci with different alleles are shown.

Locus/allele		Species			
		C. lacustris	*C. nouhuysi*	*C. randi*	*C. s. stercusauscarus*
ADA	b	0.25	0.75	—	—
	c	0.75	0.25	0.61	0.75
	d	—	—	0.39	0.25
CK	a	—	1.00	0.90	0.25
	b	0.75	—	0.10	0.75
	c	0.25	—	—	—
FUM	b	0.18	—	—	1.00
	c	0.82	1.00	1.00	—
GAPD	a	1.00	1.00	1.00	0.88
	b	—	—	—	0.12
αGPD	a	0.30	0.75	—	0.25
	b	0.70	0.25	1.00	0.75
LDH	a	0.73	0.50	1.00	1.00
	c	0.27	0.50	—	—
MDH	b	0.30	0.50	0.39	0.55
	c	0.70	0.50	0.61	0.45
GPI-1	a	—	1.00	—	—
	b	—	—	—	—
	c	—	—	0.39	1.00
	d	1.00	—	0.61	—
GPI-2	c	—	0.62	0.36	0.21
	d	1.00	0.38	0.64	0.79
IDH	b	1.00	0.87	1.00	1.00
	c	—	0.13	—	—
ME	a	—	—	0.36	1.00
	b	1.00	1.00	0.64	—
MPI	a	—	—	—	0.25
	b	0.90	1.00	1.00	0.75
	c	0.10	—	—	—
PGM	a	0.50	—	—	—
	b	0.50	1.00	1.00	1.00
XDH	b	1.00	0.75	0.75	0.75
	c	—	0.25	0.25	0.25

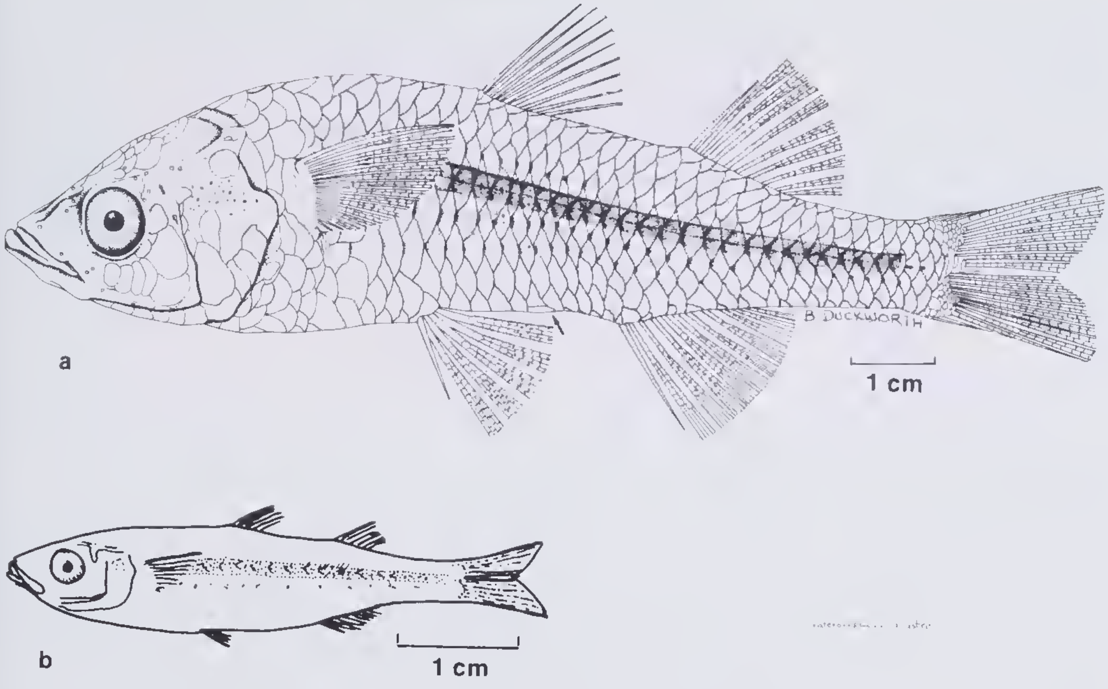

Figure 3a, b *Craterocephalus lacustris,* Lake Kutubu, Papua New Guinea.

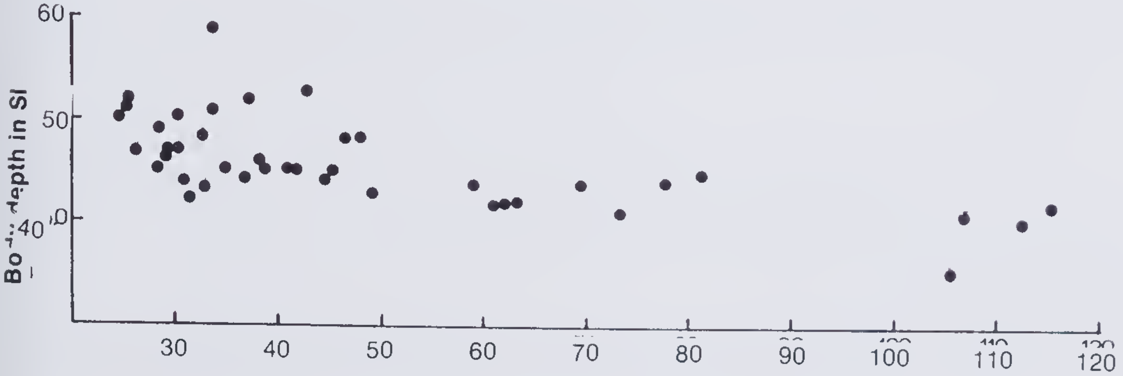

Figure 4. Graph to show relationship between standard length (SL) and maximum body depth as a proportion of SL of *C. lacustris.*

Distribution

All specimens of *C. lacustris* examined were collected in Lake Kutubu. Allen & Hoese (1986) in their description of Lake Kutubu, point out that the lake is drained by the Soro, Hegigio and ultimately the Kikori Rivers, to the Gulf of Papua. Presumably the species may occur in those rivers also. Kailola (1975) reported that this species was also present in Boboa (Lake Murray) and Balimo Lagoon. However, specimens available from that region to the present authors were not *C. lacustris.*

Table 3. Matrix table of R (Rogers, 1972) values for *Craterocephalus* species from Papua New Guinea (calculated from gene frequencies).

	C. lacustris	*C. nouhuysi*	*C. randi*	*C. s. stercusmuscarum*
C. lacustris	0.00	—	—	—
C. nouhuysi	0.25	0.00	—	—
C. randi	0.17	0.18	0.00	—
C. s. stercusmuscarum	0.25	0.30	0.19	0.00

Craterocephalus nouhuysi (Weber)

Figure 5

Atherinichthys nouhuysi Weber, 1910: 229, type locality: Bibis (van der Sande) River, West Irian, lectotype in ZMA (103.175). Paralectotypes in ZMA unless otherwise indicated: Alkmaar, Lorentz River, West Irian, paralectotypes ZMA 103.176 (12) (two specimens exchanged, now AMNH 9577, AMS I.17319-001 [alizarin]); paralectotype, ZMA 103.177 (1), side branch to the right of Lorentz River; paralectotypes ZMA 103.178 (8), rivulet near Alkmaar, Lorentz River; paralectotype ZMA 103.179 (1), Lorentz River, a little north of Alkmaar; paralectotype ZMA 103.180 (1), Beaufort River, 225 km upstream from Bibis River; paralectotype ZMA 103.181 (9), Lorentz River, south west Irian; Weber, 1913a:555; Regan 1914:276.

Craterocephalus nouhuysi: — Jordan and Hubbs, 1919:46; Weber and de Beaufort, 1922:278; Schultz, 1948:20; Munro, 1958:155; Hoedeman, 1960:212; Munro, 1967:172; Nijssen *et al.*, 1982:72.

Remarks

Type designation

Hoedeman (1960), in his list of type specimens in ZMA, designated a holotype and paratypes of *Atherinichthys nouhuysi* Weber. Nijssen *et al.* (1982) correctly redesignated the same specimens as lectotype and paralectotypes. The specimens are listed in the synonymy above.

Material examined

Paralectotypes ZMA 103.176 (5) Alkmaar, Lorentz River, West Irian; ZMA 103.177 (1); ZMA 103.178 (4); ZMA 103.179 (2); ZMA 103.180 (1); ZMA 103.181 (2); WAM P 27806-005 (15), Tributary of Ok Tedi River, 15 km S of Tabubil, Papua New Guinea. Material examined for osteology: paralectotype ZMA 103.176 (1); WAM P.27806 (3). Size range 62.1-95.4 mm SL.

Diagnosis

A freshwater species of *Craterocephalus stercusmuscarum* group most closely related to *C. randi.* Differing from all Papua New Guinea species in having longest basihyal

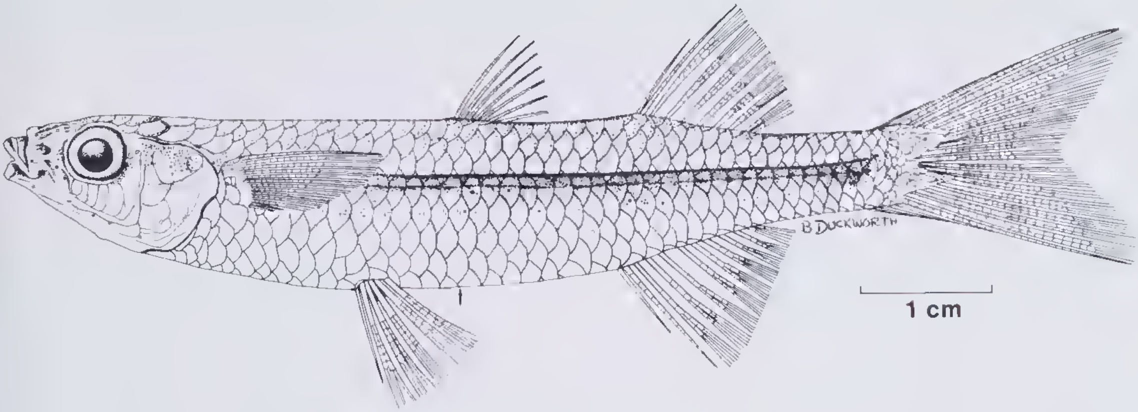

Figure 5. *Craterocephalus nouhuysi,* Tabubil, Papua New Guinea.

bone and rudimentary basihyal cartilage. Sensory canals of nasal and post temporal bones almost completely enclosed. Also differing in shape of nasal bone (see Figure 2). Transverse scale count always 7. Unique amongst the southern drainage species in having *GPI-1*^{a} allele. Differing genetically from *C. randi* in frequencies at several loci *(ADA, α GPD, LDH).*

For genetic comparison with other species, see Tables 2 and 3.

Description

One of the two largest of all members of the genus and superficially resembling *C. randi.* Mouth small with gape restricted by labial ligament. Dorsal process of premaxilla long, slender, reaching well into interorbital space. Teeth in jaws small, barely visible. Gill rakers short, stumpy but slightly longer in angle of arch. Body scales large, dorsoventrally elongated with circuli apparent posteriorly. Dorsum of head with large, almost rectangular scales. Preopercle and opercle scaled.

For morphometrics and meristics, see Table 1.

Colour

Live specimens yellowish with midlateral stripe silvery above and dark below, extending from snout to hypural joint with midlateral band running from snout through eye to hypural joint, but not ending in crescent. No spots along sides of body; body above and below midlateral band uniform in colour. Dorsum of head, snout and upper lip dusky; opercles and eye silvery; preopercle sometimes iridescent. Paired fins clear, caudal fin golden. Preserved specimens cream to yellowish with dark midlateral stripe, paler through opercle, eye and snout. Melanophores on scales above midlateral stripe not forming reticulate pattern; no pigmentation below midlateral stripe. Paired fins and caudal fin with faint markings along rays. Eye dark to silvery. Dorsum of head, snout and upper lip dusky with lower lip cream to whitish.

Distribution

Known originally from Lorentz River in West Irian, now also from the upper tributaries of Fly River (Tedi River near Tabubil). The specimens from the latter are similar to the paralectotype material from the type locality, with only minor differences in some of the body proportions. Although the two river systems are quite separate, the coastal lowlands may allow dispersal. It is therefore possible that this species may also occur in rivers between. Further collecting is necessary to determine whether the present distribution is indeed disjunct.

Comments

The unique sharing of the *GPI-1*^{a} allele together with an osteological similarity in the sensory canals between *C. kailolae* and *C. nouhuysi* is difficult to explain. The former belongs to the *eyresii* group, the latter to *stercusmuscarum*. *C. kailolae* occurs in the northern drainage of Papua New Guinea, with all the other members of the species group occurring in Australia. Similarly, the distribution of several species of *Pseudomugil* shows that they too are disjunct (Saeed, Ivantsoff and Allen, 1989).

Craterocephalus randi Nichols and Raven
Figure 6

Craterocephalus randi Nichols and Raven, 1934:3, type locality: Kubuna (Kubuna river), British Papua; holotype in AMNH (12477), paratypes (4), in AMNH (12525); Whitley, 1938:226; Schultz, 1948:20; Munro, 1958:155, 1967: 174.

Craterocephalus annator Whitley, 1938:226, type locality, Fly River, Papua, about 50 km above d'Albertis Junction; holotype in AMS (IA.7228), paratypes (7), in AMS (IA.7228); Schultz, 1948:20; Munro, 1958:155, 1967:174.

Material examined

Holotype AMNH 12477, Kubuna (Kubuna River), British Papua. Partypes AMNH 12525 (4), as for holotype; Holotype of *C. annator* AMS IA.7228 Fly River, Papua, 30 miles above d'Albertis Junction. Paratypes *C. annator* AMS IA.7228(7), as for holotype; AMS IB.7054-7059(9) Lake Murray (Mawa) New Guinea; MQUWI 70-41a (16) Weam (Torassi and Bensbach Rivers); KFRS FO.4009 (9) Nomad, Papua

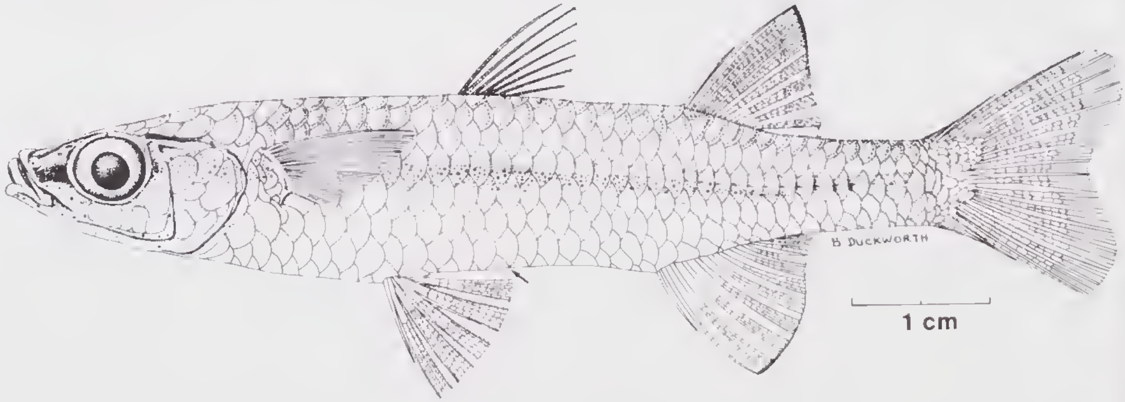

Figure 6. *Craterocephalus randi*, Kubuna, Papua New Guinea.

New Guinea; KFRS FO.4012 (7) Sinamre; downstream from Rumginae; MQUWI 70-41b (2) Balimo, north of Fly River. 25 specimens examined, size range 36.2-71.9 mm SL. Other material examined but not used for measurements and counts: WAM P.28139-005 (1), 10 km north of Kiunga; WAM P.28140-003 (6), 2 km north of Kiunga; WAM P.28141-004 (5) Elevelak, 17 km east of Kiunga; WAM P.28147-004 (8), Fly River, near Dora Village, in the vicinity of Kiunga; WAM P.28149-005 (3), 5 km west of Oboe near Kaviananga, south of Kiunga. Material used for osteology: MQU W170-41a (3), Fly River, Papua New Guinea.

Diagnosis

Freshwater species belonging to *C. stercusmuscarum* group, most closely resembling *C. stercusmuscarum stercusmuscarum* on counts and measurements and *C. lacustris* on electrophoretic data. Uniquely distinct from other Papua New Guinea species in shape of nasal bone (see Figure 2) and with lateral ramus of premaxilla more highly elevated than in other species; basihyal bone long; cartilage about half length of bone. Ventral wings of fused 5th ceratobranchial medial position and lateral in all others. Sharing only with *C. nouhuysi* and *C. pimatuae* elongate anal plate and interdorsal pterygiophores with well developed ventral processes. Differing from other Papua New Guinea species by gene frequencies at several loci *(ADA, CK, αGPD, GPI-1, GPI-2).*

For genetic differences see Tables 2 and 3. Only distinguishable by combination of meristic and morphometric characters.

Description

Slender bodied freshwater fish, externally most closely resembling *C. s. stercusmuscarum.* Mouth small, gape restricted by labial ligament. Dorsal process of premaxilla moderately short, not reaching into interorbital space. Teeth moderately long, in two rows in upper and lower jaws. Gill rakers very short, pointed and very sparse. Scales with circuli apparent in smaller specimens. Preopercle and opercles scaled. Dorsum of head with large scales.

For meristics and morphometrics see Table 1.

Colour

Live specimens closely resembling *C. s. stercusmuscarum,* often with deep golden abdomen, jet black spots along sides of body and silvery sheen. Eye usually dark, opercles silvery-blue; midlateral band obvious and unbroken from snout, through eye and pectoral fin to caudal peduncle, ending in upward pointing crescent. Preserved specimens similar to *C. s. stercusmuscarum,* often with intense spotting along sides of body frequently fading with time when preserved. Reticulate pattern on scales above midlateral band. Midlateral band as in live specimens. Fins dusky with melanophores apparent on rays; tips of caudal dusky; base of all fins dark. Opercle silvery below midlateral band and cream above. Dorsum of head and snout dark; lips and chin peppered with melanophores.

Distribution

Known from the Fly, Bensbach, Kubuna and Strickland Rivers, from Lake Murray (also see Kailola, 1975). This species appears to be fairly common in the lower reaches of southern rivers in Papua New Guinea. Further collecting may prove its range to be more extensive as there are areas of the country still not readily accessible.

Comments

Craterocephalus randi has been often confused with *C. stercusmuscarum* (e.g. Allen and Hoese, 1980; Taylor, 1964). The colour pattern of both species is very similar but varies in intensity from locality to locality, within a locality and from time to time. Genetically, *C. randi* is distinct from *C. stercusmuscarum* at *FUM* (fixed gene difference) with alternate alleles at *CK*, polymorphic versus monomorphic at *GPI-1*. Genetically *C. randi* appears to be most closely allied to *C. lacustris*, differing at *PGM* locus. The status of *C. annator* had been questioned by Ivantsoff in 1978 although the Fly River population is usually pale in colour and without marking, unlike *C. randi* from other localities. Present electrophoretic study shows that the placement of *C. annator* into the synonymy of *C. randi* is correct as no differences could be found between specimens from Kubuna (the type locality for *C. randi*) and those from Fly River streams and tributaries (the type locality of *C. annator*).

Craterocephalus stercusmuscarum stercusmuscarum (Günther)

Figure 7

Atherina stercus muscarum Günther, 1867: 64, type locality: Cape York, Queensland; syntypes in BMNH (1867.5.6.61-62 [2]).

Atherina stercus-muscarum: — Macleay, 1881: 40.

Atherinichthys maculatus Macleay, 1883: 207, type locality: Lillismere Lagoon,Burdekin River; types lost.

Craterocephalus maculatus: — McCulloch, 1913: 52.

Craterocephalus stercus-muscarum: — Jordan and Hubbs, 1919: 45.

Craterocephalus stercus-muscorum: — Nichols and Raven, 1934: 4.

Craterocephalus stercusmuscarum: — McCulloch, 1929: 110; Whitley, 1957: 16; Munro, 1958b: 102; Lake, 1971: 28; Grant, 1982: 773; Pollard, 1974: 1-32; Merrick and Schmida, 1984: 148.

Craterocephalus worrelli Whitley, 1948: 86, type locality: Mataranka, Roper River system, Northern Territory; holotype in AMS (1B.1915); Munro, 1958b: 102; Allen, 1975: 92.

Craterocephalus tanii?: — Hansen, 1987: 167 (misnomer, presumably for *randi.*)

Craterocephalus randi: — Allen and Hoese, 1980: 55 (misidentification).

Craterocephalus stercusmuscarum stercusmuscarum: Ivantsofft *et al.*, 1987b: 172.

Material examined

Holotype of *C. worrelli*, AMS 1B.1915*, Mataranka, Roper River System, Northern Territory; CSIRO A.1224-6 (3)*, Mataranka, Roper River System; AMS 1B.3700 (1)*, Darwin; AMS 1B.4125-7 (25), Bamaroogjaja Swamp, South Alligator River; AMS 1.17728-001 (3)*, Muddy Lagoon off Jim Jim Creek; AMS 1.17727-001 (10), Lily Lagoon near Barramundie Creek; AMS 1.177730-001 (10), Red Lily Lagoon, near Daly River Police Station; DR 1969-119 (1), Wildman Creek at Oenpelli-Darwin Road; AMS 1.16859-007 (62), Magela Creek, Jabiru. All of the above localities in the Northern Territory, Australia.

BMNH 1867.5.6.61-62 (2), Cape York Peninsula, syntypes of *Atherina stercusmuscarum;* AMS 1.18542-001 (6)*, Black River, about 25 km north of Townsville; MQU W175-21 (15)*, Cairns environs; MQU W176-41 (4)*, Rockhampton; MQU W176-40 (2)*, Bob's Creek, Rockhampton; AMS 1B.5055 (5)*, Barron River, Kuranda; AMS 1B.781 (1)*, Charters Towers; AMS 1A.2386 (2)*, AMS 1B.3722 (1)*, Alligator Creek, Townsville; AMS I.12767 (45), Burnett River, Eidsvold; AMS IA.3674 (174), Lake Barrine, Atherton Tableland; AMS IB.28732 (2), Pioneer River, Mackay; AMS IB.3503 (2), Gayndah; AMS I.18014-001 (5), O'Shanassy River; AMS I.17989-002 (24), Leura Homestead, McKenzie River; AMS I.17957-005 (1), Gregory River near Riversleigh Station. All of the above localities in Queensland, Australia.

*Specimens used for measurements and counts.

Material used for osteology: MQU W175-21 (4) Cairns; MQU Ia-129 (1) Hervey Creek, south of Cairns, Australia.

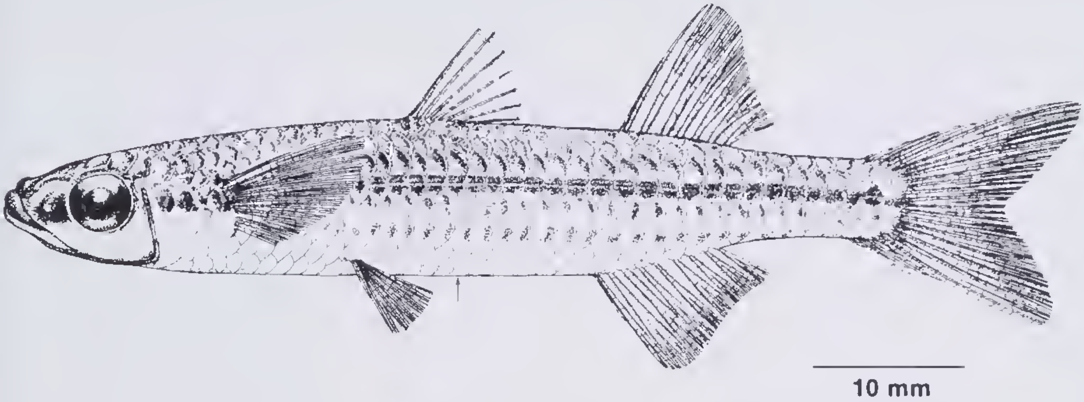

Figure 7. *Craterocephalus stercusmuscarum stercusmuscarum* Mataranka, Northern Territory.

Diagnosis

Widespread species of Australian hardyhead closely related to Papua New Guinea species but distinguished from them by shape of nasal bone, anal plate not elongate (Figure 2), gill rakers leaf-like and covered with spinules; with small teeth in 2-3 rows in both jaws. Distinguished genetically at *FUM* locus and in some allele frequencies *(ADA, CK, αGPD, ME, MPI).*

For genetic differences see Tables 2 and 3.

Description

Slender freshwater species, closely related to all southern Papua New Guinea species and to the Australian subspecies *C. s. fulvus.* Lips fleshy, mouth small, with gape restricted by labial ligament. Premaxilla not reaching vertical through anterior margin of orbit; dorsal process moderately long, just reaching interorbital space in most specimens. Teeth small, in 2 or 3 rows in upper and lower jaws. Other bones of mouth edentulous. Wings of fused 5th ceratobranchial lateral, not high and rounded anteriorly. Gill rakers moderately long and leaf-like but less than half diameter of pupil with distinct spinules present. Small, round scales, in even rows on side of body. Distinct concentric circuli on all body scales.

For morphometrics and meristics see Table 1.

Colour

Live specimens extremely variable from locality to locality, within locality and from time to time; ranging from greenish yellow and translucent, with only faint markings but with midlateral stripe obvious, to solid silvery gold with deep golden abdomen and distinct black spots. All fins yellowish. Black mark near vent in females when running ripe, abdomen of male becoming bright gold when sexually mature (Lake, 1978). Preserved specimens yellow to light brown with grey or dusky fins. Centre of each scale if pigmented forming black spot, with latter often appearing confluent with adjacent spot to form black lines along side of body. Midlateral band running from snout through eye, opercle to hypural joint. Dorsum of head black and dorsal surface of body darker than ventral. Preserved specimens losing colour with time.

Distribution

Craterocephalus stercusmuscarum stercusmuscarum is a widespread Australian species inhabiting rivers and creeks of northeastern Queensland and extending as far south as Dee River at Dululu. This species is also common in the rivers west of the Dividing Range draining into the Gulf of Carpentaria and the northern rivers of Northern Territory including the Roper, Alligator and Edith Rivers. Occasionally single specimens which may be attributed to *C. s. stercusmuscarum* are found further to the south in South Australian waters (Finnis River, Nilpena Springs) but genetic affinities of the latter are yet to be determined.

Comments

The justification for the recognition of two subspecies of *C. stercusmuscarum* is recorded in Ivantsoff *et al.* (1987) but in the context of the newly described subspecies, *C. s. fulvus.* The redescription of *C. s. stercusmuscarum,* however was omitted. Additional studies (electrophoretic and osteological) now allow a detailed comparison of this species, not only with its other subspecies but also with *C. randi,* its other close relative.

The confusion between *C. s. stercusmuscarum* and *C. randi* has already been discussed. Failure to recognize the variability of coloration had also led to a description of several species which are now regarded as indistinct from *C. stercusmuscaraum.* A thorough description of *Atherinichthys maculatus* by it's author (Macleay, 1867) has left no doubt that it is indistinct from Günther's flyspecked hardyhead (Jordan and Hubbs, 1919). Examination of the type of *C. worrelli* and subsequent collection of additional specimens from the type locality also leaves no doubt that *C. worrelli* is not different from *C. s. stercusmuscarum.* Genetic analysis of Mataranka specimens shows that they are indistinct from other populations of *C. s. stercusmuscarum* and are genetically conservative.

Discussion

Most of the land mass which is now Papua New Guinea, is geologically young. However, some areas date from Eocene and Oligocene (Dow, 1977; Pigram and Davies, 1987). Whilst the northern half of Papua New Guinea is an accretion of islands derived from the Asian plate, the southern half is the leading edge of the Australian tectonic plate. The two collided during Tertiary (Pigram and Davies, 1987).

The species of hardyheads from the southern drainages of Papua New Guinea are closely related to *C. s. stercusmuscarum* from northern and north eastern Australia. This relationship is not unexpected as Australia and Papua New Guinea have been connected by the Torres Land Bridge intermittently during Tertiary and Quaternary, with the present marine transgression separating the landmasses only about 7-10 thousand years ago.

It is well documented that a large lake (Lake Carpentaria) formed in the Torres Land Bridge during the last glacial maximum when the sea level was below —53 m (Smart, 1977; Jones and Torgersen, 1988). Whether this lake was brackish or fresh is debatable. It may have been closed to the sea and containing only internal drainage fresh water (Jones and Torgersen, 1988) or it may have always been joined to the Arafura Sea by a narrow channel with brackish water (Galloway and Löffler, 1972). With this internal drainage, whether brackish or entirely fresh, dispersal was possible for euryhaline fish species such as atherinoids and allowed them to cross from one land mass to the other. It is now known (Allen and Cross, 1982; Saeed *et al.*, 1989) that some species of rainbowfishes and blue-eyes are found on either side of Torres Strait. Genetic comparison of populations of these species of fish should nonetheless be made to determine whether divergence has already begun.

Radiation of *Craterocephalus* species and possibly others appears to be a recent phenomenon, from about Plio/Pleistocene. During Miocene, most of southern New Guinea was under shallow marine transgression (Dow, 1977). Crowley (in press) suggests that invasion of freshwaters by the ancestor of the *C. stercusmuscarum* group occurred in that area (northern Australia/southern Papua New Guinea).

With the subsequent fall of sea level, swampy lowlands around the mouth of Fly River emerged. These lowlands, together with seasonal flooding during Pleistocene and Holocene appear to have allowed movement of fish between the rivers which drained into the same flood plain, much as species today move between rivers of the Gulf of Carpentaria during the wet season when the area becomes a vast flood plain (Simpson and Doutch, 1977). Judging by genetic distance (Table 3), there appears to have been very little opportunity for speciation to occur. Isolation occurred nevertheless, resulting in distinct and localized species such as *C. lacustris* and *C. pimatuae.* The Torres Strait Barrier had allowed for recent separation between *C. randi* and *C. s. stercusmuscarum* with the genetic distance between them being quite small (R=0.19) but similar to the distances between all Papua New Guinea species in the southern drainage (Figure 8b). No specimens of *C. pimatuae* were available for electrophoresis. The comparison of Figure 8a and 8b is therefore not possible since one of the species is excluded from the genetic study. The latter study, nonetheless gives an indication of the recency of speciation between Australian and New Guinea hardyheads available for analysis.

Examination of cluster analysis (Figure 8a) shows that the osteological differences set *C. pimatuae* apart from other Papua New Guinea species. Considering the apparent osteological conservatism of atherinids (see Todd, 1976) the differences of *C. pimatuae* suggest that separation of this species had taken place prior to separation of other Papua

New Guinea hardyheads. This hypothesis cannot be verified until fresh material is available for electrophoresis.

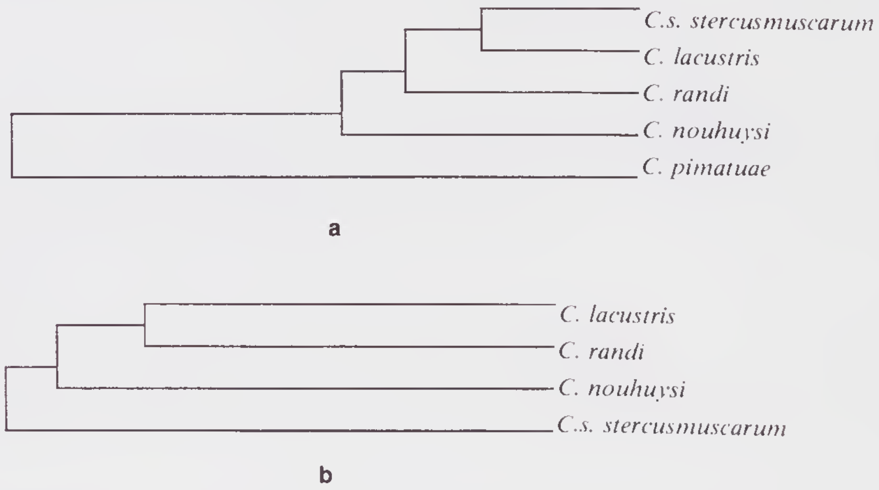

Figure 8. Cluster analysis of Papua New Guinea species of *Craterocephalus* and *C. s. stercusmuscarum* using a) osteological characters and b) Rogers' genetic distance values.

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Scruttonia (Rugosa, Cnidaria) from the Devonian of Western Australia

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Abstract

Phillipsastrea delicatula Hill, 1936, from probably the early Frasnian (early Late Devonian) of the Lennard Shelf, Western Australia, is assigned to the cosmopolitan rugose coral genus *Scruttonia*. Its occurrence there supports the previously reported cosmopolitan nature of Late Devonian rugose coral faunas and the faunal similarities between eastern and Western Australia in the Devonia.

Introduction

During the study of a Frasnian (early Late Devonian) coral fauna from the Keepit district of New South Wales, in the New England Fold Belt (Wright *et al.* in press), it was of considerable interest to compare the Keepit fauna with the famous faunas of the same age from the Lennard Shelf of the Kimberley region of Western Australia (Hill and Jell 1970), in order to assess biogeographic relationships. Examination of coral specimens from Western Australia revealed that the somewhat neglected species *Phillipsastrea delicatula* Hill, 1936 is congeneric with corals belonging to *Scruttonia* from the Keepit region. *Phillipsastraea delicatula* was proposed by Professor Dorothy Hill (1936: 30) in the first of her papers on the Western Australian coral faunas, and has only been redescribed by Hill (1954).

The purpose of this paper is to draw attention to this occurrence of *Scruttonia* in Western Australia; to describe and illustrate the available material; and to report on the biogeographic implications of the distribution of the genus.

Systematics

Phylum Cnidaria

Subclass Rugosa Edwards and Haime, 1850
Family Phillipsastreidae C.F. Roemer, 1883
Genus *Scruttonia* Cherepnina, 1975

Type Species

Smithia bowerbanki Milne-Edwards and Haime, 1851; from the lower Frasnian (early Late Devonian) of south Devon, England.

Diagnosis

McLean (1989) has given a diagnosis for the genus.

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Remarks

The detailed morphology of the cosmopolitan genus *Scruttonia* has been described by Pedder (1986) who reviewed and gave a list of species assigned to the genus. The type species has been described by Scrutton (1968) and Rohart (1981); Pedder (1986) tentatively assigned material showing strong carinae to this species, whereas Scrutton (1968) noted that the septa are never truly carinate in British material (see Rohart [1981] for illustration of septal structure of topotype material of the type species). Diagnostic features of the genus thus include thamnasterioid growth form, carinate or non-carinate septa, lack of horseshoe dissepiments and a narrow symmetrical zone of trabecular fanning close to the inner margin of the non-everted or weakly everted dissepimentarium.

There has been divergence of opinion about the validity of *Scruttonia,* as Birenheide (1978) considered it a symonym of *Haplothecia,* whereas Scrutton (1978), Coen-Aubert (1980), Rohart (1982) and McLean (1989) considered the genera separate; Hill (1981) and Pedder (1986) have tentatively accepted the genus as distinct. Pedder (1986) noted that the two genera are not typical phillipsastreids, and could be referred to a new subfamily.

Several genera of Chinese Devonian rugose corals are difficult to distinguish from *Scruttonia,* as discussed by Pedder (1986), Küster (1987), McLean (1989) and Wright *et al.* (in press). *Haplothecia (Kuangxiastraea)* Yü and Kuang, 1982 was considered by Pedder (1986) to be a genus distinct from *Scruttonia,* but not satisfactorily separated from *Sichuanastraea. Billingsastraea (Sichuanastraea)* He, 1978 was considered by Küster (1987) to be synonymous with *Scruttonia. Haplothecia (Lanceothecia)* Yü and Jiang in Jiang (1982) is a *nomen nudum* and, according to Pedder (1986: 655), possibly a junior subjective synonym of *Haplothecia (Kuangxiastraea).*

Scruttonia delicatula **(Hill, 1936)**

(Figure 1a, b)

Phillipsastraea delicatula Hill, 1936: 30, figures 4-5
Phillipsastrea delicatula; Hill, 1954: 14, pl. 1, figure 19

Type Material

Hill (1936) designated as holotype "F. 326 [catalogued as F. 328] = 6924" in the collections of the Geological Survey of Western Australia; according to Hill (1936: 30), the specimen was mentioned by Glauert (1910a, b, 1925) and Hosking (1925). This specimen, known only from Hill (1936, figure 4), is missing (S.K. Skwarko pers. comm. 1989).

Other material mentioned by Hosking (1925) and Hill (1936) included Western Australian Museum (WAM) numbers 4435-6, collected by J.E. Wells in 1922. These two (?) specimens and the holotype were stated by Hill (1936) to come from 'Barker Gorge, Napier Range, Kimberley'. However, this numbering refers to only one specimen (K.J. McNamara, pers. comm., 1989); the thin section figured by Hill (1936, figure 5) bears the inscription 4435/6. The only thin section material of the species I have been able to study is the figured longitudinal thin section and a small transverse section prepared from the specimen WAM 4435.

Hill (1954) mentioned two further specimens (CPC 539 and R 225B; Bureau of Mineral Resources, Geology and Geophysics, Canberra collections) collected by H.B. Woodward in 1906 from the Sparke Range, Margaret River, west Kimberleys, and illustrated the former specimen (Hill 1954, pl. 1, figure 19a, b). These specimens are missing, and were probably destroyed in the 1953 BMR fire at Acton (D.L. Strusz, pers. comm., 1988).

Thus, the only relic of this uncommon species in WAM 4435, fortunately a paratype.

Age

Playford and Lowry (1966: 61) state that *S. delicatula* is from the Givetian to early Frasnian part of the Pillarar Limestone. I suggest that the latter age is the more likely. Material from the Barker Gorge may well have been reworked, as the coral specimen is set in a matrix of quartz grains.

Diagnosis

Scruttonia with up to 19x2 septa with mostly zig-zag carinae; trabeculae form a prominent half-fan near inner edge of dissepimentarium, which is not everted; tabularium diameter about 1.3mm, with depressed tabulae flanked by axially-inclined tabellae.

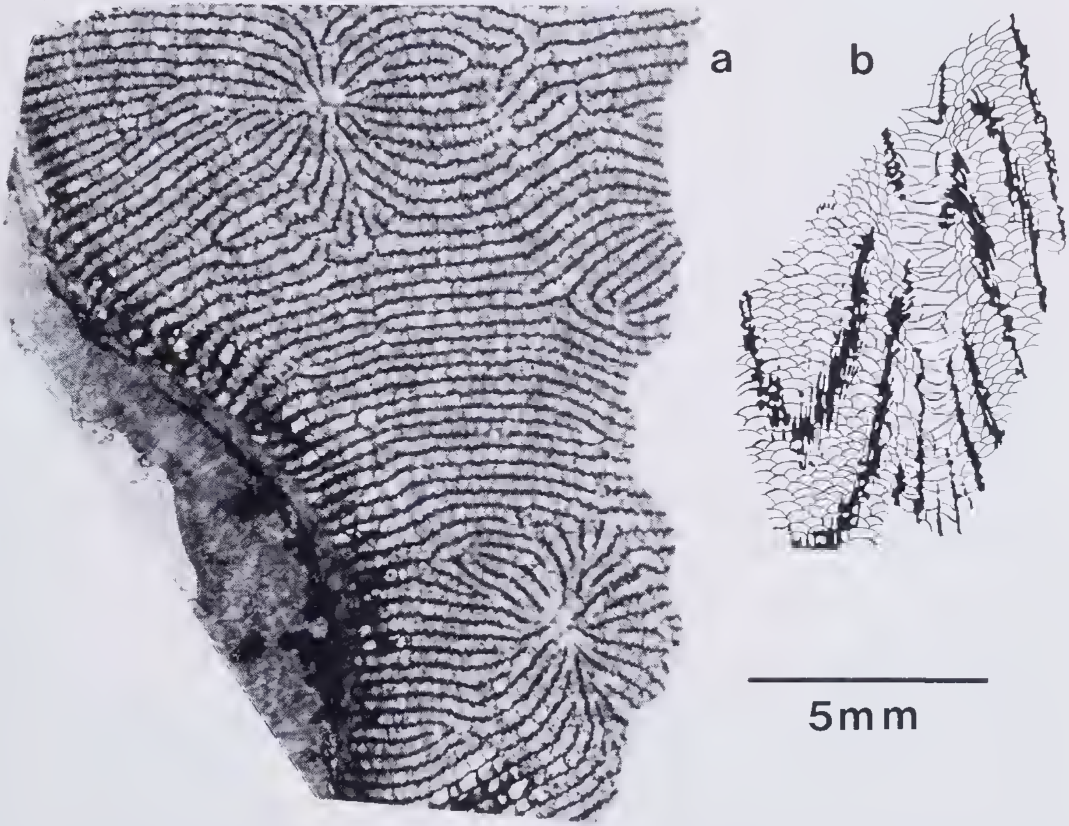

Figure 1a-b. *Scruttonia delicatula* (Hill, 1936), paratype WAM 4435. Pillara Limestone, Barker Gorge, Napier Range, Kimberley district, Western Australia. Probably early Frasnian. 1a, transverse section, x6. 1b, drawing of longitudinal view, x6. Bar scale 5mm.

Description

Apparently strongly thamnasterioid, although the confluent septa cannot be seen joining adjacent corallites in presently available material (see, however, Hill [1936, figure 4] and Hill [1954, pl. 1, figure 19a] for highly confluent septa in this species); about 14x2 carinate septa, possibly up to 19x2; the major septa are slightly withdrawn from the axis; minor septa do not enter the tabularium; both orders of septa show slight, variable development of mostly zigzag carinae, and both are slightly dilated at the colony margin. Septal insertion is marked in the two corallites ilustrated (Figure 1a); up to 7 major septa occur in the counter quadrant, and about 4 in the alar quadrant. Coarse trabeculae form a half-fan (Figure 2) towards the inner part of the dissepimentarium, with trabeculae normal to dissepimental surfaces in the coenosteum. Horizontally disposed, gently arched dissepiments form the coenosteum between corallites, without any eversion at corallite margins; several rows of inclined dissepiments; large axially-inclined tabellae merge with the rather widely spaced tabulae which vary from transverse and complete to sagging; Dt about 1.3mm.

Remarks

This small fragment of a colony is quite inadequate for establishing all the specific characters. The transverse section (Figure 1a) shows two apparently immature corallites in which septal insertion is suggested by arrangement of short septa flanking longer septa; unfortunately, it is uncertain which are the counter, cardinal or alar septa (or even whether some septa are major or minor), but there are apparently up to 19 major septa. The longitudinal section (Figure 2) is oblique, and hence the trabecular structure is incompletely known. Although *Scruttonia* is defined as having a symmetrical trabecular fan, the trabecular half-fan seen in *S. delicatula* (Figure 2) is also illustrated for *S.* sp. cf. *S. bowerbanki* by Pedder (1986, figures 78.20, 78.21) and for *S. boloniensis* Milne-Edwards and Haime by Rohart (1981, pl. 2, figure 1b).

Comparison

This Western Australian species has a greater number of more carinate septa than *S. bowerbanki* as currently known from the work of Scrutton (1968), Tsien (1977), Coen-Aubert (1980a), Rohart (1981) and Pedder (1986). *S. boloniensis* is distinct in its equally spaced corallites; very long, equally withdrawn major septa; and larger tabularia (Rohart 1981).

Implications

The shared occurrence of *Scruttonia* provides another link in the previously recognised similarities at the general level in Late Devonian faunas between Western Australia and New South Wales (e.g. Talent 1984, p. 76). This conforms with the generally recognised cosmopolitan aspect of Late Devonian coral faunas (Oliver and Pedder 1989, figure 3). Unfortunately, the fauna associated with *S. delicatula* is not known (other than sparse data in Glauert 1910b), so the affinities of the entire fauna cannot be assessed. However, further comparisons of the Keepit and Western Australian coral faunas reveal surprisingly few faunal elements common to these two regions

(Wright *et al.* in press). Roberts (1971:1) stated that the Frasnian brachiopods of Western Australia belonged to a world-wide 'platform' fauna, noting (Roberts 1971: 32) that the eastern Australian Late Devonian brachiopod faunas are not well known in detail (see also Veevers 1959).

Pedder (1986: 659) concludes that *Scruttonia* is restricted to the Frasnian, and thus the occurrence of *delicatula* in Western Australia is likely to be of this age.

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Redescription of *Aulactinia veratra* n. comb. (=*Cnidopus veratra*) (Coelenterata: Actiniaria) from Australia.

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Abstract

The actinian described as *Actinia veratra* Drayton, 1846, and currently referred to as *Cnidopus veratra,* belongs to the genus *Aulactinia.* Discrepancies in the literature, particularly concerning ectodermal specializations of the column, led to taxonomic uncertainties about its placement. Nomenclatural re-evaluation was necessitated by recent synonymization of the genus *Cnidopus* with *Epiactis. Cribrina verruculata* Lager, 1911, is synonymized with *Aulactinia veratra.*

Introduction

In this study we evaluate the taxonomic and nomenclatural status of the actiniid sea anemone originally described as *Actinia veratra* Drayton in Dana, 1846, and currently commonly referred to as *Cnidopus verater.* The genus *Cnidopus,* created by Carlgren (1934) for *Epiactis ritteri* Torrey, 1902, has been synonymized with *Epiactis* (Fautin and Chia 1986).

Carlgren (1934: 351) erected *Cnidopus* on the basis of "very numerous nematocysts present at the sides of the protuberances and between them in the lowest parts of the column", which he identified as "probably atrichs" (= atrichous isorhizas). These cnidae actually possess small spines (Bigger 1976, 1982) and so are correctly termed holotrichous isorhizas (= holotrichs). Carlgren (1949) omitted this species from his catalog of Actiniaria, but later (1950a, b) referred *Actinia veratra* to *Cnidopus.* In the process, he inexplicably changed the species name to *verater,* which Ottaway (1975) considered a deliberate emendation that should not supercede the original spelling. Carlgren subsequently (1950b, 1952) referred the Japanese sea anemone called *Epiactis prolifera* Verrill, 1869, (e.g. by Uchida and Iwata 1954) to the genus as *Cnidopus japonicus.*

Fautin and Chia (1986) returned *C. ritteri* to *Epiactis* because they found that the type species of the genus, *E. prolifera,* has holotrichs in the lower column. They urged that the other two species attributed to *Cnidopus* be studied to determine if they, too, actually belong to *Epiactis.* We examined Australian specimens of *C. veratra* to establish the

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appropriate generic placement of this species; although it has not been formally re-examined, Dunn (1972) concluded from the literature and correspondence with Uchida that the Japanese species, *"C. japonicus"*, should be returned to *Epiactis*.

Materials and methods

Sea anemones from the intertidal zone of Pt. Peron, Western Australia (32°16′ S, 115°40′ E), and Barwon Head, Port Philip Bay, Victoria (39°25′ S, 144°50′ E) were examined alive and then preserved. Preserved specimens for comparison were sent to us from North Beach at Wollongong, New South Wales (34°25′ S, 150°52′ E), and from Portobello, South Island, New Zealand (45°51′ S, 170°39′ E).

Cnidae measurements were made from tissue smears of 10 individuals, although not all tissues of each individual were studied. Paraffin sections cut at 8 μm were stained with hematoxylin and eosin for histological study.

Voucher specimens in the Department of Invertebrate Zoology and Geology, California Academy of Sciences are as follows: *Aulactinia veratra* from Western Australia catalog #066250 (x4, including histological sections from three); from New South Wales #065139 (x1), #065140 (x1), #065141 (x1), #065154 (x2, including histological sections from both); unidentified actiniid from New Zealand #065138 (x7). Four voucher specimens from New South Wales, including histological sections from one, in the Western Australian Museum bear catalog number WAM 861-89.

Aulactinia veratra new combination.

Synonymy

Actinia veratra Drayton in Dana 1846: 129-130. Drayton in Dana 1848: 129-130. Dana 1849: pl.1, figure 3. Dana 1859: 6.

Phymactis veratra Milne-Edwards 1857: 275. Andres 1883: 228.

Cribrina verruculata Lager 1911: 233-234.

Bunodactis verruculata Carlgren 1949: 65.

Cnidopus verater Carlgren 1950a: 124-125. Carlgren 1950b: 137-138, figure 7, 8; pl. III, figure 3. Carlgren 1952: 387. Dakin *et al.* 1952: 136, 137, pl. 22. Carlgren 1954: 571, 576, 593. Ottaway 1975: 58-59. Bennett 1987: 175.

Cnidopus veratra Ottaway 1975: 58-59.

Description

Pedal disc

Well developed, more or less circular, pale tan. Diameter approximately equal to that of column; to 35 mm in specimens examined.

Column

Height 8-15 mm in preserved specimens, average 20 mm in live specimens. Typically green, less commonly brown or reddish brown in color; lighter adhesive areas in longitudinal rows run entire length of column. Histologically adhesive areas composed

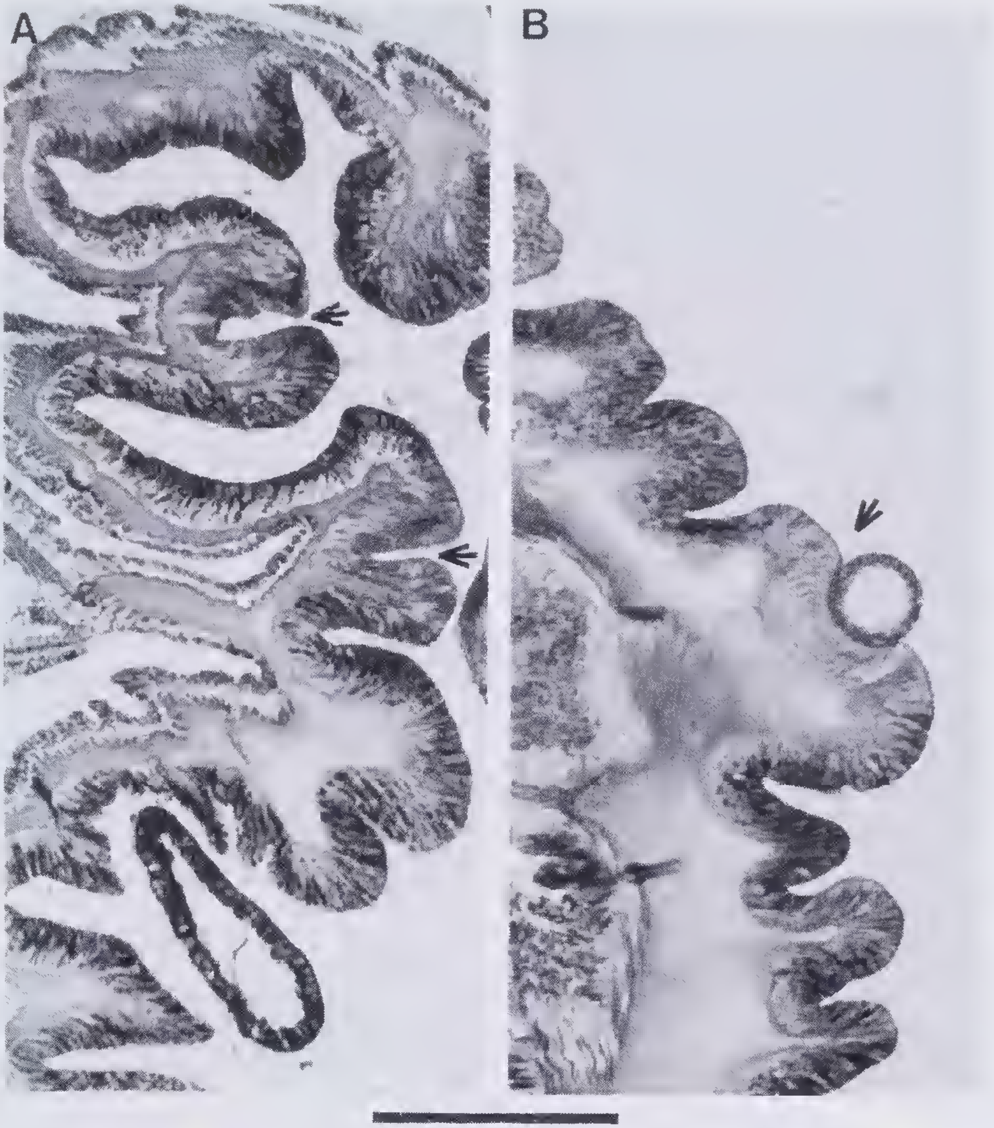

Figure 1. Sections through adhesive areas on column: A) verrucae in upper column; B) sucker in lower column. (CAS 066250). Scale bar = 360 μm.

of less vacuolated and more tightly packed cells than regular ectoderm (figure 1); some appear as true complex verrucae (figure 1A), others as suckers (figure 1B). No spherules or pseudospherules at margin.

Endodermal sphincter muscle strong, circumscribed to circumscribed-diffuse, generally palmate, on marginal side of distinct fosse (figure 2).

Oral disc

Flat, mouth central. Tentacles restricted to marginal half.

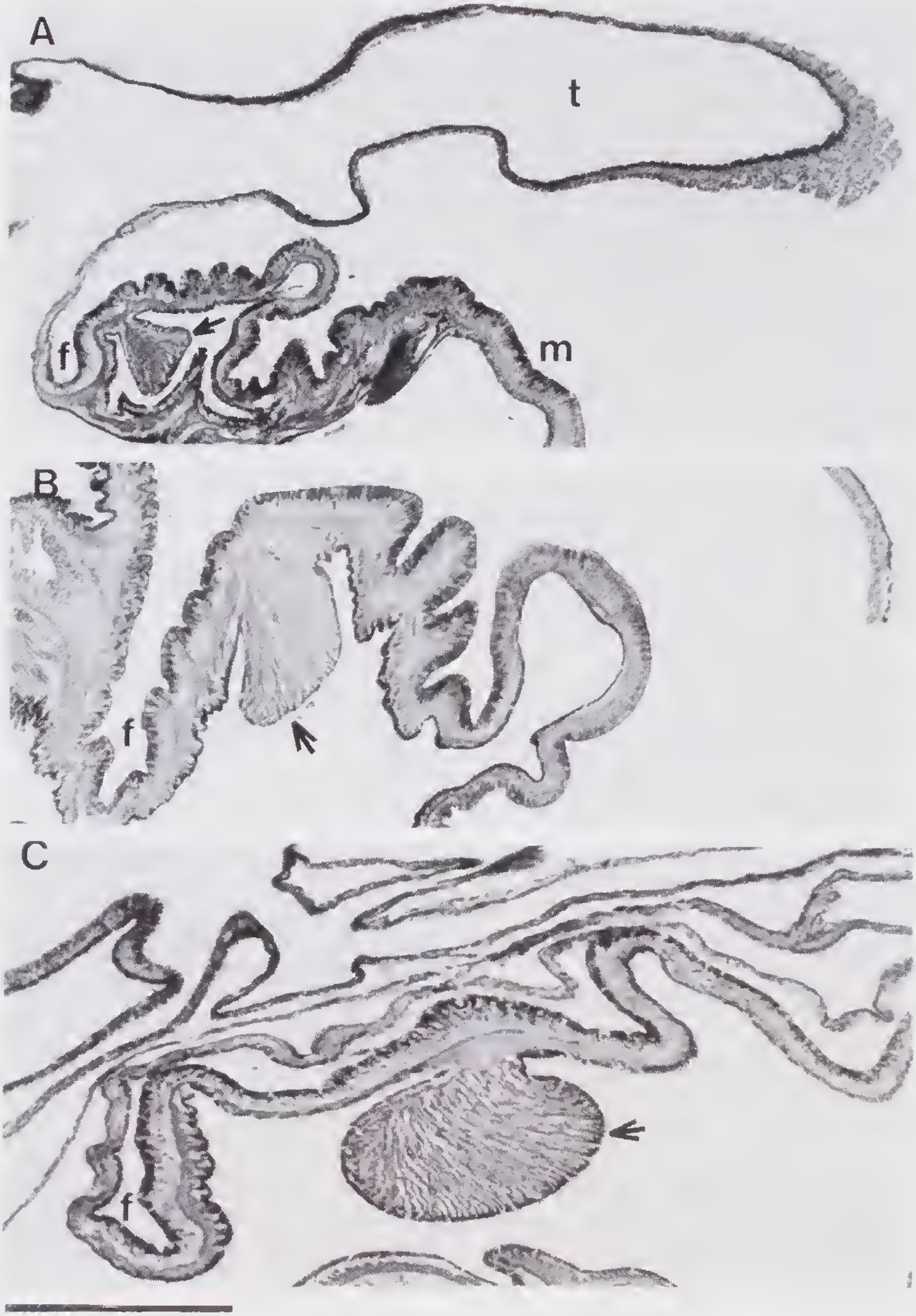

Figure 2. Longitudinal sections through upper column illustrating variability of sphincter muscle (arrow). Sphincter is consistently on marginal side (m) of fosse (f) (CAS 066250). Scale bar = 645 μm for A; 345 μm for B, C.

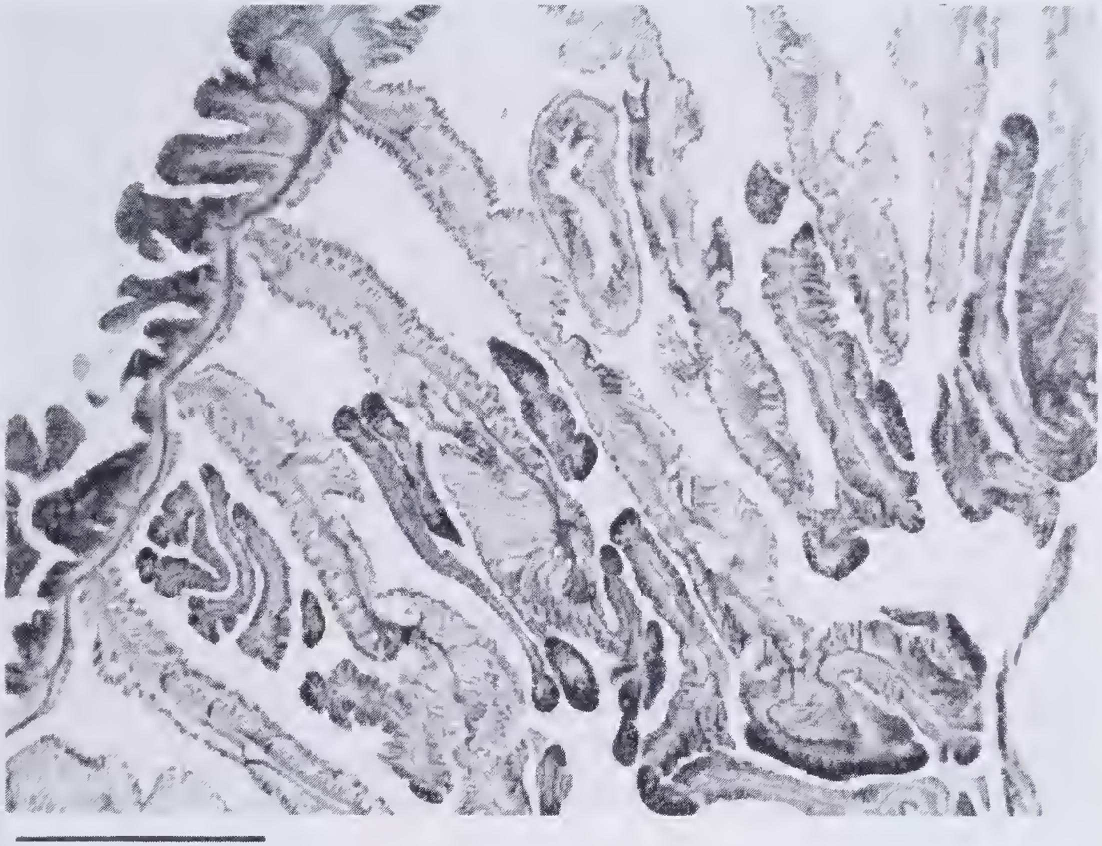

Figure 3. Cross section showing mesenteries (CAS 066250). Scale bar = 720 μm.

Tentacles

Conical, blunt-tipped, regularly arrayed, same color as rest of animal. Central ones held erect; marginal ones droop over edge. Fairly short: 5-12 mm in preserved specimens; all of one individual approximately equal length. Observed number varied from 24 to 96, but may be more numerous (Carlgren [1950b] counted 152 in a large specimen, and Hand [unpub.] recorded as many as 150, consistent with a developing fifth cycle of mesenteries that we observed). Longitudinal muscles ectodermal.

Mesenteries and internal anatomy

Maximum five orders of mesenteries (figure 3); first three complete, highest order may be rudimentary and confined to proximal end; two pairs of directives. Mesenteries mostly hexamerously arrayed, with occasional irregularities. Stronger mesenteries except directives fertile; sexes presumably separate (all four fertile individuals sectioned female). Mesenteries added from proximal end, so narrower distally; oral and marginal stomata large. Retractor muscles diffuse (figure 3); parietobasilar muscles wide with short free flap.

Actinopharynx ribbed; rose colored in one specimen, cream in others. Directive mesenteries attached to two distinct, symmetrical siphonoglyphs.

No zooxanthellae.

Cnidom

Spirocysts, basitrichs, holotrichs, and microbasic *p*-mastigophores.

Size and distribution of cnidae

See Table I and Figure 4. Column holotrichs were primarily in the lower portion, but occurred occasionally in the mid-column. Nematocyst size did not appear to correlate with animal size.

Table 1. Distribution and size of nematocysts. Measurements are in μm; values in parentheses indicate nematocysts that fell outside the typical size range. Letters refer to illustrations in Figure 4; n is total number of animals examined; N refers to the ratio of animals possessing a particular cnidae type to the total number examined for that type.

TENTACLES			
Spirocysts (A)	9.0-22.0 x 1.9-4.0	n = 94	N = 8/8
Basitrichs (B)	10.0-21.0 x 2.0-4.0 (5.0)	n = 85	N = 8/8
Basitrichs (C)	21.0-31.5 x 2.0-4.0 (5.0)	n = 88	N = 8/8
ACTINOPHARYNX			
Basitrichs (D)	9.7-17.3 x 1.6-3.8	n = 25	N = 4/8
Basitrichs (E)	18.2-32.1 x 2.2-5.2	n = 75	N = 8/8
MESENTERIAL FILAMENTS			
Microbasic *p*-mastigophores (F)	9.9-19.8 x 1.8-4.0	n = 42	N = 5/7
Basitrichs (G)	20.1-48.7 x 2.2-5.4	n = 68	N = 7/7
Microbasic *p*-mastigophores (H)	15.5-30.4 x 2.9-5.5	n = 45	N = 7/7
COLUMN			
Basitrichs (I)	7.5-19.9 x 2.0-4.0	n = 95	N = 8/8
Basitrichs (J)	20.0-32.0 (36.0) x 2.0-4.0	n = 55	N = 7/8
Holotrichs (K)	21.1-35.0 x 3.7-7.4	n = 37	N = 4/8

Geographical and ecological range

Aulactinia veratra is known from the intertidal zone of Australia and New Zealand; we observed it in the middle and lower reaches of this zone, Carlgren (1950a) reported it in the upper part. It may be locally abundant on rocky shores, often in the same areas as *Oulactis muscosa* (see Dakin *et al.* 1952, Bennett 1987). It occurs in areas "of moderate wave energy" (Thomas and Shepherd 1982: 167), particularly in rock pools, crevices, and the undersides of ledges.

In New Zealand it has been reported from Auckland (Carlgren 1954), Kaikoura Peninsula (Ottaway 1975), and Otago Peninsula (Ottaway 1975). If it has been confused with *Isactinia olivacea* and possibly other actinians, it may actually be more widespread

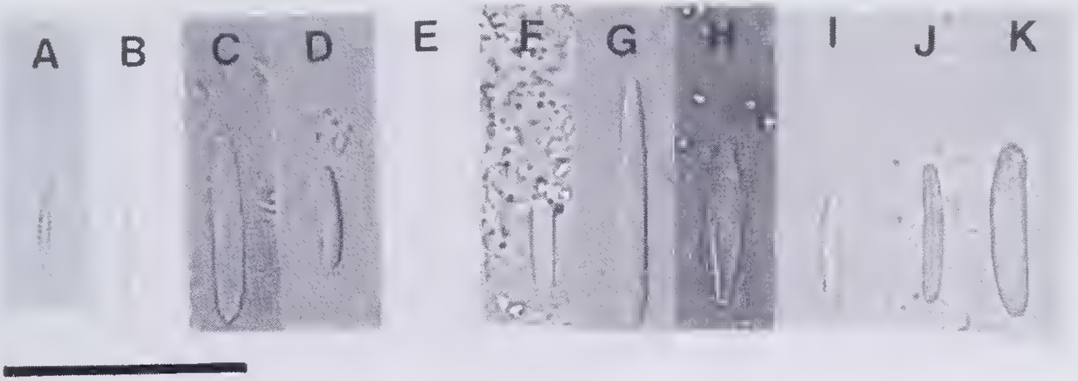

Figure 4. Cnidae types. Letters refer to categories in Table 1. Scale bar = 36 μm.

in New Zealand (Ottaway 1975). This is likely, since "it is found all round the temperate Australian coasts", according to Bennett (1987: 175).

Discussion

Taxonomy

The specimens examined, including those from Wollongong, type locality of *Actinia veratra,* conform well to the most complete descriptions of the species in terms of size, color, external morphology, musculature, and internal anatomy (Carlgren 1950a), b; Hand unpub.) except that Carlgren (1950b) recorded fertile directives. Carlgren (1950b) failed to list spirocysts, which is certainly an omission since those cnidae are characteristic of most actinians, and definitely of actiniids. We (Table 1) found a somewhat greater size range in several categories of cnidae than did Carlgren (1950a, b), although our range for holotrichs is narrower. Considering that, from what we know of Carlgren's work, his data probably came from small numbers of both cnidae and animals, the agreement is excellent. Mesenterial filaments contain, according to Carlgren (1950b), basitrichs of two sizes and microbasic *p*-mastigophores, whereas we found the reverse. It is difficult to ascertain detail in such small structures, so we deem it likely that we all confounded small basitrichs and small microbasic *p*-mastigophores, both of which occur.

There is confusion in the literature concerning the nature of the column projections of *A. veratra.* Carlgren stated (1950b: 138) that the "outgrowths could possibly be interpreted as verrucae . . . [but] certainly are vesicles". Subsequently (1950a: 124) he "correct[ed] [this] mistake . . . In fact the outgrowths *seem* [emphasis added] to be verrucae, though perhaps not so strong as usually in the verrucous genera". Still, he did not alter his generic assignment of *A.veratra,* although he (1949: 61) had defined *Cnidopus* as having a "[c]olumn smooth in its upper part, in its lower, from the limbus upward, provided with transverse and longitudinal rows of low protuberances square at the base". Similarly, according to Hand (unpub.), anemones of the genus *Cnidopus* have "low protuberances" on the column "which are not identical to verrucae", yet he defined

C. veratra as having "numerous warts". Verrucae are, by definition, warts (Latin for wart is *verruca*) (Stephenson 1928). Dakin *et al.* (1952) and Bennett (1987) described *C. veratra* as papillose. This uncertainty, and the related conflicting information about whether debris adheres to the outgrowths (*vide* Carlgren 1950a), is not surprising. In our specimens, the projections were clearly identifiable as verrucae in life. Their ambiguous character when preserved is probably because both verrucae (figure 1A) and adhesive spots (figure 1B) — which do not project in life — are present. Debris attaches at least to the adhesive spots (figure 1B). [We agree with den Hartog (1987) that the definition of verrucae should be based on histological structure, and that adhesiveness should not be considered, if for no other than the pragmatic reason that structure can be determined in preserved specimens, whereas adhesiveness cannot always be.]

Additional ambiguity may have been created by confusion with *Isactinia olivacea.* Parry (1951) characterized two species under that name; Carlgren (1954: 593) believed there to be "at least three" among her specimens, one of them "undoubtedly *Cnidopus verater*". Ottaway (1975: 59) concluded that "*Isactinia olivacea* . . . is easily confused with *Cnidopus veratra* . . . and possibly also with *Isanemonia australis* Carlgren, 1950[a]". The specimens sent to us from New Zealand, and tentatively identified as *Isactinia olivacea* by P.K. Probert (Portobello Marine Laboratory, University of Otago), have adhesive verrucae, but the genus *Isactinia* is characterized by a smooth column (Carlgren 1949). Ottaway (1975: 56) described the column of *Isactinia olivacea* as "smooth, but with verrucae in longitudinal rows", while quoting Carlgren's (1949) definition of the genus. Members of *Isactinia* have spherules (*sensu* England 1987) at the margin; our New Zealand specimens lack them. *Isanemonia australis* (as defined by Carlgren 1950a; see also Ottaway 1975) is smooth-columned, too. The sphincter and parietobasilar muscles of our New Zealand specimens differ from those of *A. veratra.* Intertidal New Zealand actiniids clearly still need study, and we do not feel qualified at this time to list either of these species as partial and/or erroneous synonyms of *A. veratra.*

Nomenclature

Because specimens of "*C. veratra*" have verrucae, they fit neither within the genus *Cnidopus* nor *Epiactis* (Carlgren 1949), with which *Cnidopus* has been synonymized (Fautin and Chia 1986). They can, however, be assigned to the actiniid genus *Aulactinia* (Dunn *et al.* 1980: 2078):

> All or most of column with more or less distinct adhesive verrucae . . . No marginal spherules . . . Sphincter more or less circumscribed, sometimes circumscribed-diffuse . . . All stronger mesenteries fertile, although directives sterile in some species . . . Mesenteries grow from proximal end and therefore may be more numerous proximally than distally. Cnidom: Spirocysts, basitrichs, microbasic *p*-mastigophores, atrichs in some.

Holotrichs (= atrichs), which were not present in all individuals we sampled, may be inducible (Fautin and Chia 1986), and therefore probably should not be considered a character defining a taxon (Fautin 1988). Our specimens also conform to England's

(1987) redefinition of *Aulactinia,* which includes those species previously called *Bunodactis* that lack marginal spherules. Indeed, Carlgren (1950b: 138) noted that individuals of "*C. verater*" "recall specimens of the genus *Bunodactis* . . . There [sic] is, however, impossible to refer them to this genus as I have never found any atrichs there and the outgrowths of the specimens certainly are vesicles". We found both "atrichs" and verrucae in them.

Aulactinia veratra does not differ appreciably from the species described by Lager (1911) as *Cribrina verruculata,* except that she said the latter had "Randsäckchen" (acrorhagi). She listed smaller cnidae from the column and larger from the "Randsäckchen". The former fall within the range of our small column basitrichs and the latter of our large column basitrichs. In our experience of this animal, verrucae at or near the margin may be misinterpreted as spherules. Lager admitted that her specimens were poorly preserved and that her descriptions were, in some cases, incomplete. Of 18 species she recorded from Southwest Australia, she described 15 as new, but many have since been synonymized (see, for example, Dunn 1981). Carlgren (1949), whose student Lager was, assigned *C. verruculata* to *Bunodactis.* The type locality of *C. verruculata* is within 45 km of the Western Australian site where we collected specimens for this study. There are no type specimens of *B. verruculata* at the Western Australian Museum (where some of Lager's types are), nor in the Swedish Museum of Natural History and the Zoological Museum in Lund, Sweden. Carlgren (1954: 571) asserted "that it is not easy to identify Lager's species" because type specimens of "the species described by Lager were probably lost during the war" except for some in Stockholm (presumably he was referring only to those kept in Europe). Even so, we have no reservations in synonymizing *Cribrina verruculata* with *Aulactinia veratra.*

Acknowledgments

We are grateful to Loisette Marsh for assistance in collecting the original specimens of *A. veratra,* to David Ayre for supplying additional animals, and to P. Keith Probert for providing anemones from New Zealand. Thanks also to Elliot Dawson for much-needed information, to Jeannie DeMouthe for tutelage in preparing figures, and to *Cadet Hand and Ken England for advice that improved the manuscript. This research was supported by a U.C. Regents Fellowship to S. Edmands.*

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Notes on mites parasitic or phoretic on Australian centipedes, spiders and scorpion

A. Fain*

Abstract

A collection of mites (Acari) found on Australian centipedes and spiders and on a scorpion was studied.

Leptus waldockae sp. nov. (Erythraeidae) is described from its larval form taken from a scorpion, *Lychas alexandrinus* Hirst, 1911 (Buthidae) in Western Australia; *Dinothrombium southcotti* sp. nov. (Trombidiidae) is described from the larva found attached to a theridiid spider in Queensland; *Ljunghia pulleinei aname* subsp. nov. (Laelapidae) is described from adult forms found on a spider *Aname diversicolor* (Hogg, 1902) in Western Australia.

Introduction

The mites studied herein were found on centipedes, spiders and a scorpion in Australia. Some of them (i.e. the deutonymphs of *Histiostoma feroniarum* (Dufour, 1839) and of *Caloglyphus* sp.) are purely phoretic and not pathogenic, whilst the other species are feeding on their hosts and should therefore be considered as parasitic.

All these mites were sent to the author by Miss J.M. Waldock, Technical Assistant of the Arachnology Department of the Western Australian Museum, Perth.

The holotypes of the new species or subspecies are deposited in the Western Australian Museum (WAM). Paratypes are also deposited there, in the Institut royal des Sciences naturelles de Belgique, Brussels (IRSNB) and in the British Museum, Natural History (BMNH). The hosts are in WAM.

All measurements are in micrometers.

Systematics

Family Erythraeidae

Genus *Leptus* Latreille, 1796

Leptus waldockae sp. nov.

(Figures 1—8)

Holotype

WAM 89/178, larva on slide, from the body of a scorpion, *Lychas alexandrinus* Hirst, 1911 (Buthidae), WAM 89/222, from Learmonth, WA, 22°15'S, 114°05'E, 1,3 km W of, Western Australia. (Coll. D.B. Brooks & J. Waldock, 20 September 1988).

Paratypes

Eight larvae, with the same data as the holotype, of which five paratypes in WAM, one paratype in BMNH and two paratypes in IRSNB.

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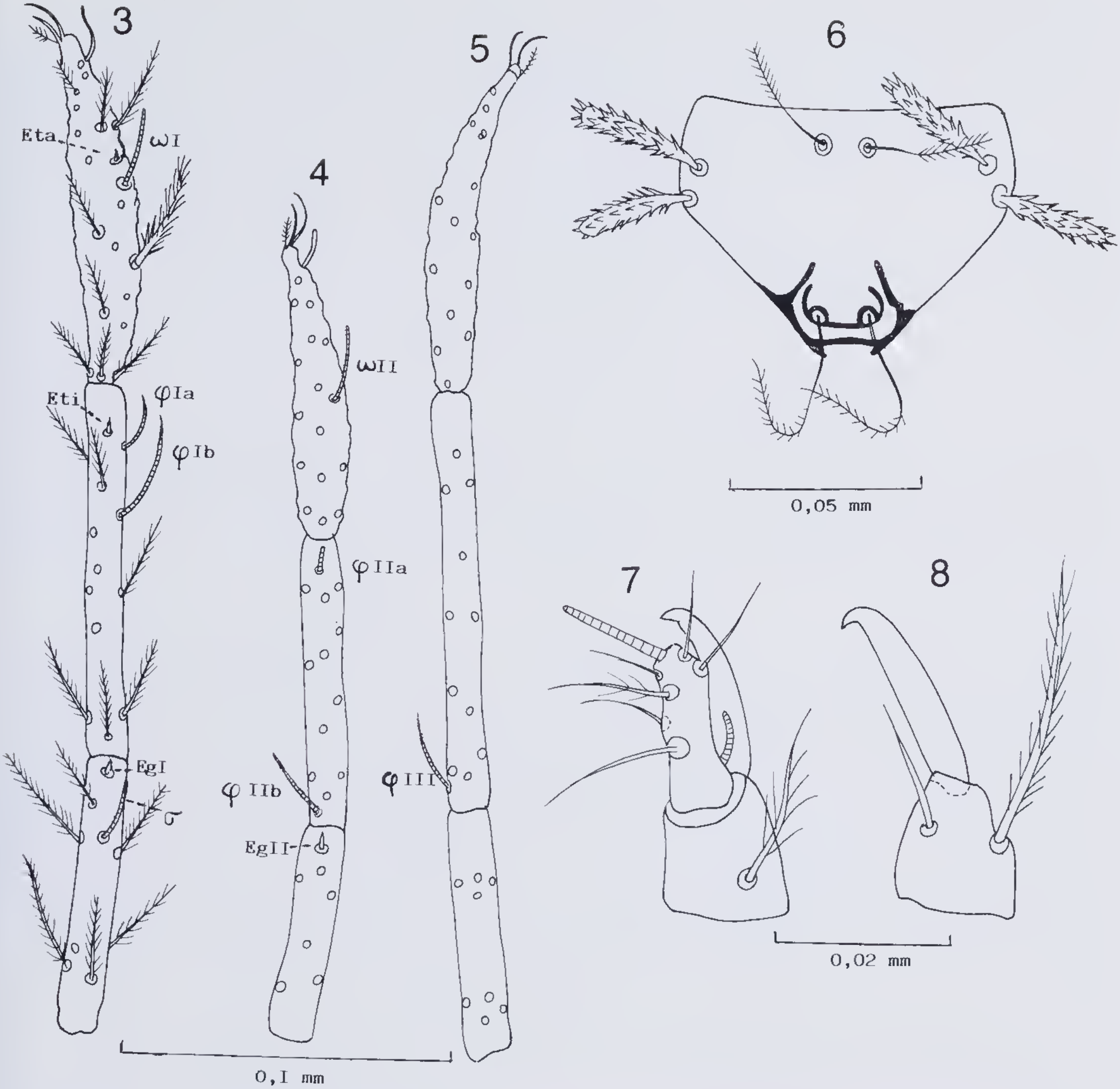
Figures 1-2. *Leptus waldockae* sp. nov. Larva in ventral (1) and dorsal (2) view.

Diagnosis

This new species is represented only by its larval stage. Until now about 80 species of *Leptus* have been described in the world from their larval stage. Many of them were inadequately described and are difficult to recognize from the original description.

The larvae of *Leptus* parasitize a wide range of arthropods in all the parts of the world *L. waldockae* is close to the cosmopolitan group *ignotus* characterized by the presence of



Figures 3-8. *Leptus waldockae* sp. nov. Larva: Tarsus, tibia and genu of leg I (3), of leg II (4), of leg III (5); dorsal shield (6); palptarsus and palptibia in ventral view (7) and dorsal view (8).

two solenidia on tibiae I and II, one solenidion on genu I and no solenidion on genu II and the presence of one barbed seta on palpfemur. It differs, however from this group by the presence of two barbed setae on palpgenu.

In Australia four species of *Leptus* have been recorded from the larval stage, i.e. *Leptus chelonethus* Womersley, 1934 (host: a pseudoscorpion in WA); *L. bathypogonus* Womresley, 1934 (host: an Asilid, *Bathypogonus,* in WA); *L. anomalus* Southcott, 1946 (found in the soil in South Australia); *L. torresianus* Southcott, 1988 (from Cicadas in north Queensland).

L. waldockae differs from *L. chelonethus* by the longer legs, the shorter dorsal setae (42 long in that species), the greater length of AL (35) compared to PL (30) whilst in the species of Womersley the AL is shorter (33) than the PL (48).

It is distinguished from *L. bathypogonus* by the much smaller length of the legs, the scutum and the setae AL and PL and the greater length of the dorsal setae.

It differs from *L. torresianus* by the presence of two solenidia on tibia I and one solenidion on genu I (for three and two respectively in that species) and two barbed setae on palpgenu (for only one in that species).

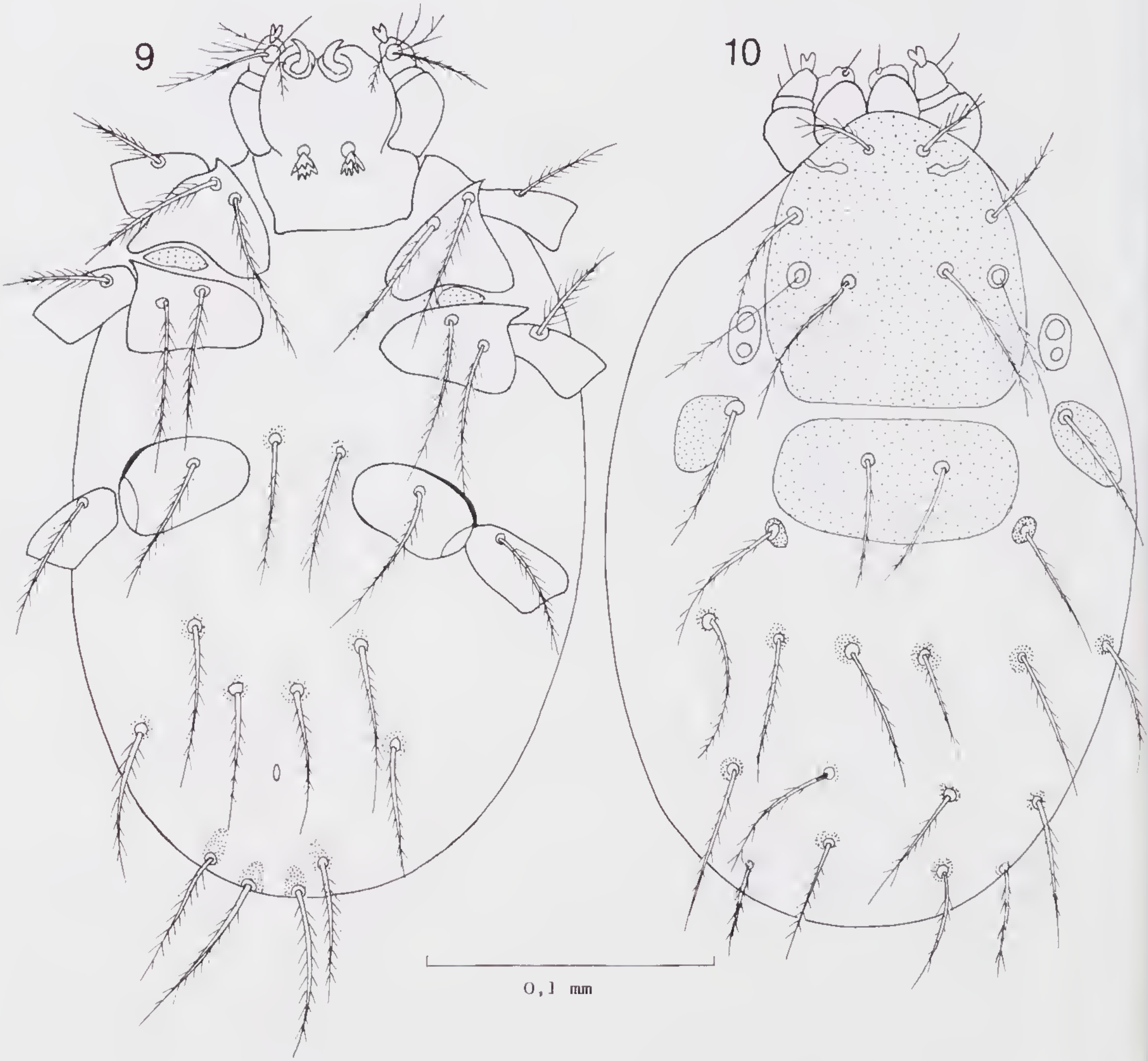


Figure 9-10. *Dinothrombium southcotti* sp. nov. Larva in ventral view (9) and dorsal view (10).

It differs from *L. anomalus* mainly by the presence of two solenidia on tibia I (for one in that species) and also by the following characters: scutum relatively longer and distinctly triangular posteriorly (rounded in *L. anomalus*), legs distinctly shorter, barbed setae of scutum slightly unequal, the anterior longer than the posterior (equal in *L. anomalus*), the coxal setae I distinctly shorter, solenidion of tarsus of leg I shorter, basal solenidion of palptarsus much shorter.

André (1953) described a new species, *Leptus pyrenaeus*, from a scorpion, *Buthus occitanus* L, in Banyuls, France. The present species is clearly distinct from the latter especially by the much smaller number of setae on the dorsum and the venter (about 120 and 75 respectively in *L. pyrenaeus*), the smaller size of these setae, the shape of the scutum with postero-lateral margins almost straight (concave in *L. pyrenaeus*).

Description

The standard data proposed by Southcott (1961) for the scutum are used herein and the measurement ASBM is added here, which is the perpendicular distance between the bases of the anterior sensilla and the anterior border of the scutum in the midline (Fain *et al.* 1987a and 1987b). The lengths of the legs include the claws and the coxae.

Larva holotype

This larva is unfed. Length of the body, including gnathosoma 585, width 240. Length of two paratypes: 630 and 750. Dorsum with 65 barbed setae, slightly club-shaped and placed on 10 rows of five to eight setae 21 to 30 long. Diameter of eye lens 16. Shield: see table 1. *Venter* with 31 barbed setae of which eight are in podosomal region; those on the opisthogaster 15 to 25 long and bear longer barbs than dorsal setae. Coxal setae I-III 36, 12 and 21 long respectively. *Gnathosoma* 160 long. Palps: Femurs bearing one barbed seta 40 long; genu 48 long devoid of a crest and bearing 2 barbed setae, a dorsal 46 long and a ventral thinner 30 long; tibia with apical curved spine and three setae, of which two barbed (a dorsal and a ventral) and one bare (dorsal); tarsus 16 long, with six setae (five

Table 1. Standard data of *Leptus waldockae* sp. nov.

	Holotype	Paratype n°1	Paratype n°2	Paratype n°3
L	60	63	63	57
W	84	84	76	81
AL	35	40	35	39
PL	30	34	28	34
A Sens	25	33	34	—
P Sens	57	58	56	56
AW	72	75	70	72
PW	81	81	75	78
SBa	12	11	11	12
SBp	12	11	11	12
ISD	42	40	37	33
A-P	9	9	8	8
ASBM	10	11	9	10

bare and one barbed) and two unequal solenidia (an apical and a subbasal, 12 and five long respectively). Legs I to III 480, 408 and 495 long; tarsus, tibia and genu of leg I 105, 110 and 78 long. Number of barbed setae on legs I-III: trochanters 1-1-1, basifemora 2-2-1, telofemora 5-5-5, genua 8-8-8, tibiae 14-14-14. Solenidia *ω1* 22; *ω2* 16; *φ1a* 16; *φ1b* 28; *σ1* 21.

This new species is named for Miss J. Waldock, who collected the mite.

Leptus sp.

Three specimens of larvae of *Leptus* sp. were strongly macerated and not identifiable. They were collected on the following hosts:

Leptus sp. (WAM 69/1616) from *Urodacus armatus* (♂) (Scorpionidae) (N.T. Museum), collected in Alice Springs, 8 January 1958 (23°42′S, 133°52′E)

Leptus sp. (WAM 69/1614) from *U. yaschenkoi* (♀), Lake Victoria, N.S.W. (34°04′S, 141°11′E), 23 June 1969. (Coll. Sir Robert Blackwood).

Leptus sp. (WAM 69/1617), from *U. hoplurus* (♀), Marloo Stn., (28°19′S, 116°11′E). 2 February 1969 (Coll. L.E. Koch and A.M. Douglas).

Family Trombidiidae

Subfamily Trombidiinae

Genus *Dinothrombium* Oudemans, 1910

Dinothrombium Oudemans, 1910: 48; Newell, 1979: 425
Isothrombium André, 1949: 354
Angelothrombium Newell & Tevis, 1960: 293; Newell, 1979: 425; Southcott, 1986: 31

The type species of *Dinothrombium* is *Acarus tinctorius* L, 1767.

Thor and Willmann (1947) listed 22 species in the genus *Dinothrombium*, all known only from the adult stage. These species were found in all the parts of the world except Australia. Hirst (1928), however, had described several new species in this genus from Australia but Womersley (1934) showed that they actually belonged to other genera. Newell and Tevis (1960) described a new genus and species, *Angelothrombium pandorae*, from both adult and larval stages, and collected in the U.S.A. Later, Newell (1979), synonymized this genus and species with *Dinothrombium tinctorium*.

The genus *Isothrombium* André (1949) (type species: *I. oparbellae* André, 1949, from a solpugid, *Oparbella fagei* Vachon, in Western Africa) has been synomized with *Dinothrombium* by Southcott (1986).

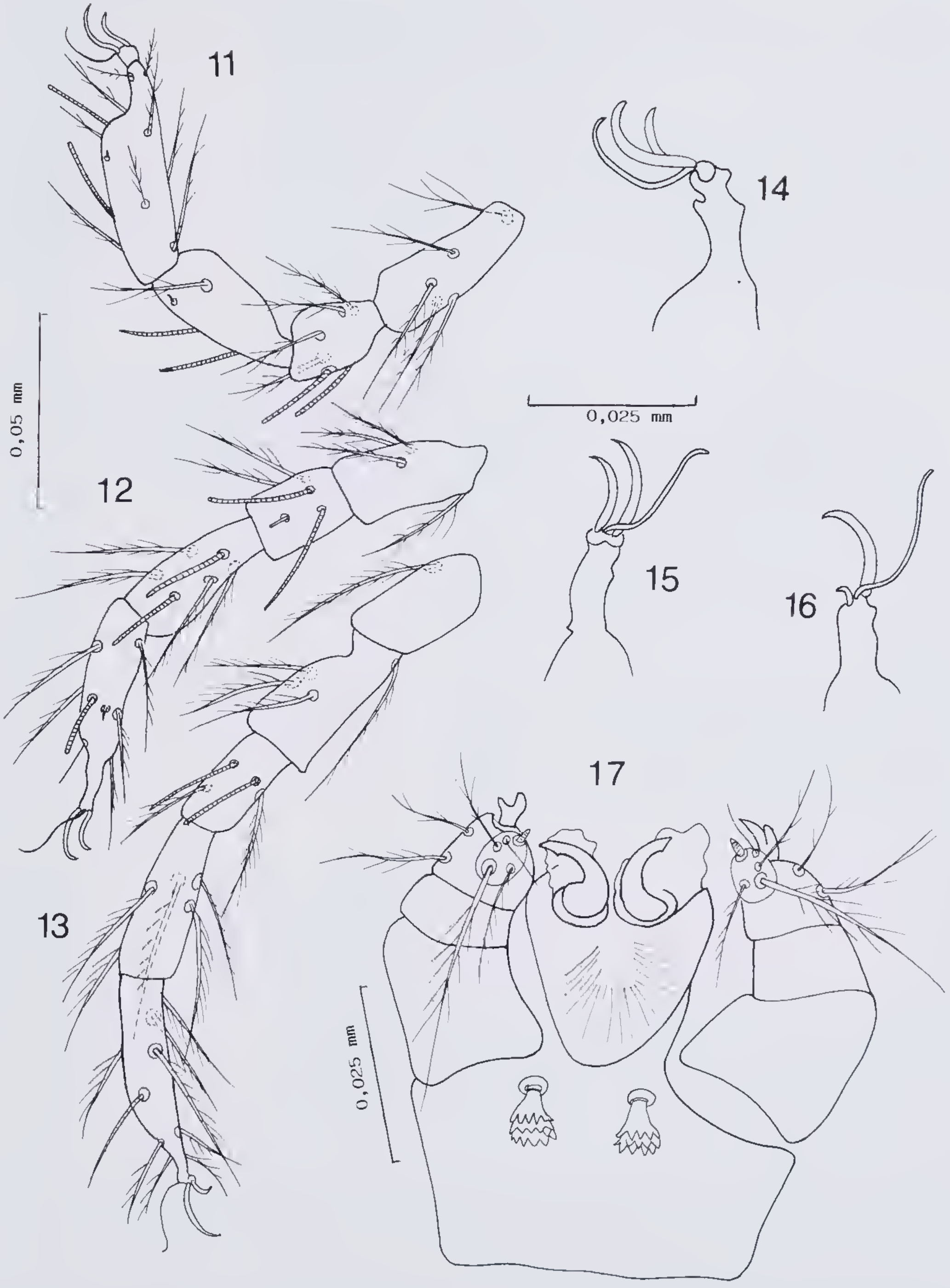
The genus *Dinothrombium* was, until now not known from Australia. I describe, herein, the first Australian species.

Dinothrombium southcotti sp. nov.

(Figures 9-17)

Holotype

WAM 89/298, larva on slide, ex an unidentified spider (WAM 89/297), from Wolfdene, Qld. (27°47′S, 153°11′E). (Coll. A.E. de Jong, 13 August 1988).



Figures 11-17. *Dinothrombium southcotti* sp. nov. Larva: Leg I (11); leg II (12); leg III (13); ambulacrum of leg I (14), of leg II (15), of leg III (16); gnathosoma (17).

Paratypes

6 paratypes larvae WAM 89/299-304, with the same data as the holotype. Amongst these specimens, 3 paratypes are in WAM, one in the BMNH and two in the IRSNB.

Diagnosis

The larva of *D. southcotti* differs from the two other species known in the genus by the following characters (see below). It is to be noted that the descriptions of *D. oparbellae* and *D. tinctorium* (larva of *Angelothrombium pandorae*) do not mention the basic measurements of the dorsal shields. The following key, therefore is based mainly on the figures given by the authors.

Key to the larvae of *Dinothrombium*

1. Posterior region of idiosoma with 4 barbed setae much longer than the other hysterosomal setae .... *D. oparbellae* (André, 1949)
   Posterior region of idiosoma without long terminal setae 2
2. Intercoxal setae II 1,5 times as long as coxal setae I-III. Most setae of palptarsus and palptibia are bare. Opisthogaster with 4 pairs of setae. Anterior scutum wider than long. Setae QL longer than PL. Setae QL more spaced. Cheliceral blade not toothed .... *D. tinctorium* (L.1767)
   Intercoxal setae II shorter than coxal setae. Most setae of palptarsus and palptibia are barbed. Opisthogaster with 5 pairs of setae. Anterior scutum longer than wide. Setae QL shorter than PL. Setae QL less spaced. Cheliceral blade toothed .... *D. southcotti* sp. n.

Description

Most of the larvae are ungorged. Holotype 300 long (including the gnathosoma) and 180 wide. In three paratypes length and width are 294 x 170; 291 x 190; 283 x 149. *Dorsum:* Outside of scuta dorsum bears nine pairs of setae, 45-50 long, all barbed. First pair situated on a small oval shield, the other setae are situated on smaller rounded platelets. *Venter:* Coxae I-III with 2-2-1 barbed setae 55 to 60 long. Opisthogaster with five pairs of barbed setae 45 to 60 long. Legs I-III are 245-240-260 long (claws and coxae included). Tarsi with three claws, the posterior claw of tarsi III very short. Chaetotaxy of legs (number of barbed setae): trochanters 1-1-1, femora 5-4-4, genua 4-3-3, tibiae 5-5-5, tarsi 19-14-14. Number of solenidia: tarsi 2-1-1, tibiae 2-2-0, genua 2-2-2. A short eupathidia is present on tarsi I and II, tibia I and genu II. *Gnathosoma:* Palpal tibia with apical bifid spine and three setae (two barbed and one bare). Palptarsus very short with one apical solenidion, one thin and short bare seta and three barbed setae of which one very long. Base of gnathosoma with pair of strong and short setae ending into numerous small teeth. Cheliceral blade with small preapical tooth.

This species is named for Dr R.V. Southcott in recognition for his comprehensive work on trombidiid mites.

Genus *Cliotrombium* Southcott, 1986

Clinotrombium antares Southcott, 1986

(Figures 18-19)

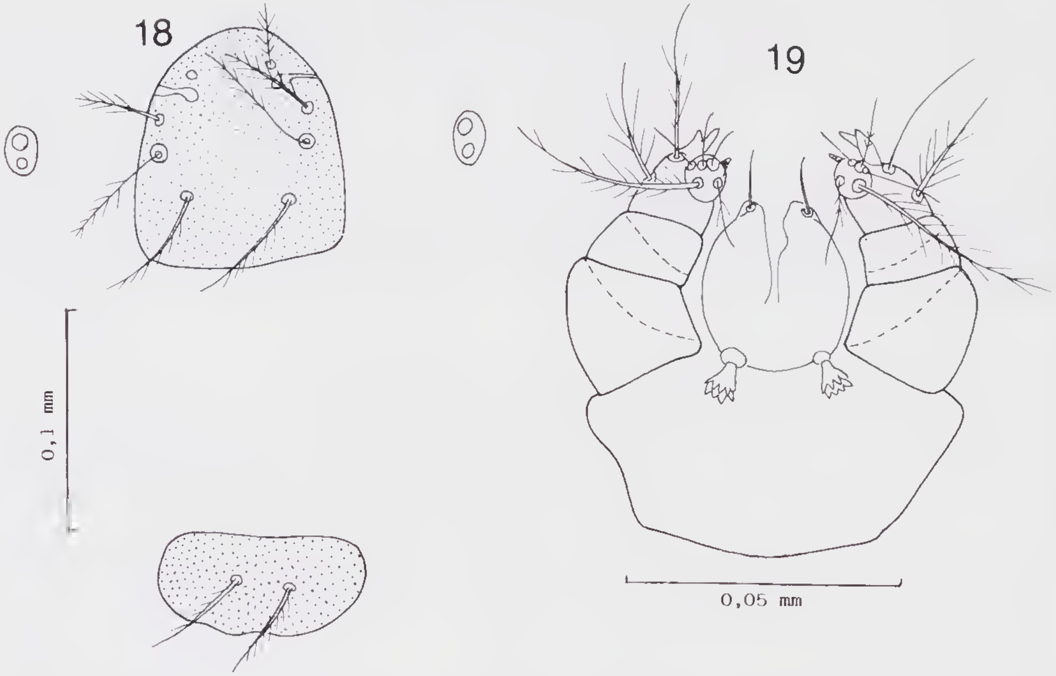
This species was described from a single larva attached to a small spider, from South Australia.

The present specimen, also a larva (WAM 89/318), was attached to a small unidentified spider (WAM 89/317) found under a rock at Mt Cookc, WA (32^0, 25′S, 116^{0}18′E) (Coll. B. Hendrick, 6 May 1989).

Table 2: Measurements (in micrometers) of the larvae of *Dinothrombium southcotti* sp. nov. and *Clinotrombium antares* Southcott, 1986

	Dinothrombium southcotti				*Clinotrombium antares*	
	Holotype	Para 1	Parat. 2	Parat. 3	Specimen WAM 89/318	Original description
Anterior scutum						
L	96	99	100	98	106	110
A	90	93	90	—	93	104
AM	30	28	30	30	41	34
AL	37	34	39	39	45	54
PL	66	75	68	65	57	78
Sens	60	60	56	54	60	73
AMB	26	29	25	25	36	40
AW	75	77	75	—	67	83
PW	34	39	38	36	49	55
SB	69	75	74	69	66	74
MA	33	33	30	29	25	29
AP	30	26	27	26	36	39
SA	19	19	18	21	57	
SP	15	16	18	16	21	
LN	13	15	15	15	23	17
PSB	45	45	42	42	51	54
Posterior scutum						
PSL	42	39	39	39	45	46
PSW	84	87	84	81	90	80
QL	52	54	52	54	48	66
QW	27	29	30	27	24	25
PLN	15	15	15	13	18	17

The specimen corresponds with the description and the figures of *C. antares* given by Southcott except for some minor differences such as a smaller length of PL and AW (57 and 67 long instead of 78 and 83 in *C. antares* (see table 2).



Figures 18-19. *Clinotrombium antares* Southcott. Larva: Dorsal shields (18); gnathosoma (19). (Specimen from Western Australia).

Family Laelapidae

Genus *Ljunghia* Oudemans, 1932

Ljunghia hoggi Domrow, 1975

This species has been described from a mygalomorph spider, *Aganippe subtristis* Pickard-Cambridge (Idiopidae); from Seacliff, Adelaide, South Australia.

The present specimens (eight females and two nymphs, WAM 89/320-9) were collected from a spider (*Eucyrtops* sp.) (WAM 89/319), at 5 km NW of Stoneville, WA (Coll. D. Mead-Hunter and G. Harold, 6 May 1989). They agree with the description of Domrow except that the dorsal shield bears 24 pairs of setae (podonotal 17, opisthonotal 7) instead of 25 pairs in the typical series.

Ljunghia pulleinei Womersley, 1956, emend. nov.

Ljunghia pulleini Womersley, 1956

Womersley (1956) and Domrow (1975) (see below) incorrectly spelled this name *pulleini*. The person concerned was the arachnologist Robert Henry Pulleine. We correct therefore the species name in *pulleinei* (Art. 32c of the International Code of Zoological Nomenclature, 1985).

This species has been described from a spider *Selenocosmia stirlingi* Hogg (Theraphosidae) from South Australia. Domrow (1975) redescribed this species and recorded the discovery of new specimens from another spider, *Aname* sp. (Nemesiidae). This author noted that the specimens from *Aname* differed from the typical series by the lack of the subterminal pair of setae on the scutum and the smaller length of the body setae.

The present specimens were collected from a spider *Aname diversicolor* (Hogg, 1902) in WA. They present the same characters as the specimens from *Aname* studied by Domrow. It seems therefore that the differences with the typical series are stable and I think that it justifies their separation in a new subspecies that I describe below.

Ljunghia pulleinei aname subspec. nov.

(Figure 20)

Holotype

WAM 89/187, female on slide, ex a spider *Aname diversicolor* (♂) (WAM 89/223), from Woorolo, WA (31°48′S, 116°19′E), collected by A.R. Gilliespie, 6 February, 1978.

Paratypes

15 females and three males (WAM 89/188-204), with same data as holotype; four females, five males and eight nymphs (WAM 89/226-42) from the same host (♂) (WAM 89/225) from Cooralya Stn, WA (24°27′S, 114°04′E). Coll. G. Maslim, 12 April 1989.

Holotype and 13 females, six males and six nymphs in WAM, two females in the BMNH and four females, two males and two nymphs in the IRSNB.

Diagnosis

In this new subspecies there are only 16 pairs of setae on the dorsal shield and the setae *j6* are much shorter, moreover the setae *j3*, *j4* and *Z5* and some setae outside of the shield are distinctly longer than in *L. pulleinei s. str.*

Description

Female (holotype: Idiosoma 675 long and 440 wide. Dorsal shield 495 long and 270 wide bearing 16 pairs of setae (14+2). Lengths of setae: *j1* 42; *j2* 54; *j3* 185; *j4* 180; *j5* 35; *j6* 54; *z1* 38; *z2* 180; *z3* 190; *z5* 42; *s1* 50; *s3* 70; *s4* 200; *s5* 200; *J4* 9; *Z5* 100. Setae on the soft cuticle outside the shield 120 to 220 long. Other characters as in typical form.

Male: Idiosoma 510 long and 330 wide. Dorsal shield as in female. Ventral surface as in typical form.

Family Histiostomatidae

Genus *Histiostoma* Kramer, 1876

Histiostoma feroniarum (Dufour, 1839)

The only specimen (a deutonymph or hypopus) of the collection (WAM 89/146-72) was mixed with deutonymphs of *Caloglyphus* sp. collected from three centipedes *Cormocephalus aurantiipes* (Newport, 1844) (WAM 80/1934-5 and 82/61) from Mt Cooke, WA (Coll. E.G. Cockett, 23 March 1968) (32°25′S, 116°18′E) (see below).

This species has a cosmopolitan distribution and it has already been recorded from Australia from various habitats. The deutonymph was found on a millipede (Womersley, 1941).

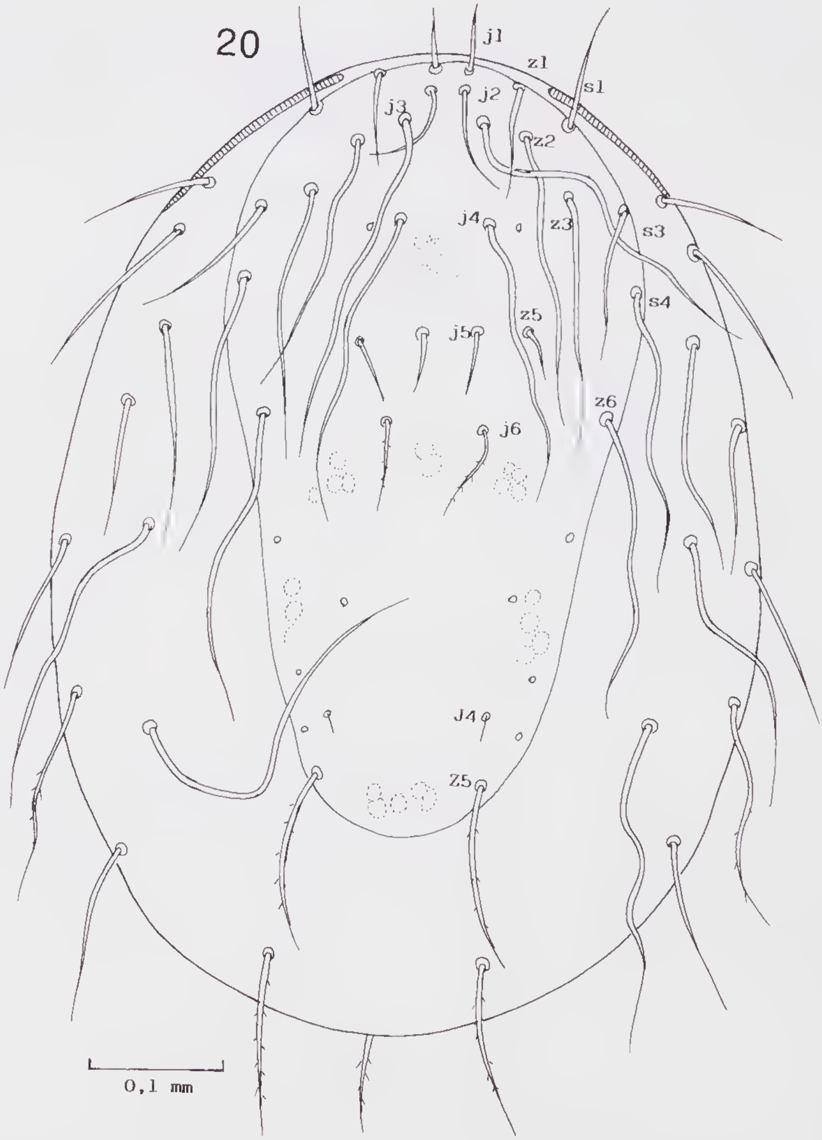


Figure 20. *Ljunghia pulleinei aname* subsp. nov. Female in dorsal view.

Family Acaridae

Genus *Caloglyphus* Berlese, 1923

Caloglyphus sp.

This species is represented only by deutonymphs (hypopi). The specific identification of the deutonymphs of this genus is very difficult and I prefer not to name the specimens of this collection in the absence of the adults. Womersley (1941) collected numerous adults of *Caloglyphus berlesei* (Michael, 1903) in Australia. Perhaps our deutonymphs belong to this species.

The present specimens were attached to the following hosts:

25 deutonymphs (WAM 89/146-71) from three centipedes *Cormocephalus aurantiipes* (WAM 80/1934-5 and 82-61) from Mt Cooke, WA (see above).

Two deutonymphs (WAM 89/175-76) from *Cormocephalus hartmeyeri* Kraepelin, 1908 (WAM 80/891) from Nannup, WA (33°59′S, 115°46′E) (Coll. M. Colreavy, 4 June 1978).

Nine deutonymphs (WAM 89/206-14) from *Aname diversicolor* (Hogg, 1902) (WAM 89/224) from Bates Junction, near Albany, WA (35°01′S, 117°53′E) (Mr Proctor don. 14 November 1988).

Acknowledgements

I thank Mr D. MacFarlane, British Museum (Nat. Hist.) who provided literature necessary for this study.

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Two new and unusual species of the bee genus *Leioproctus* Smith (Hymenoptera: Colletidae), with notes on their behaviour

Terry F. Houston*

Abstract

Two new species of *Leioproctus sensu stricto*, *L. excubitor* from Western and Central Australia and *L. macmillqni* from south-western Australia, are described and figured. Males of both species have extraordinary antennae, *excubitor* having the first flagellar segment greatly attenuated as in stenotritid bees and *macmillani* having most segments highly setose and produced into lobes. Males of *excubitor* have other unusual modifications including a very broad highly depressed metasoma and spend much time perched upside-down on dead tree trunks. Both sexes of *macmillani* have the head peculiarly elongated, doubtless an adaptation to the tubular flowers of their winter-flowering food plant, *Astroloma xerophyllum*.

Introduction

Little is recorded of the ethology of the Australian species of *Leioproctus* Smith *sensu stricto* even though the subgenus is a large one with 126 nominal Australian species and possibly as many undescribed ones.

The two species described here, while not especially closely related, are both aberrant members of the subgenus. Their extraordinary features at first glance might suggest they should be placed in separate genera but closer inspection reveals their affinities with *Leioproctus s. str.* Their behaviour, too, is unusual and worthy of reporting. For these reasons, the species are described ahead of a much needed subgeneric revision.

Terminology and Abbreviations

The morphological terminology employed here follows that of Michener (1965).

Relative dimensions quoted in the descriptions are directly comparable between sexes and species. All were measured using an eye-piece graticule on a stereo-microscope with the zoom objective set to give a head width reading of 50 divisions. By doubling the figure for any given dimension, a percentage of head width is obtained. The methods of obtaining certain measurements were illustrated by Houston (1990) and abbreviations used for them are as follows: AOD Antennocular distance; ASD Diameter of antennal socket; BMW Basal width of mandible (viewed laterally); DMA Distance between anterior mandibular articulations; EL Length of compound eye (top to bottom); FL Flagellum length; F1L Length of first segment of flagellum; HL Head length; HW Head width; IAD Interantennal distance; LID Lower interorbital distance; ML Mandible length; MOD Diameter of median ocellus; MSL Malar space length; OOD Ocellocular distance; SL Scape length; SW Scape width; UFW Upper width of face; UID Upper interorbital distance; WOC Width of ocellar cluster.

LID, UFW and UID are not measurable in some instances when the inner orbits are strongly divergent ventrally or dorsally.

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Other abbreviations: ANIC Australian National Insect Collection, CSIRO, Canberra; HS homestead; TFH author's name; UQIC University of Queensland Insect Collection, Brisbane; WAM Western Australian Museum.

Systematics

Colletidae: Colletinae; Paracolletini

Genus *Leioproctus* Smith

Michener (1965) redefined the genus and its nominate subgenus and listed the species-level taxa which he assigned to them. In his notes, he made no mention of the sorts of extraordinary features which characterize the two species described in this paper although I am sure he would have done had the species been known to him. On this basis, I am confident in describing them as new.

Leioproctus (Leioproctus) excubitor, sp. nov.

Figures 1, 2

Holotype

In WAM (89/520), ♂, East Yuna Reserve, 34 km WNW of Mullewa, Western Australia, 24-26 August 1985, T.F. Houston 617-9, on wooden fence post.

Paratypes

27♂, 11♀ in ANIC; 1♂, 1♀ in UQIC; 12♂, 9♀ in WAM. See Specimens Examined.

Diagnosis

A black, non-metallic species readily recognizable by the following combination of features: first flagellar segment greatly attenuated, more so in male, equal in length to subsequent 3.5 segments (Figure 2 e, f); metasomal terga 2-4 (and 5 in male) with basal bands of white tomentum; metasoma of male markedly broadened and depressed, rather fusiform (Figure 1); fore basitarsi of male expanded dorsally and fringed with long setae (Figures 1, 2 h).

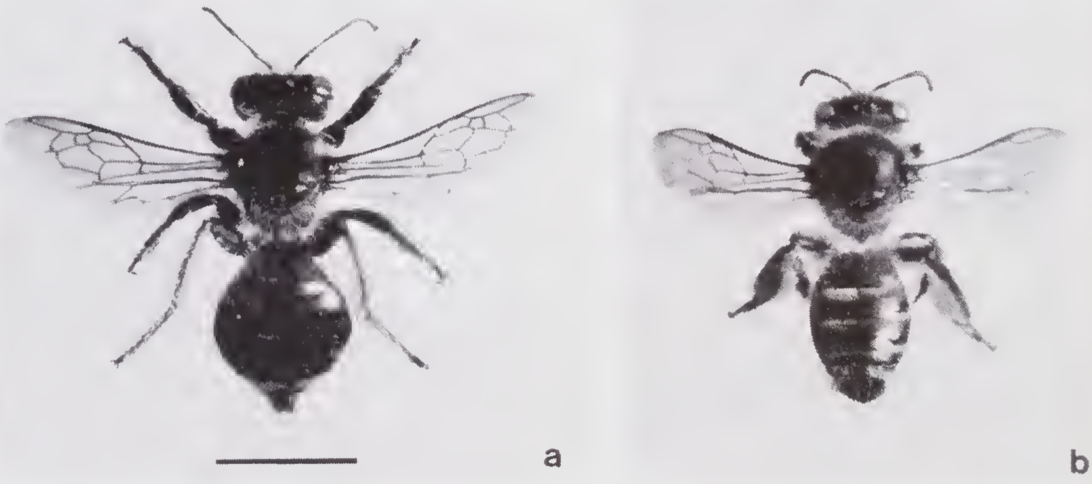

Figure 1 *Leioproctus excubitor:* (a) male and (b) female to same scale (line = 5 mm).

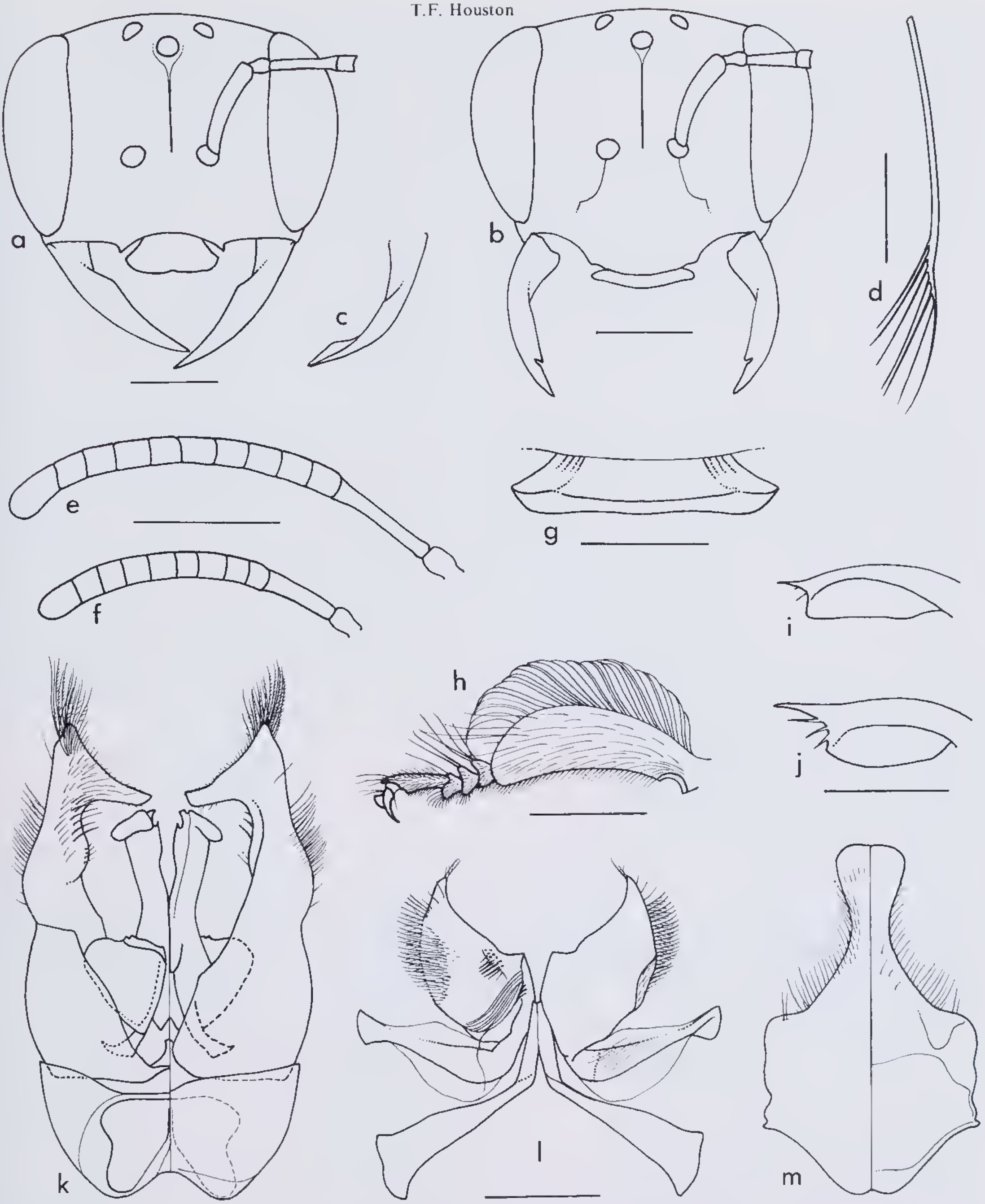

Figure 2 *Leioproctus excubitor:* (a, b) heads of male and female, respectively, anterior view; (c) mandible of male, inner view; (d) seta from outer side of hind tibia of female; (e, f) right antenna (excluding scape) of male and female, respectively, anterior view; (g) labrum of female, anterior view; (h) fore tarsus of male, inner view; (i, j) fore tibial calcar of male and female, respectively; (k-m) genital capsule, 7th and 8th metasomal sterna of male; dorsal view on right, ventral on left. Pubescence omitted in a-c, e-g. Scale lines (a-c, e, f, h) 1 mm; (d, i, j) 0.25 mm, (g, k-m) 0.5 mm.

Description

Male (holotype)

Head width 4.0 mm; body length 12 mm. Relative dimensions: HW 50; HL 35; UID 28; UFW 29; LID -; IAD 7; ASD 3.5; AOD 7; MOD 4; WOC 14; OOD 7; SL 14; SW 3; FL 40; F1L 10; ML 27; BMW 7; MSL 1.

Head form as in Figure 2 a; genae rounded, almost as wide as compound eyes viewed laterally; labrum rather flat, fringed ventrally with long simple bristles; mandible long, slender, simple (lacking subapical tooth), postero-apical margin twisted (Figure 2 a, c); proboscis ordinary; palpi well-developed, ordinary; maxillary palpus exceeding apex of galea; antenna slender (Figures 1, 2 e), first flagellar segment attenuated, about ¼ of length of flagellum, equal in length to succeeding 3.5 segments; middle segments about 1.2X as long as wide; terminal segment rounded and strongly compressed apically; propodeal enclosure with steeply sloping dorsal surface about as long as metanotum and rounding evenly onto vertical posterior surface with no separating edge or carina; venation ordinary; second submarginal cell of fore wing 2/3 as long as third; femora stout; fore basitarsus twice as long as segments 2-5 together, swollen and convex anteriorly (Figure 2 h), slightly concave on inner surface; mid basitarsus strongly broadened and flattened; hind basitarsus straight and slender, 6X as long as high, slightly wider distally than proximally; segments 2-4 of fore and mid tarsi strongly contracted; fore tibial calcar with very short apical spine (Figure 2 i); metasoma strongly depressed, very wide, rather orbicular in dorsal view (Figure 1); third and fourth terga each with a longitudinal furrow margined laterally by a carina on each lateral margin.

Coloration. Integument almost wholly black, nonmetallic; labrum and diffuse areas of metasomal sterna and first tergum dark brown; flagellum mid-brown ventrally; wings lightly suffused with brown apically.

Sculpture. Integument generally finely coriarious; head and thorax dull, metasoma weakly to moderately shining; frons with open, small puncturing; vertex closely, minutely punctured; scutum, scutellum and metanotum like frons but puncturing sparse; propodeal enclosure dull, minutely roughened, with areolate posterolateral margins; metasomal terga with fine setigerous punctures concentrated basally, very sparse apically.

Pubescence. Lower face covered by long, silvery-white, plumose hair, completely obscuring integument; white plumose setae occur more sparsely on genae, posterior of head, mandibles laterobasally, scutum anteriorly, mesosoma laterally, ventrally and posteriorly, metasomal tergum 1, coxae and trochanters; metasomal terga 2-5 with rather diffuse bands of short silvery-white tomentum basally and very short, erect, simple, brown setae posteriorly; frons, vertex, scapes, scutum and scutellum with long, sparse, erect, sooty-brown setae; fore basitarsus densely fringed anteriorly with very long, silvery-white to brownish setae (Figure 2 h); fore femur largely bare ventrally with a regular longitudinal fringe of long black setae; fore and mid tibiae and basitarsi with sparse, simple, black setae on outer surfaces.

Terminalia. See Figure 2 k-m.

Female (paratype WAM 87/1441) Head width 3.45 mm; body length *ca.* 10 mm. Relative dimensions: HW 50; HL 40; UID 28; UFW 32; LID 32; MOD 3.5; WOC 13.5; OOD 7; IAD 6.5; ASD 4; AOD 9; SL 15; SW 2.5; FL *ca.* 30; F1L 7.5; ML 24; BMW 7; MSL 1.

Head form as in Figure 2 b; gena about 0.7X as wide as compound eye viewed laterally; vertex gently depressed between compound eyes and lateral ocelli; clypeus straight in profile, gently convex transversely; supraclypeal-interantennal area elevated, convex, somewhat triangular; antennae slender with first flagellar segment attenuated, about ¼ as long as flagellum (Figure 2 f); mandible slender, bidentate, subapical tooth subtended by a deep incision; labrum very short with strong transverse carina separating concave anterior surface from flat bare ventral surface (Figure 2 g), postero-ventral margin fringed with simple bristles; proboscis and palpi ordinary as in male; propodeum as in male; fore tibial calcar as in Figure 2 j; inner hind tibial spur coarsely pectinate with 6 long, well-spaced teeth; legs ordinary; metasoma depressed but otherwise ordinary (Figure 1), 3rd and 4th terga with lateral furrows and carinae as in male; pygidial plate rounded apically, flat and granular dorsally; sting very stout and strongly compressed.

Coloration. Integument as in male but labrum black.

Sculpture. Much as in male; clypeus coarsely punctured, weakly shining; supraclypeal area with triangular, impunctate glossy area medially; propodeal enclosure with margins areolate only laterally.

Pubescence. Long, white, plumose setae occur on the following — lower face up to mid frons (dense laterally, sparse medially), posterior of head, scutum anteriorly and posteriorly, pronotal tubercles (densely), metanotum, ventral and lateral areas of thorax (except upper anterior mesepisternum), metasomal tergum 1 (except apically), terga 5 and 6 laterally and sterna 2-4 apically, coxae, trochanters and femora; sparse, long, erect, plumose, sooty brown setae occur on upper frons, vertex, scutum, metanotum and upper anterior mesepisternum; prepygidial fimbria dense, setae highly plumose, black-brown; metasomal pubescence otherwise as in male; fore and mid tibiae and all tarsi with dark brown setae; fore basitarsus with dense, fine, simple bristles on inner and ventral surfaces and coarse bristles along dorsal margin; hind tibial scopa moderately dense, composed of long, coarse, apically pectinate setae (Figure 2 d), setae dark brown except on ventral and posterior surfaces of tibia; hind basitarsus with long, plumose setae proximally and dorsally grading into simple bristles ventrally.

Variation

Minor. Head widths range from 3.5-4.0 mm in males (n 14) and 3.3-3.6 mm in females (n 10). Number of teeth on inner hind tibial spur of female ranges from 5-10 (n 20).

Remarks

L. excubitor belongs to a small group of closely related species none of which has been described until now. All inhabit the arid zone of Western Australia, are black, non-metallic, have the first flagellar segment elongated to some degree and the sting strongly compressed.

L. excubitor is by far the most unusual of these in respect of the following characters of the male: broad lower face; long, sickle-shaped mandibles; greatly attenuated first flagellar segment (occurs also in female); modified, fringed fore and mid tarsi; and very broad, highly depressed metasoma. It is unusual (although not alone) amongst bees in exhibiting reversed sexual size dimorphism (RSSD): males are larger than females whereas in most bees the reverse is the case. RSSD was recently reported in another species-group of *Leioproctus* (Houston 1990).

Attenuation of the first flagellar segment occurs in various members of several bee families but is rare in the Colletinae and is nowhere as pronounced as in *L. excubitor*. It is one of several morphological features characterizing bees which engage in fast hovering and darting flight (Rozen 1968) but *excubitor* does not exhibit such behaviour nor any of the other morphological features.

Etymology

The specific epithet is Latin for 'sentinel' and alludes to the perching habits of males.

Distribution

Arid and semiarid regions of southern Western Australia, extending from coastal areas between Geraldton and Carnarvon inland through the Gibson Desert to the ranges of Central Australia.

Specimens Examined

The holotype and the following paratypes. Western Australia: 2♂, 7♀ (WAM 87/1439-41, 89/514-9), same data as holotype but collected on flowers of *Comesperma scoparium* (1♂, 6♀) and *Acacia* (1♀) and on collector's net (1♂), UQIC, WAM; 1♂ (WAM 89/521), same data as holotype but collected 13-16 Sept. 1984, sitting on collector's trouser leg, WAM; 5♂ (WAM 89/524-8), 11 km ENE of Anketell HS (28.02 S, 118.51 E), 4-6 Sept. 1981, TFH, on flowers of *Eucalyptus oldfieldii* (2♂) and on trunks of dead mulga (3♂), UQIC, WAM; 1♀ (WAM 89/533), Balline Stn, 27.59 S, 114.13 E, 24-25 July 1979, A.M. & M.J. Douglas, WAM; 2♂ (WAM 89/529-30), Boolagoorda, 4 km NW of Hamelin HS, 5 Aug. 1982, B.P. Hanich, on wooden mast on hill, WAM; 1♀ (WAM 89/532), 5-7 km NW of Boolathana HS (24.39 S, 113.42 E), 27 Aug. 1980, C.A. Howard & TFH, on flowers of *Asphodelus fistulosus*, WAM; 26♂, Drummonds Cove nr Geraldton, Sept. 1972, N. McFarland, ANIC; 1♂ (WAM 89/531), NE end of Lake Throssell, 27.22 S, 124.21 E, 13 Sept. 1982, B. Hanich & TFH, on flowers of *Ptilotus*, WAM; 1♂ (WAM 87/1438), 10 km S of Nerren Nerren HS (27.08 S, 114.38 E), 19 Aug. 1980, C.A. Howard & TFH, perched on dead mulga branch, WAM; 1♂, 1♀ (WAM 89/522-3), 13 km S of Wannoo (26.49 S, 114.37 E), (♂, 28-31 July 1985, on flowers of *Dampiera incana* var *incana*; ♀, 21-23 Aug. 1985, on flowers of *Schoenia cassiniana*), WAM. Northern Territory: 3♀, 24.03 S, 133.37 E, 46 km SW by S of Alice Springs, 23 Sept. 1978, J.C. Cardale, ANIC; 1♀, 24.03 S, 133.59 E, 41 km S by E of Alice Springs, 4 Oct. 1978, J.C. Cardale, ANIC; 1♂, 7♀, 23.32 S, 133.38 E, Mt Solitaire, 30 km NW by W of Alice Springs, 29 Sept. 1978, J.C. Cardale, (1♂, 4♀) on flowers of *Ptilotus*, ANIC.

Leioproctus (Leioproctus) macmillani, sp. nov.

Figures 3 a-c, 4, 5

Holotype

In WAM (87/1452), ♂, Gnangara [State Forest], *ca.* 20 km NNE of Perth, Western Australia, 11 July 1982, R.P. McMillan, on flowers of *Astroloma xerophyllum*.

Paratypes

2♂, 1♀ in ANIC; 1♂, 1♀ in UQIC; 11♂, 6♀ in WAM.

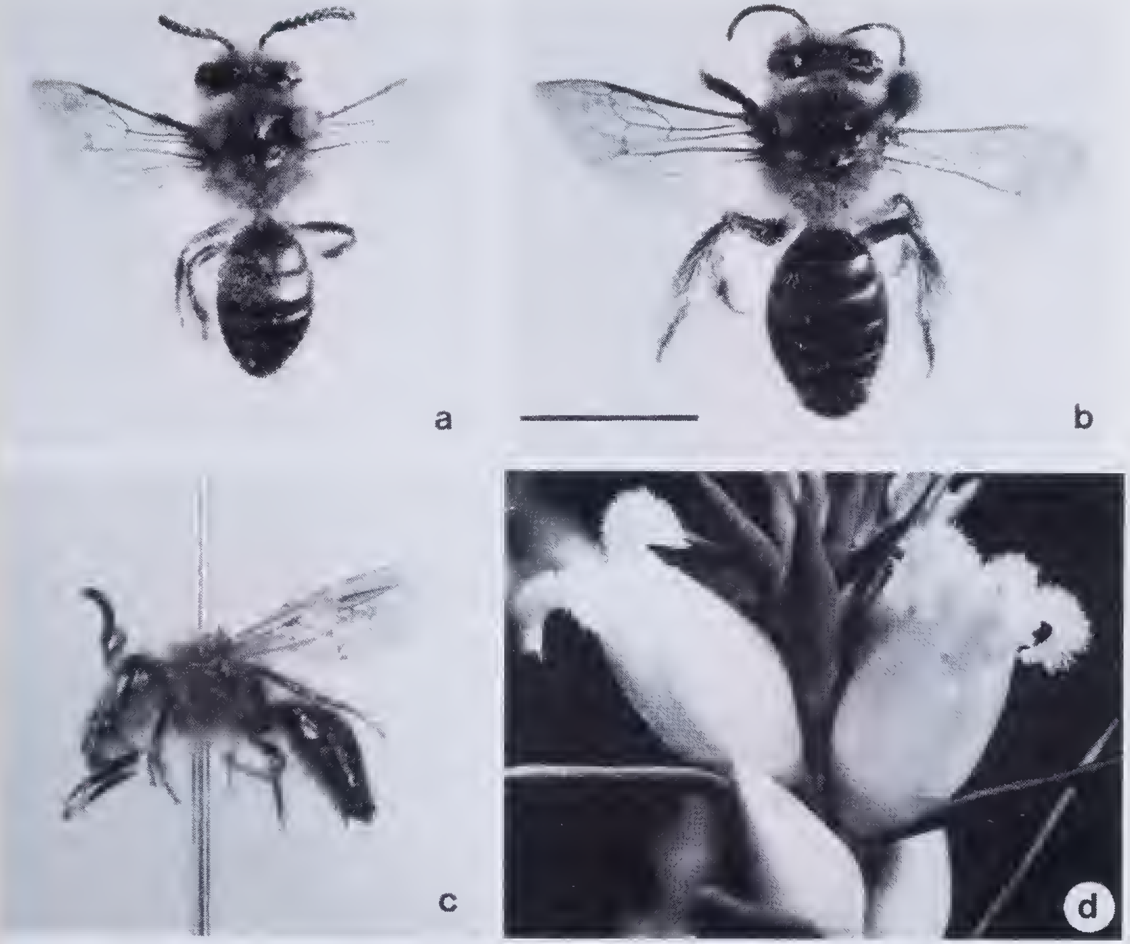

Figure 3 *Leioproctus macmillani:* (a, b) male and female, respectively, in dorsal view and (c) male, lateral view, all to same scale (line = 5 mm); (d) flowers of forage plant, *Astroloma xerophyllum.*

Diagnosis

Both sexes readily distinguishable by the extraordinarily long malar areas, about half as long as compound eyes (Figure 5 a-c); male with antennal flagellum complexly pectinate (Figure 4 a-c).

Description

Male (holotype)

Head width 3.1 mm; body length *ca.* 9.0 mm. Relative dimensions: HW 50; HL 46; UFW 33; LID -; DMA 26; MOD 3.5; WOC 13; OOD 10; IAD 7; ASD 4; AOD 10; EL 26; MSL 12; SL 15; SW 3.5; FL *ca.* 46; ML 21; BMW 6.

Head form as in Figure 5 a, b; gena *ca.* 0.6X as wide as compound eye viewed laterally; vertex slightly depressed between compound eyes and lateral ocelli; supraclypeal-interantennal area and clypeus strongly convex transversely, fairly straight in profile;

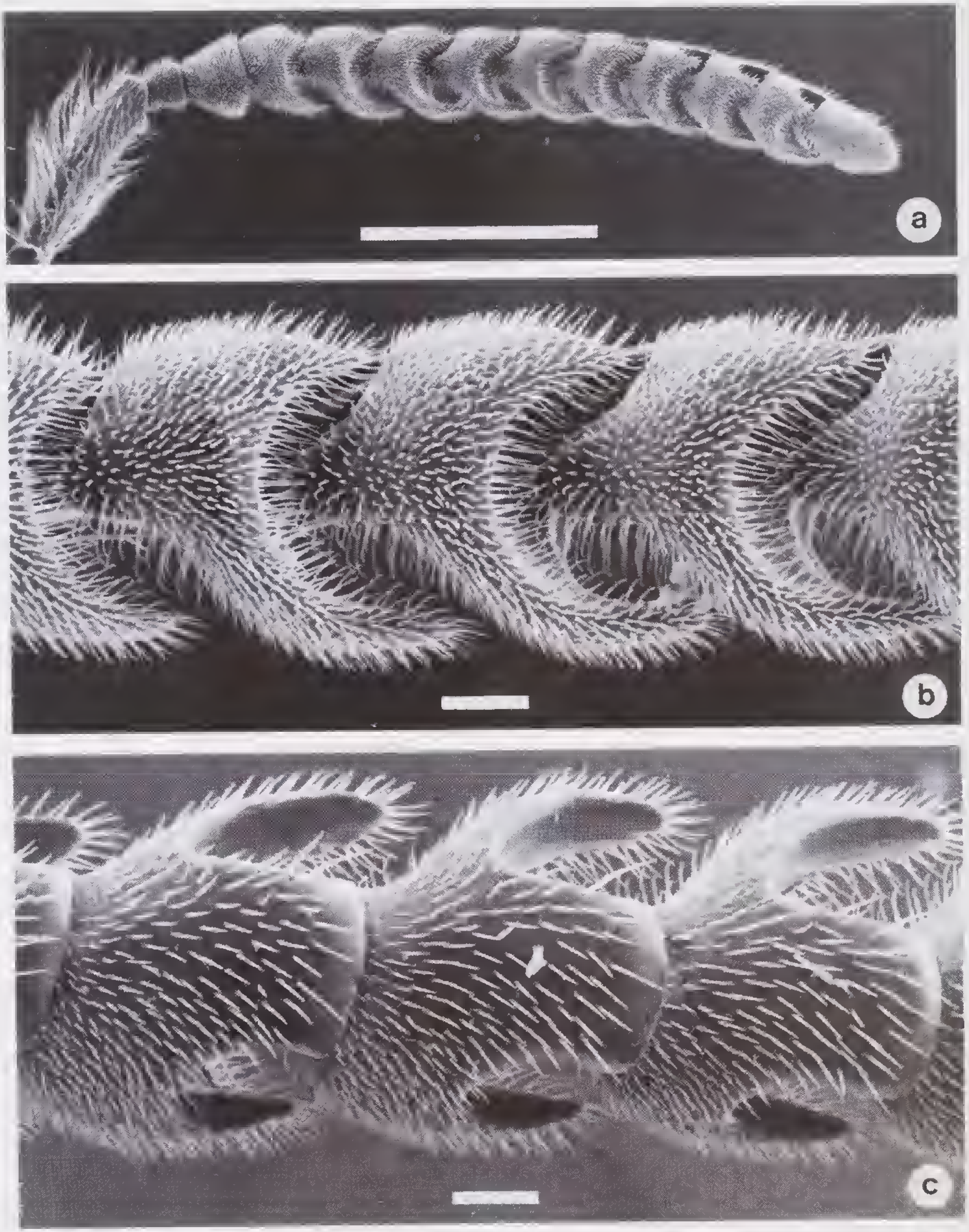

Figure 4 *Leioproctus macmillani*, antenna of male: (a) whole antenna, anterior view; (b) middle flagellar segments, anterior view; (c) same in dorsal view. Scale lines (a) 1 mm; (b, c) 0.1 mm.

labrum 0.8X as long as wide, ventral margin rounded, basal area strongly convex, smooth and bare, apical area flatter, minutely roughened and highly setose (much as in female, Figure 5 d); mandible slender, distinctly bidentate; proboscis elongate (Figure 3 c), prementum 0.56X as long as head width, annulate area of glossa separated from apex of prementum by about twice its own length; palpi well-developed, slender, ordinary; maxillary palpus attaining apex of galea; antennal scape slender, attaining mid ocellus; flagellum (Figure 4 a-c) almost as long as head width, extraordinarily modified, segments 2-10 each with a complex, somewhat cup-shaped ventral lobe projecting basally into concavity of preceding segment and produced apically into a small point anteriorly and a large prong posteriorly, segments 1 and 11 simpler but still lobed ventrally, all segments highly setose on outer surfaces, bare on inner surfaces; metanotum ordinary, not tuberculate although posterior margin bulges slightly; propodeal enclosure with steeply sloping basal area rounding imperceptibly onto vertical posterior surface; metasoma ordinary (Figure 3 a, c), first tergum with fairly abrupt anterior face deeply grooved medially and much longer than dorsal surface; venation ordinary; legs fairly ordinary, slender; fore basitarsus about as long as segments 2-5 combined with concavity of antenna cleaner unusually large (Figure 5 e); fore tibial calcar (Figure 5f) correspondingly large; hind basitarsus fairly straight, slender, *ca.* 8X as long as high.

Coloration. Integument predominantly black, metasoma faintly metallic blue-green except narrow apical margins of terga; labrum apically and mandibles largely orange-brown; inner surfaces of fore tibiae and all tarsi yellow-brown; flagella and wing veins dark brown; wings faintly brown-tinted.

Sculpture. Clypeus and supraclypeal area weakly shining with close, medium puncturing; frons and vertex minutely roughened and punctured, dull; malar areas and lateral margins of clypeus below tentorial pits impunctate, glossy; scutum and scutellum largely glossy centrally, setigerous punctures concentrated more peripherally; genae, thorax laterally and ventrally and propodeum (except enclosure) weakly shining, coriarious with open setigerous puncturing; propodeal enclosure coriarious, some weak transverse striae basally, posterolateral borders areolate; metasomal terga rather dull, foveate-imbricate (grading to imbricate on hind margins) with sparse, indistinct puncturing.

Pubescence. Frons, vertex, scapes, thorax generally, propodeum and legs proximal to apices of femora with moderately dense, long, erect, highly plumose, greyish-buff setae; similar but whiter setae occur on genae and metasomal terga 1 and 2; lower face with similar but shorter, more adpressed, white setae; ventrolateral areas of face also with several very long, blackish, erect, plumose bristles; malar areas bare; tibiae and tarsi with sparse, erect, simple and plumose setae; metasomal tergum 1 apically and terga 2-4 generally with erect, short, fine, simple setae intermixed with longer blackish bristles; terga 5-7 with long, blackish, plumose bristles; metasomal sterna sparsely setose, lacking conspicuous fringes.

Terminalia. See Figure 5 h-j.

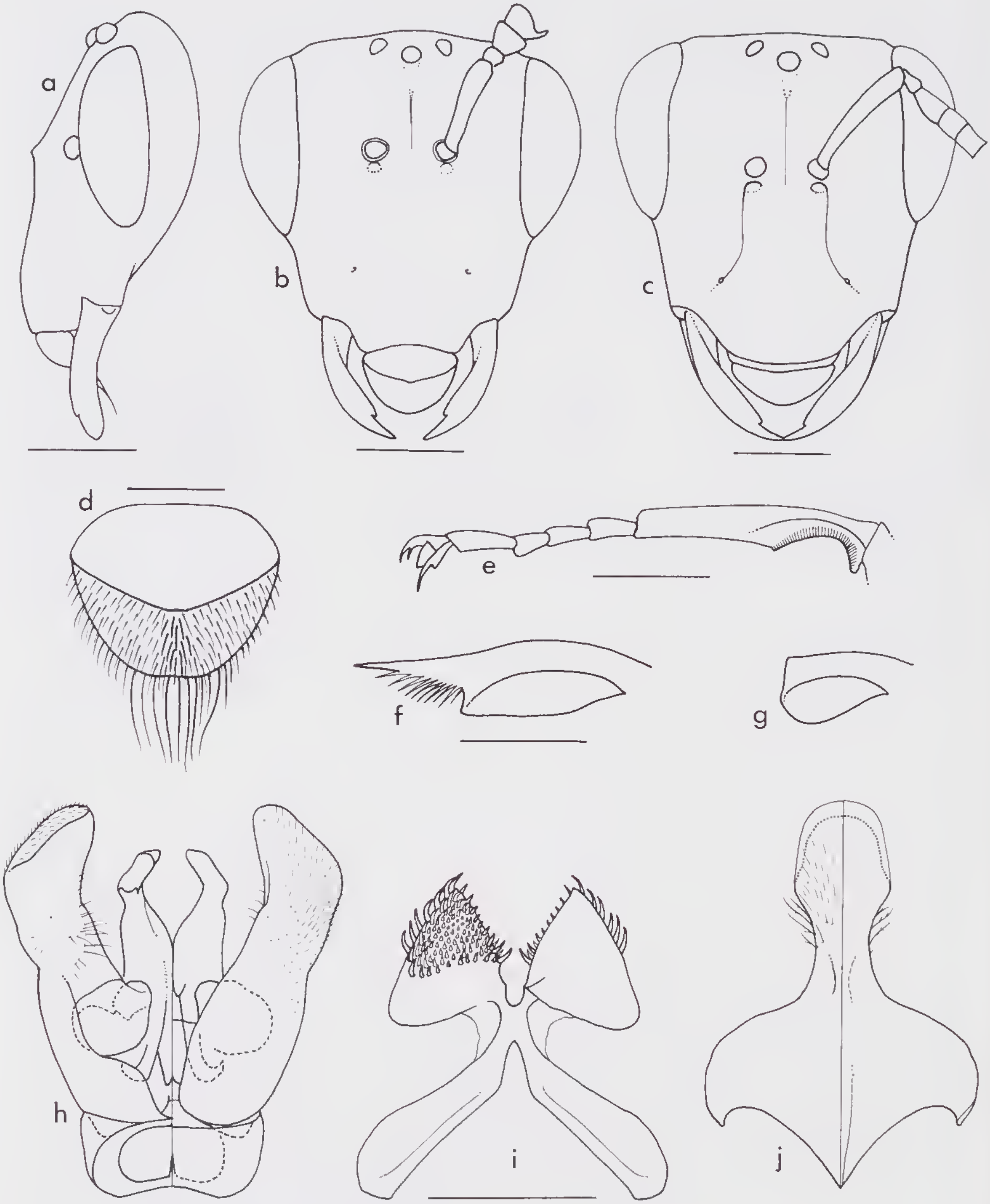

Figure 5 *Leioproctus macmillani:* (a) head of male, left lateral view; (b, c) heads of male and female, respectively, anterior view; (d) labrum of female, anterior view; (e) fore tarsus of male, inner view; (f, g) fore tibial calcar of male and female, respectively; (h-j) genital capsule, 7th and 8th metasomal sterna of male; dorsal view on right, ventral view on left. Pubescence omitted from a-c, e. Scale lines (a-e) 1 mm, (d, e, h-j) 0.5 mm, (f, g) 0.25 mm.

Female (paratype WAM 89/500)

Head width 3.55 mm; body length *ca.* 12 mm. Relative dimensions: HW 50; HL 48; UID 30; UFW 34; LID -; DMA 29; MOD 3.5; WOC 12; OOD 8.5; IAD 5; ASD 4.5; AOD 10; MSL 13; BMW 6.5; ML 25; SL 18; SW 3; FL 36.

Form (Figure 3 c) generally similar to that of male except as follows: head form as in Figure 5 c; flagellum ordinary, slender, first segment 1.5X longer than wide, segments 3-9 1.2X as long as wide, each slightly concave dorsally; prementum 0.72X as long as head width; fore basitarsus straight, slender, 5X longer than greatest width and 1.4X longer than remainder of tarsus, concavity of antenna cleaner occupying only about 1/5 of its length; hind basitarsus slender, *ca.* 5.5X as long as greatest height and 1.9X as long as remainder of tarsus; fore tibial calcar truncate (Figure 5 g); inner hind tibial spur with 5 or 6 slender teeth; pygidial plate notched at apex.

Coloration. As described for male but labrum wholly orange-brown; legs dark brown grading to yellow-brown more distally; hind tibiae yellow-brown.

Sculpture. As described for male except as follows: clypeus and supraclypeal area shining, closely to sparsely punctured; vertex weakly shining between ocelli and compound eyes; metasomal terga 2-4 with indistinct fine punctures grading from close anteriorly to sparse posteriorly; pygidial plate acinose centrally, smooth marginally.

Pubescence. As described for male except as follows: setae of legs chiefly golden but dark brown on outer (dorsal) surfaces of tibiae; fore basitarsus with dense, short, fine setae of inner surface contrasting with sparse, long, curved bristles of dorsal and outer surface (bristles on outer ventral edge especially thick); fore tarsal segments 2-4 also with long curved bristles; scopa of hind legs fairly sparse; metasoma with long, erect white setae, sparse on tergum 1, absent on remainder; terga 2-4 with sparse, short, white tomentum anteriorly (appearing silvery in oblique light); ventrolateral areas of terga and whole sterna (except basally) with long, plumose, golden setae; prepygidial fimbria sparse, of plumose blackish setae.

Variation

Slight. Head widths range from 3.1-3.3 mm in males (n 15) and 3.4-3.5 mm in females (n 8). Number of teeth on inner hind tibial spur of female varies from 5-8 (n 12).

Remarks

The unusually modified antennae of the male of this species are strikingly similar to those of male of *L. (Cladocerapis) bipectinatus* (Smith), the most notable difference being that *macmillani* lacks the sometimes forked or irregular finger-like processes arising from the smooth inner surface of each flagellar segment of *bipectinatus.* As females of *macmillani* possess stiff bristles on the fore tarsi, one of the diagnostic features of *Cladocerapis,* the possibility that *macmillani* should be assigned to that subgenus as a close relative of *bipectinatus* was considered. Certainly the species shares many characteristics with *Cladocerapis* species. However, it does not have the 'clypeus and supraclypeal area flat, at least partly smooth, shining and impunctate' as do *Cladocerapis* species (Michener 1965). Additionally, as far as is known, all species of *Cladocerapis* are oligolectic on *Persoonia* (Proteaceae). Consequently, I regard *macmillani* as an aberrant member of the subgenus *Leioproctus* which has independently acquired some of the characteristics of *Cladocerapis* and *bipectinatus* in particular. In any event, as Michener (1965) noted, *Cladocerapis* is closely related to *Leioproctus sensu stricto.*

Etymology

The specific epithet is in honour of Mr R.P. McMillan, an honorary associate of the Western Australian Museum, who collected the first specimens and who has made a significant contribution to the Museum's entomological collections.

Distribution

South-western Australia on the coastal plain north of Perth and in the Jurien Bay —Leeman region.

Specimens Examined

The holotype and the following paratypes. Western Australia: 1♂, 1♀ (WAM 89/500-1), same data as holotype, WAM; 2♀ (WAM 89/512-3), Beekeepers Reserve, Eneabba-Leeman-Jurien area, 2-5 Sept. 1987, M. Lyons, WAM; 4♂, 3♀ (WAM 87/1453-4, 89/495-9), 11 km NE of Wanneroo, 18 July 1982, C.A. Howard & TFH, on flowers of *Astroloma xerophyllum*, ANIC, WAM; Melaleuca Park, 10 and 11 km NE of Wanneroo (6♂, WAM 87/1451, 89/502-6, 11 June 1984; 3♂, 2♀, WAM 89/507-11, 7 Aug. 1989), TFH, on flowers of *Astroloma xerophyllum* (5♂, 2♀) and *Andersonia heterophylla* (4♂), UQIC, WAM.

Observations and Discussion

Leioproctus excubitor

This species inhabits semiarid and arid regions. It exhibits no clear plant preferences, females having been collected from flowers of four plant species representing four families, males from a further three species and families. Both sexes have been collected from late July to late September.

Males are unusual in perching for prolonged periods on prominent erect dead sticks, wooden posts, poles and other slender vertical objects (twice I found males sitting on my trouser leg after I had stood still for several minutes). Males always perch on sunlit surfaces and face vertically downwards. They were observed to occupy sites for up to 2 hrs from mid morning to early afternoon (and may have occupied them longer).

When perched, males have the legs splayed, the wings folded and the abdomen slightly cocked.

Slender dead trunks of mulga *Acacia* trees which have lost all but the main branches and have no bark are common perching sites. Once I encountered two such trees each attended by three or four males at a time. Each bee flew to the base of the tree, then upwards as if inspecting the sunlit side of a main stem. It would then alight on the stem at a height of *ca.* 2 m, facing upwards and quickly turn 180° to face downwards, remaining settled for a few seconds to several minutes before taking off and repeating the manoeuvre on the same or an adjacent branch. The males occasionally circled one another in flight but no aggressive interactions were observed. The silvery-white facial hair of males is very conspicuous when they are in flight.

The function of this male perching behaviour is unknown. Most probably it is a mating strategy (lekking) but no male-female encounters were observed at perching sites or elsewhere.

Males sometimes (if not regularly) roost in borer holes in dead wood: one live and one dead dry male were found in a vacated borer's gallery in a dead dry branch of a mulga *Acacia* tree.

Leioproctus macmillani

This species is most unusual in terms of its morphology and ecology. First, it appears to be oligolectic on a single species of winter-flowering plant, *Astroloma xerophyllum* (D.C.) Sonder (family Epacridaceae). This is the only species on which females are known to forage. It grows as a low shrub on sand in *Banksia* heaths north of Perth and can be locally abundant. Its flowers are white (Figure 3 d). Males have been observed to patrol this species and to take nectar from the tiny white flowers of *Andersonia heterophylla* Sond. (Epacridaceae). Few other bees are active during June and July on the coastal plain north of Perth (between latitudes 30°-32° S) when *macmillani* reaches the peak of its activity. These months are characterized by the frequent passage of cold fronts from the Indian Ocean bringing heavy showers, strong winds and cool temperatures. Flight and foraging appear to be limited to intermittent fine, sunny days.

Second, the peculiar elongation of the lower part of the head below the compound eyes is unparalleled in the Paracolletini although similar or even more exaggerated elongation occurs in certain exotic halictid bees in the genera *Chlerogella* Michener and *Thrincostoma* Saussure (Michener 1978). The cephalic elongation in *macmillani* is

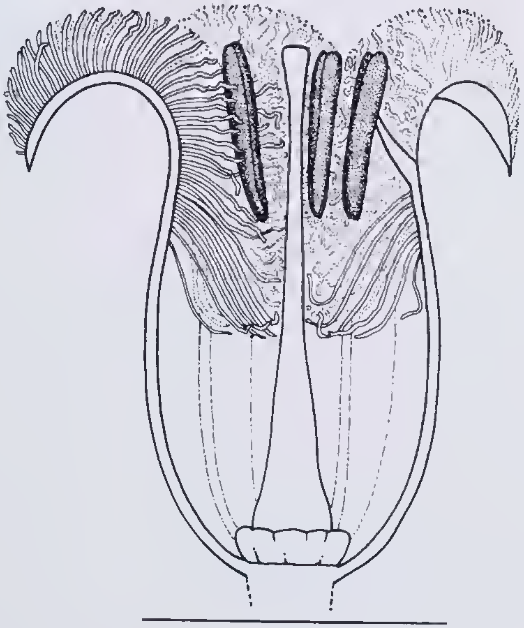

Figure 6 Flower of *Astroloma xerophyllum* (calyx and bracteoles omitted) with corolla tube sectioned to show internal structure. Scale line 5 mm.

associated with elongation of the proboscis and doubtless is an adaptation to the tubular flowers of the food plant. The corolla tube of *A. xerophyllum* is narrowed and densely bearded distally (Figure 6) and the small lumen is almost occluded by the style and anthers. Close observation of several foraging females revealed a consistent pattern of behaviour on flowers of *A. xerophyllum*. On alighting, a female thrusts her fore tarsi into the throat of the corolla and audibly vibrates her flight muscles. Then the fore legs alternately pump up and down drawing pollen out of the tube and the mid legs sweep it back to the scopa. Finally, the proboscis is extended and the female thrusts her head deep into the corolla tube to take nectar. A few times, females were observed to rotate about the long axis of the flower as they took nectar.

The use of vibration to aid pollen collection by bees is common on flowers with poricidal anthers. Bee vibration of non-poricidal anthers is comparatively rare but is recorded for plants having 'shaving brush' clusters of anthers (Buchmann 1985). Flowers of *A. xerophyllum* fit neither of these categories, having only five anthers dehiscing by means of longitudinal slits and wholly enclosed within the corolla tube (Figure 6). *Leioproctus macmillani* thus exhibits a novel variety of buzz pollination.

Third, *macmillani* is unusual in having most segments of the antennal flagellum of the male highly modified. The modifications result in a significantly increased area of plate organs and sensory hairs and may be adaptive in giving males a heightened olfactory sense. This could enable males to be more efficient at locating females by their scent, compensating for relatively lower temperatures and/or the scarcity of suitable flight periods. However, the existence of similar but even more ornate modifications of the antennal flagellum in males of *L. bipectinatus*, a summer-active species inhabiting coastal areas of eastern Australia, does not support this hypothesis.

Acknowledgements

I am indebted to Mr Clay Bryce (WAM) for production of the scanning electron micrographs (Figure 4) and to Ms J.C. Cardale (ANIC) for the loan of material in her care.

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A new species of *Nyctophilus* (Chiroptera: Vespertilionidae) from Lembata Island, Nusa Tenggara, Indonesia.

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Abstract

Nyctophilus heran sp. nov. is described from a single specimen collected in November 1989 from Pulau Lembata. Superficially it is most similar to *N. geoffroyi*, with which it is compared.

Introduction

Long-eared bats of the genus *Nyctophilus* are believed confined to Australia and New Guinea, where the number of species recognised ranges from 8 species (Corbet and Hill 1987) to 14 species (Parnaby 1988). Interestingly the first *Nyctophilus* named was *Vespertilio timoriensis* (Geoffroy, 1806) from specimens collected by Peron and Lesueur during the Baudin expedition of 1800-1804. The locality of these type specimens was reported to be Timor, Nusa Tenggara, Indonesia, however, it has not since been reported from Timor. Hill and Pratt (1981) consider that the exact provenance of the above specimens reported from Timor remains uncertain. Hill and Pratt (1981), however, attribute two specimens from near Wau, Morobe Province, New Guinea, to *Nyctophilus timoriensis.*

Nyctophilus together with the monotypic New Guinea genus *Pharotis* have been placed in the tribe Nyctophilini within the Nyctophilinae (Koopman and Jones 1970). Increasingly these two genera are considered distinct from the North American long-eared genera *Antrozous* and *Bauerus* (Antrozoini) (Hill and Harrison 1987).

As noted by Hill and Pratt (1981) *Nyctophilus* is easily recognised by its "square, truncated muzzle, low, fleshy noseleaf and its large usually clearly conjoined ears". *Nyctophilus* may be distinguished from *Pharotis* by a much lower anterior noseleaf which has a slightly concave distal margin rather than one that is evenly convex; a convex rather than concave anterior margin of the tragus; the absence of deep pits immediately behind the posterior nasal elevation and longer rostrum (Thomas, 1914). Tate (1941) recognised four species groups of *Nyctophilus.* These were:

(i) *timoriensis* group (including the forms *timoriensis, major* Gray, 1844; *sherrini* Thomas, 1915; and *gouldi* Tomes, 1858). These forms have unspecialised noseleaves (see Thomas 1915) except for *gouldi* which has moderately specialised noseleaves.

(ii) *bifax* group (*bifax* Thomas, 1915 and *daedalus* Thomas, 1915). These have unspecialised noseleaves and M^3 specialised, reduced and shortened.

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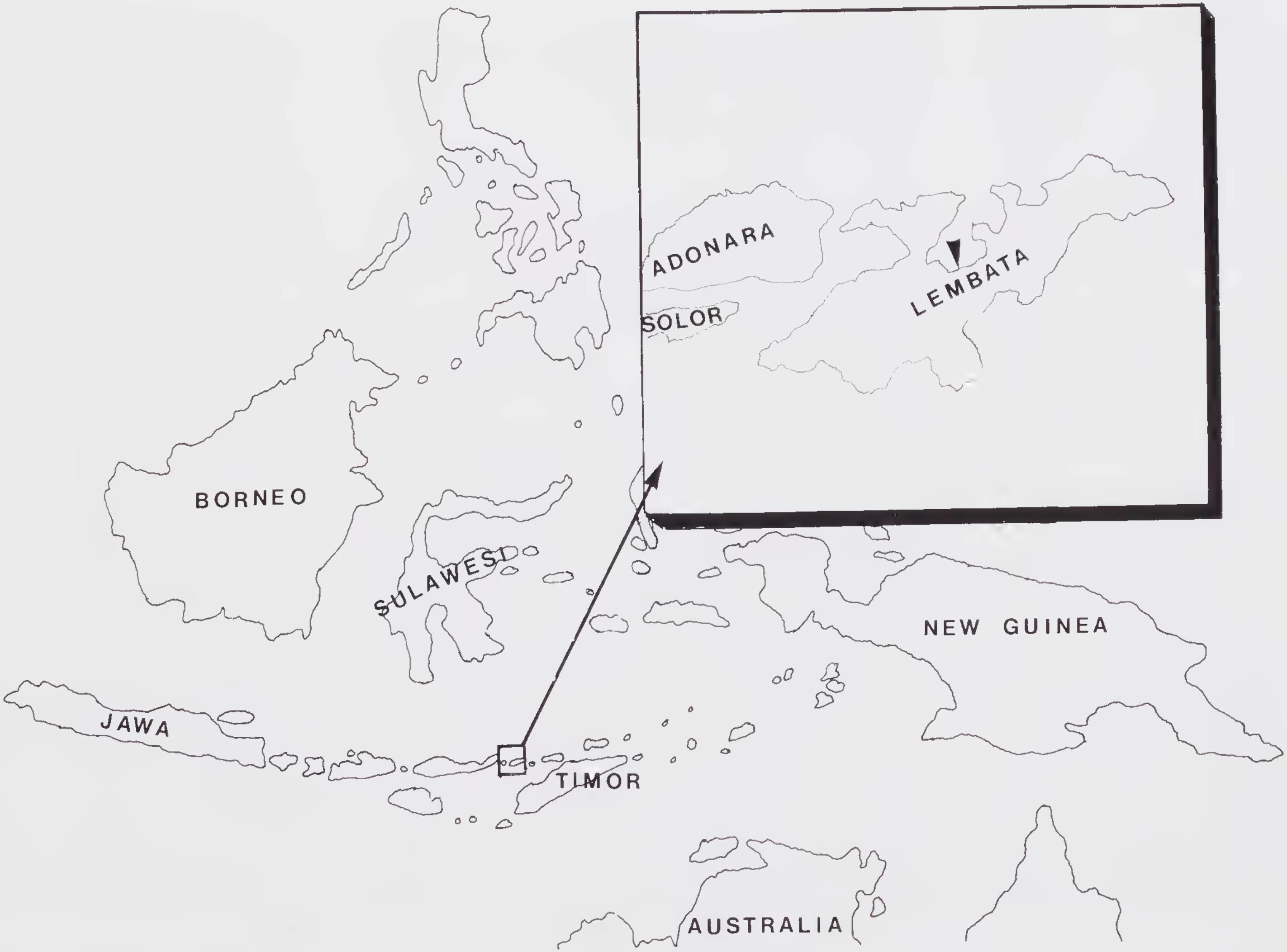

Figure 1: Map showing Pulau Lembata. Type locality of *Nyctophilus heran* sp. nov. is indicated by the arrow head.

(iii) *microtis* group (*bicolor* Thomas, 1915; *microtis* Thomas, 1888 and possibly *walkeri* Thomas, 1892). These have slightly specialised noseleaves and in the case of *walkeri* very small ears.

(iv) *geoffroyi* group (*geoffroyi* Leach, 1821, *unicolor* Tomes, 1858, *australis* Peters, 1861, *pacificus* Gray, 1831, *pallescens* Thomas, 1913). These have specialised noseleaves, where the posterior leaf is high, bifurcate and each lobe connected by a flexible membrane.

Parnaby (1988) recognises these above forms and additionally recognises *N. arnhemensis* Johnson, 1959, *N. microdon* Laurie and Hill, 1954 and *N. howensis* McKean, 1975 as well as a new species from Papua/New Guinea. All modern authors have synonymised *unicolor, australis, pacificus* and *pallescens* with *N. geoffroyi* (e.g. Mahoney and Walton (1988).

N. arnhemensis is stated by Parnaby (1988) to be similar to both *N. microtis* and *N. bifax. N. microdon* according to Koopman (1982, 1984) has a high band connecting the ears, long ears (24-28mm) and a noseleaf that is higher and clearly divided into two parts; the condylobasal length ranges from 13.5-13.6mm. Parnaby (1988) notes that it also has a large rectangular tragus and a distinctive penile morphology and with teeth conspicuously small [C^1-M^3 4.87 (4.8-5.0mm)]. In this regard, *N. microdon* could be considered somewhat intermediate between Tate's (1941) *Nyctophilus* species groups (iii) and (iv). *N. howensis* is a large robust form known only from the holotype which is a damaged skull. It is a large bat that perhaps falls in Tate's (1941) *timoriensis* group.

Between October 1987 and November 1989 five expeditions have been carried out in search of terrestrial vertebrates in Nusa Tenggara. Islands visited were Lombok, Sumbawa, Moyo, Sangiang, Sumba, Flores, Andonara, Lembata and Timor. These expeditions have recorded large numbers of bats which have greatly altered our understanding of the patterns of distribution of bats in this regions (Kitchener *et al.* 1990, a & b).

In November 1989, a single specimen of *Nyctophilus* was collected on Lembata (Lomblen) I. This specimen was compared to the known species using information contained in the following publications: Thomas (1915), Tate (1941), Laurie and Hill (1954), McKean (1975), Hill and Pratt (1981), Hill and Koopman (1981), Koopman (1982, 1984) and in an unpublished thesis by H. Parnaby (1988). The present study benefited greatly from access to the latter work, particularly in regard to glans penis morphology and craniometrics.

As a result of these comparisons the Lembata *Nyctophilus* is herein described as a new species.

Methods

Measurements (in mm) used and measurement points are detailed in Kitchener *et al.* (1986). Pelage was described using Ridgway (1912).

Systematics

Nyctophilus heran sp. nov.

Holotype

Western Australian Museum catalogue number (WAM) M 32252* an adult male, skull and mandibles separate, carcase fixed in 10% formalin and preserved in 70% ethanol, liver and blood samples separately in ultrafreezer; collected in a Harp Bat Trap on 5 November 1989 by the authors.

Type locality

Kampong Merdeka, Desa Hadakewa, Pulau Lembata, Nusa Tenggara, Indonesia (8°22′S, 123°31′E) (Figure 1) at sea level. Collected over a small stagnant pool in a small dry stream some 200 m from mangroves. The stream was bordered on both sides by kebun (gardens) with occasional coconut and banana trees.

Diagnosis

Nyctophilus heran sp. nov. differs from all described species of *Nyctophilus,* apart from *N. geoffroyi,* by having a high postnasal foliation that bifurcates distally into a Y-shaped structure which has each arm connected by a flexible septum; by having a baculum which has its shaft thin and narrowing to a simple distal point that is not bifurcate and unexpanded.

It differs from *N. geoffroyi* in having a glans penis that lacks a pronounced dorsal crest which projects to the distal end; the distal end less rounded and does not overshoot the ventral mound — which has a median cleft (Figure 4); bulla smaller, such that bulla length/greatest skull length less (0.233 *v.* 0.247-0.275) and less inflated; postpalatal spine more pronounced; mesopterygoid anterior edge more sharply angled towards base of postpalatal spine; hypocone more pronounced on M^{1-2}; a number of skull and dental measurements exceed the largest reported for male *N. geoffroyi:* e.g., greatest skull length (16.7 *v.* 16.4), zygomatic breadth (10.6 *v.* 9.9), braincase height (6.2 *v.* 5.8), and C^1-M^3 length (6.1 *v.* 5.8).

It differs from *N. microdon,* the only other *Nyctophilus* with a moderately high postnasal foliation (which while bifurcated is not Y-shaped), by having a tragus which is not squared at its apex; narrower interorbital width (<3.9); generally broader skull: e.g., zygomatic width larger (>9.5), C^1-C^1 breadth greater (>4.2), bulla longer (>3.5); dentition more robust: e.g., C^1-M^3 longer (>5.5).

It also differs from *N. t. timoriensis, N. timoriensis sherrini,* (see Table 1) and *N. major* by being generally smaller: e.g., forearm length shorter (<40), greatest skull length shorter (<17), C^1-C^1 breadth narrower (<4.8) and C^1-M^3 shorter (<6.4); glans penis has no dorsal fissure such as in *major* and *sherrini,* and ventral lobe lower.

It also differs from *N. walkeri* in being substantially larger: e.g., forearm length larger (>37); ear larger (>17); greatest skull length longer (>14); zygomatic width greater (>9.1); interorbital width greater (>3.3); C^1-C^1 wider (>40); C^1-M^3 length greater (>5.0); bulla longer (>3.0); glans penis lacks a pronounced distal ventral groove, ventral lobe more pronounced.

* Final deposition of this holotype, at completion of this series of expeditions, will be the Museum Zoologicum Bogoriense, Bogor, Indonesia.

Table 1: Skull, mandible, dentary and external measurements for the holotype of *N. heran* sp. nov., *N. timoriensis* putative cotype, a specimen from New Guinea and *N. geoffroyi* from southwest Western Australia and Tasmania.

		N. timoriensis		*N. geoffroyi*
	N. heran	*	**	N = 6 (range)
	holotype ♂	New Guinea ♀	"Timor"? ♂	West Aust./Tas. ♂♂
Skull & dentition				
greatest skull length	16.70	19.2	19.8	14.45 - 15.86
interorbital breadth	3.76		5.4	3.04 - 3.53
zygomatic breadth	10.64	11.7	11.4	8.59 - 9.47
mastoid breadth	8.89	9.4		7.55 - 8.50
braincase height	6.18			4.94 - 5.35
mesopterygoid fossa width	2.05	2.1	2.1	1.37 - 1.78
palatal length	6.02	6.5		5.13 - 5.90
distance between bullae	1.64			1.33 - 1.41
basicranial length	8.25			6.76 - 7.41
bulla length	3.90	3.9		3.74 - 3.98
antorbital foramen breadth	4.73	5.5		4.08 - 4.48
braincase width	7.85	8.6	9.0	6.93 - 7.77
dentary length (from condyle)	11.83	12.7		9.89 - 10.61
C^1-C^1 breadth (alveoli)	4.54	5.5	5.1	3.72 - 4.36
M^1-M^1 breadth (inside)	2.90		3.35	2.41 - 2.72
M^3-M^3 breadth (cusp)	6.79			5.74 - 6.32
M^1-M^3 length (cusp)	3.90	4.8	4.6	3.28 - 3.74
C^1-M^3 length (cusp)	6.05	7.2	7.0	5.09 - 5.59
C_1-M_3 length (cusp)	6.53	7.8		5.83 - 6.01
M^3 length	0.74			0.63 - 0.73
M^3 width	1.75		1.7	1.43 - 1.69
Externals				
forearm length	39.3	48.5	46.5	34.5 - 38.4
head to vent length	51.5		60	43.3 - 44.6
tail to vent length	40.7		50.5	37.7 - 40.4
pes length	6.4		10	6.8 - 7.1
ear length	23.4			21.1 - 24.0
tibia length	18.8			16.1 - 17.9
calcar length	13.6			10.1 - 10.6
tragus length	8.1			6.6 - 7.3
metacarpal I length (MCI)	6.1			5.2 - 5.6
MCII	34.7			31.4 - 33.9
MCIII	37.8			31.1 - 35.2
MCIII/phalanx I length (PI)	14.5			12.2 - 14.3
MCIII/PII	14.0			11.5 - 11.7
MCIII/PIII	9.1			6.3 - 8.9
MCIV	38.0			30.7 - 34.3
MCIV/PI	10.5			9.4 -12.0
MCIV/PII	13.0			10.3 - 11.7
MCV	37.2			30.9 - 34.7
MCV/PI	10.4			9.1 - 10.0
MCV/PII	8.5			6.8 - 8.8

* *from Hill and Pratt (1981) - BM (NH) 80.498* ** *Tate (1941) - putative cotype, Paris Museum*

It also differs from *N. b. bifax* in having band of skin connecting ears more pronounced; glans penis ventral lobe slightly more pronounced, urethral aperture with a more pronounced median groove.

It also differs from *N. bifax daedalus* in having its greatest skull length slightly smaller (<16.8); C^1-C^1 breadth narrower (<4.9); C^1-M^3 length shorter (<6.2) and bulla slightly longer (>3.8); glans penis distal end less globose, distal and ventral lobes less prominent.

It also differs from *N. arnhemensis* in having skull slightly larger: e.g., greatest skull length longer (>16), zygomatic width considerably larger (>10.2), bulla longer (>3.5); glans penis distal lobe from cranial surface does not overshoot ventral lobe, ventral lobe more rounded at distal end rather than squarish.

It also differs from *N. gouldi* in having zygomatic width larger (>10.6); glans penis with distal and ventral lobes more pronounced.

It also differs from *N. m. microtis* and *N. m. bicolor* in having a well developed band connecting the ears, rather than scarcely developed or absent in the midline; tragus more broadened basally; greatest skull length longer (>16.1); glans penis lacks prominent ventral lobe, urethral opening on ventral surface rather than distal, ventral lobe also with a median groove.

It differs from *N. howensis* in being smaller in all skull measurements: e.g., greatest skull length (16.8 *v.* 23.2), zygomatic width (10.6 *v.* 13.9); interorbital width (3.8 *v.* 4.3); C^1-M^3 length (6.1 *v.* 8.0); palatal length (6.0 *v.* 7.6) and braincase width (7.9 *v.* 9.7).

Description

(Table 1; Figures 2-5)

Skull, mandible and dentition (Table 1; Figure 2)

Skull shape generally similar to *N. geoffroyi.* The cranium moderately inflated; sagittal crest weak, most marked in midpoint of cranium and bifurcating anteriorly to weak supraorbital ridges, does not connect with weak lambdoidal ridges; rostrum slightly more depressed and median sulcus slightly deeper than in *N. geoffroyi;* anterorbital foramen moderate, zygomatic breadth wide (10.6), zygomatic thickness moderate; anterior nasal aperture a wide V shape, projects posteriorly to a line level with the anterior edge of anteorbital foramen. Skull measurements greater than those presented for *N. geoffroyi* (Table 1) but Parnaby (1988) presents maximum measurements for *N. geoffroyi* (usually from the Tasmanian form) which exceed the values given in Table 1. However, compared to Parnaby's (1988) measurements, *N. heran* has the following values exceeding those reported for *N. geoffroyi:* greatest skull length (16.7 *v.* 16.4), zygomatic breadth (10.6 *v.* 9.9), braincase height (6.2 *v.* 5.8), and C^1-M^3 length (6.1 *v.* 5.8); bulla compared to *N. geoffroyi* are shorter such that the bulla length/greatest skull length is less (0.233 *v.* 0.247-0.275), less inflated; distance between bulla greater than in *N. geoffroyi* (1.64 *v.* 1.33-1.44); postpalatal spine large; angle of mesopterygoid edge to base of postpalatal spine moderately sharp; third commissure of M^3 slightly longer than in *N. geoffroyi* such that M^3 breadth greater (1.75 *v.* 1.43-1.69); hypocone M^1-M^2 moderately well developed more so than in *N. geoffroyi,* palate deep, slightly more excavated than in *N. geoffroyi.*

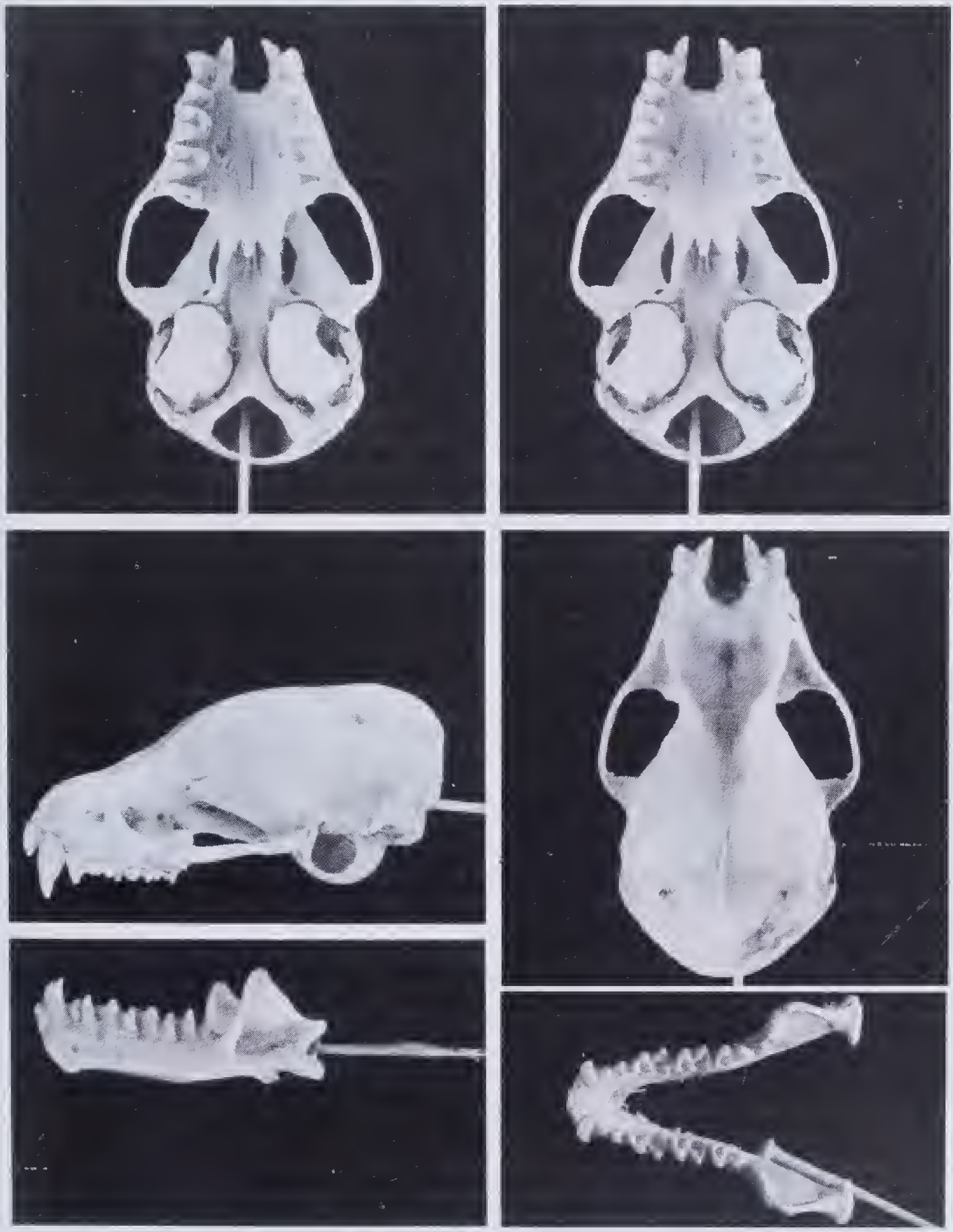

Figure 2: Skull and dentary of *Nyctophilus heran* sp. nov. holotype. Ventral view as stereopairs.

Figure 3: Photographs of *Nyctophilus heran* sp. nov. taken while alive.

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

Ears moderately long (23.4), joined by band of skin that is approximately 3 mm high at midpoint; tragus moderately long (8.1), anterior edge from apex straight, or very slightly concave, for one-third length then gently concave to base, posterior edge from apex very gently convex for half length then considerably convex towards base where margin has several protuberances, apex a rounded point, slightly narrower than in *N. geoffroyi,* lobe on inner edge at midpoint of posterior margin moderate; antitragus both moderately wide and high; anterior noseleaf moderately high; upper margin gently concave; postnasal foliation high (*c*. 1.9), bifurcating distally to a Y-shape with a central stout membrane connecting these distal arms — the general shape is similar to *N. geoffroyi;* weight (7.6 g): forearm length (39.3), head to body length (51.5) and tail to vent length (40.7); calcar (13.6) reaches approximately to midpoint of posterior margin of uropatagium. These values show *N. heran* to be an intermediate sized *Nyctophilus.*

Glans penis (Figure 4) slender, without a very prominent distal lobe, urethral groove ventral U-shaped, supported by a bifurcated low ventral lobe. It differs from *N. geoffroyi* in lacking a pronounced dorsal crest and a distal lobe that overshoots the ventral mound, and the presence of a median cleft in the ventral mound.

Baculum (Figure 5) bifurcated basal part with a gently curving thin shaft tapering to a thin distal point which is not bifurcate and has no other modifications. It is similar to *N. geoffroyi.*

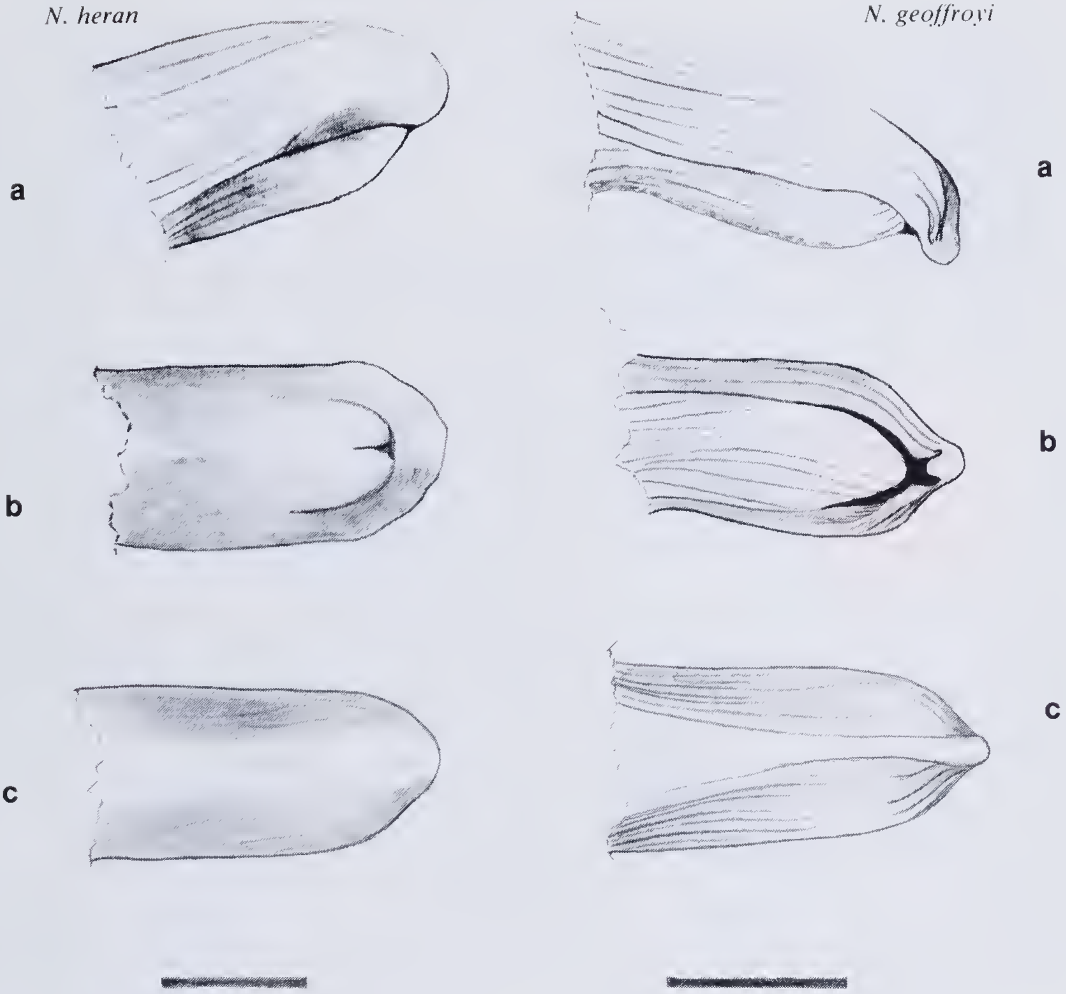

Figure 4: Drawings of glans penis, assisted by use of camera lucida, of *Nyctophilus heran* sp. nov. and *N. geoffroyi*. (a) lateral, (b) ventral and (c) dorsal views.

Pelage

Dominant colour of pelage Light Drab, which is from distal one-third of hairs on dorsum and venter. Basal two-thirds of hairs on dorsum (±6.5 long) and head (±4 long) Mouse Grey — on venter Mummy Brown (±6 long). Hair at base of ears and on band of skin connecting ears, face and chin shorter (<4), Light Buff. Skin of basal one-quarter of ear, chin and lips, Light Ochraceous-Buff.

Etymology

Nyctophilus heran is named after the Bahasa Indonesian word for surprise (heran), which was our prevailing emotion at capturing a nyctophiline bat in Nusa Tenggara.

Figure 5. Bacula of: (a), *Nyctophilus heran* sp. nov. holotype. X-ray photograph; (b), outline from (a) and (c) of *N. g. geoffroyi* (WAM M 15950) for comparison.

Remarks

The capture of a *Nyctophilus* in Nusa Tenggara has biogeographic implications and increases the number of bat genera confirmed to be in common between these islands and Australia to 12. It is perhaps not surprising that, superficially at least, *N. heran* appears most similar to *N. geoffroyi,* which is the most widespread of the Australian *Nyctophilus* species.

The collection of *N. heran* perhaps adds support to Timor as the type locality of *N. timoriensis* — a view not supported by most modern authors, for example, Goodwin (1979) did not collect it on Timor, and commented that on distributional grounds it was unlikely to occur there. We have briefly collected on Timor Barat; the first bat we collected was unrecorded for Timor, indicating that much more collecting is required on that island before a complete inventory of its bat species is available, and before *N. timoriensis* can be excluded from its bat fauna.

Acknowledgements

We are indebted to Ron Johnstone, Western Australian Museum, for his support and companionship in the field. We are particularly grateful to Harry Parnaby who kindly allowed us access to his PhD thesis and commented on the manuscript.

Gerry Allen instructed us on the use of the X-ray machine; Norah Cooper took the skull photographs. Anne Nevin typed the manuscript.

Other specimens measured

Nyctophilus geoffroyi (all ♂♂, WAM specimens) M 856, Tambellup, W.A.; M 3207, Woodanilling, W.A.; M 6022, Katanning, W.A.; M 8970, Dwellingup, W.A.; M 15950, Gingin, W.A.; M 18356, Augusta, W.A.; M 16586, Orford, Tasmania; M 25684, Plenty, Tasmania.

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Rec. West. Aust. Mus. 1991, 15(1): 109-116

A new species of *Tylos* Audouin (Isopoda: Oniscidea: Tylidae) from Western Australia

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Abstract

Tylos tantabiddyi sp. nov. is described from specimens collected at Tantabiddy on the west coast of the Exmouth peninsula, WA. This is the third species of the genus found in Australia and the first from the west coast. A key to the Australian species is given.

Introduction

The Tylidae is a family of supralittoral isopods which occurs on the coasts of all continents. Twenty three species have been established (although opinions about synonymy vary) of which eight are from the southern hemisphere (Roman 1977, Schmalfuss and Ferrara 1978, Schultz 1983,). Two more southern species have been described. The first Australian species *T. australis* Lewis and Bishop, 1990, from the south east of the continent was based on specimens collected in 1987 (Lewis and Bishop, 1990). A second species was collected by the author in Queensland in 1988 (Lewis, in press).

The family Tylidae Milne-Edwards, 1840, differs from other Oniscidea by the presence of all of the following characters:—

1. Well developed frontal process on cephalon.
2. Separate epimera on pereonal tergites 2-7.
3. Ventral uropods articulated laterally.
4. Obsolete uropod exopod.
5. Pleopod exopods with tracheal systems.
6. Antennula reduced to 1 joint.
7. Pleopod endopod 2 only, used in copulation.
8. Ability to conglobate.

(Vandel 1960, and Schmalfuss and Ferrara 1978).

As well as showing the previous characteristics, the genus *Tylos* Audouin, 1826, is diagnosed as follows:

Ability to roll into perfect ball. Head with triangular protrusion between the antennae (frontal process). Lateral quadrangular grooves which contain the antennae when the animal rolls. Four jointed flagellum. Locking ventral grooves on epimera 1. Pleon tergites not fused. Ventral pleon plates cover part of ventral area. (Schmalfuss and Ferrara 1978).

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The following abbreviations are used:
WAM= Western Australian Museum
AM = The Australian Museum, Sydney
TM = Tasmanian Museum and Art Gallery, Hobart
QMW= Queensland Museum, Brisbane
MU = Macquarie University, Biological Sciences Museum.

Systematics

Tylos tantabiddyi sp. nov.

Figures 1-7

Holotype

Male, in WAM 21-90, Tantabiddy Beach south of boat ramp, under and among weed at high tide line, 17, August 1989, collected by Fiona Lewis.

Paratypes

WAM. 22-90, AM. P39745, TM. G3374, MU. Collection data as for holotype.

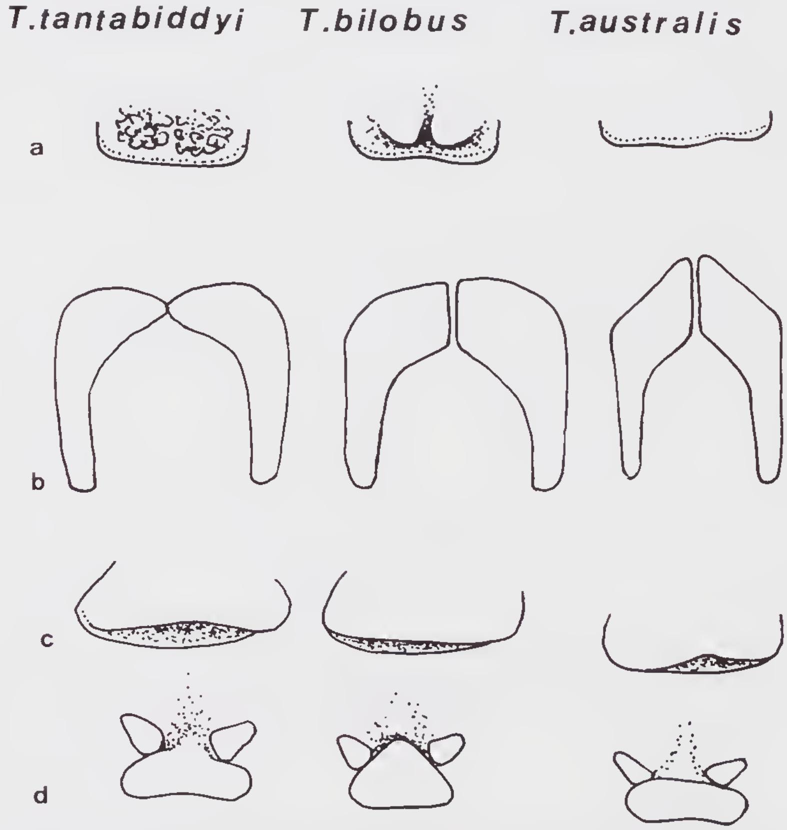

Figure 1. Differences between the three Australian species of Tylidae; a, telson; b, ventral view of 5th pleon plates; c, lateral margin of 1st, left epimera; d, frontal process of cephalon, anterior view.

Diagnosis (see Figures 1a-1c).

The morphology of the telson, fifth pleon plate, lateral margin of epimeron 1 and cephalon, distinguishes this species from the other two Australian species. This species is nearest geographically to *T. nudulus* Budde-Lund, 1906, from Christmas Island, but differs from this species, and all other described species, in having a less sharply defined frontal process, shallow tuberculated lobes on the telson and pointed medial margins of the 5th pleon plates.

Description

Size: 9mm long, 3mm broad.

Colour: (live). Dorsal surface creamy grey with very sparse black chromatophores, mainly along midline, extending laterally on pereonite seven and pleonites one and two, and in patches antero-medial to eyes.

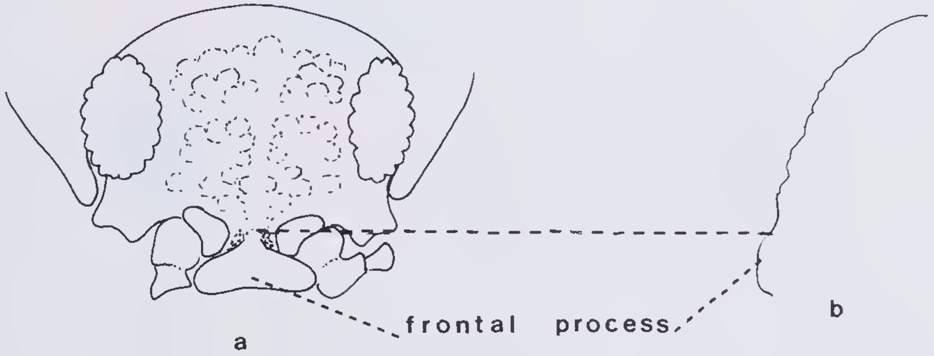

Figure 2. *Tylos tantabiddyi* spinov. Cephalon; a, anterior view, frontal process and antenna 1 labelled; b, lateral view, frontal process labelled.

Cephalon (Figures 2a, 2b). Eyes each of 27-30 ommatidia. Vertex without distinct frontal line, but with areas of large tubercles anterior and median to eyes. Frontal process triangular with apex smoothly joined to cephalon.

Antenna 1 (Figure 2a). Medial and slightly above 2nd antenna base; comprised of single, flattened, triangular article.

Figure 3. *Tylos tantabiddyi.* Antenna 2; a, peduncle and flagellum; b, lateral view, frontal process labelled.

Antenna 2 (Figures 3a, 3b). Short, slender, with flagellum of four articles, 3rd longer than 1st and 2nd, 4th minute, ending in brush organ, articles 0.03, 0.02, 0.05, and 0.01mm in length.

Left Mandible (Figure 4a). Incisor process of two pointed teeth and one round tooth, with lacinia mobilis of two teeth and rounded process, setose lobe at base with one large penicil, five smaller penicils between lobe and molar process which has one penicil.

Right Mandible (Figure 4b). Incisor process of three teeth with five small transparent teeth in arc, two penicils on lobe at base and five smaller penicils between lobe and molar process which has one medial penicil.

Maxilla 1 (Figure 4c). Lamellar, subquadrangular, terminally setose.

Figure 4. *Tylos tantabiddyi.* Mouthparts; a, left mandible; b, right mandible; c, maxilla 1; d, maxilla 2; e, maxilliped.

Maxilla 2 (Figure 4d). Outer lobe with five large, heavy teeth laterally, one with spines; seven slender teeth medially, one with spines. Inner lobe terminates in three setose penicils with large spine at base of superior penicil.

Maxilliped (Figure 4e). Endite with three lobes bearing heavy, blunt spines, with sharp spines at bases of two medial lobes and along lateral margin. Endite has four small lobes extending into short setose penicils, with tooth at base of medial two lobes.

Pereon (Figures 5a, 5b). Lightly granulated. Epimera two to four subtriangular, decreasing in size. Epimeron five rounded, epimera six and seven large and subrectangular. Lateral border of epimeron one slightly convex with groove joining ventrally to raised triangular lobe, small raised areas on ventral surfaces of epimera two and three.

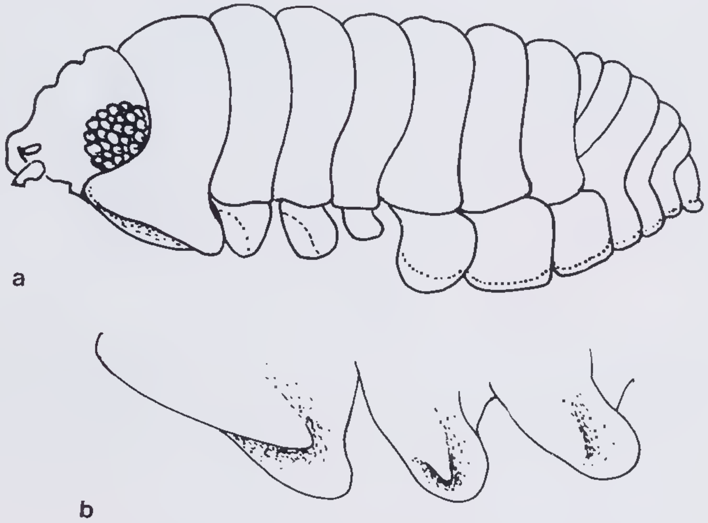

Figure 5. *Tylos tantabiddyi.* Pereon; a, lateral view; b, ventral view of epimera 1-3.

Pereopods (Figures 6a-6f). Pereopods 1-4 slender, pereopods 5-7 increasingly short and stout, with anterior process at distal end of ischium increasing in size. Dactylar organs and accessory claws on all.

Pleon (Figures 7a, 7b). Third segment squarely truncated, 4th and 5th rounded laterally. Telson rectangular, broader than long, with two subrectangular, raised areas of low tubercles close to mid line. Posterior border with evenly spaced large setae. Ventrally 5th pleon plates meet medially in a rounded point covering 5th and half of 4th pleopod.

Pleopod 1 (Figure 7b). Reduced to slender lamella curving around lateral angle of pleopod 2.

Pleopod 2 (Figure 7b). Exopod subrectangular extending to posterior pointed process medially, with folds enclosing slit openings of pseudotracheae. Endopod modified to form copulatory stylet.

Figure 6. *Tylos tantabiddyi.* Pereopods; a, first; b, third; c, dactylus showing dactylar organ of pereopod 1; d, fifth.

Pleopods 3-5 (Figure 7b). Exopods similar to 2nd, endopods lamellar.

Uropod (Figure 7c). Not visible dorsally. Wedge shaped and platelike with setose endopod.

The following key to Australian species of Tylidae uses simple morphological characters to separate the three species.

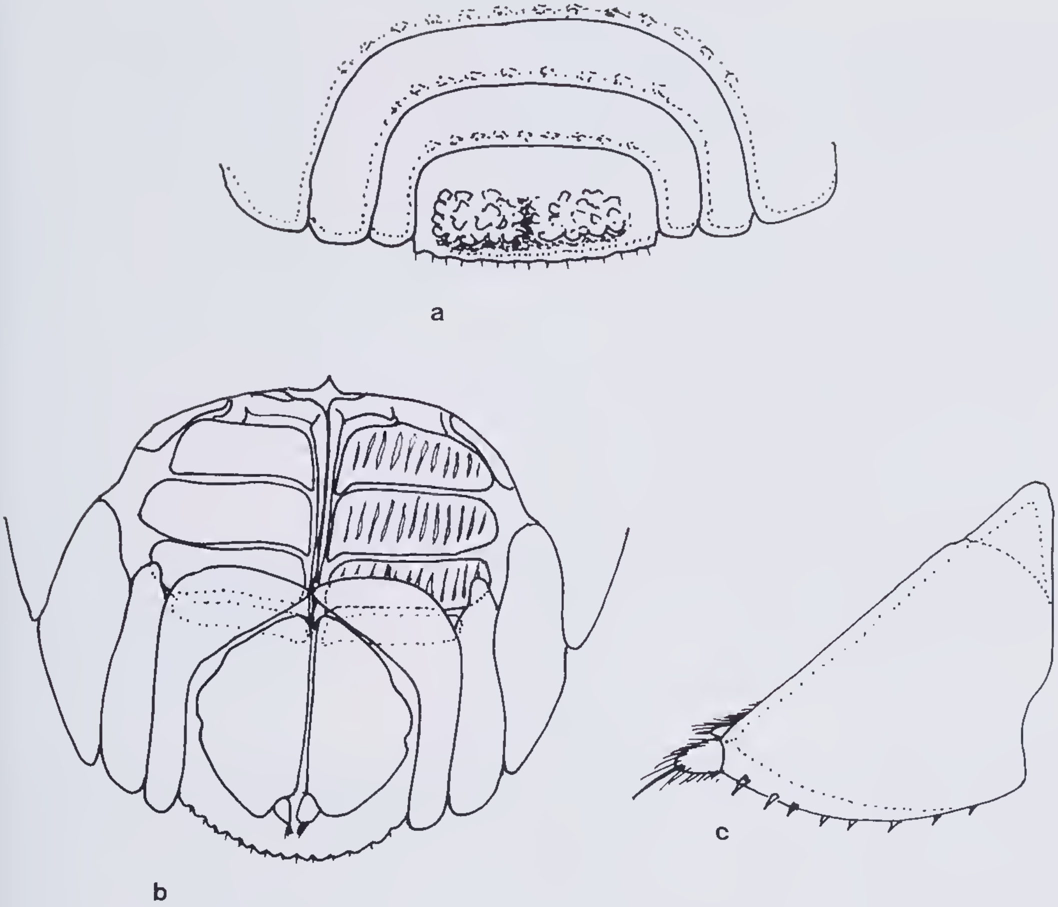

Figure 7. *Tylos tantabiddyi.* Pleon; a, dorsal view; b, ventral view; c, uropod, ventral view.

A Key to the Austrarlian Species of Tylidae

1. Telson with small tubercles . . . . *T. australis*
   Telson with two raised lobes *2*
2. Telson with raised areas of low tubercles close to midline; lateral edge of epimeron one sinuous . . . . *T. tantabiddyi*
   Telson with large lobes; lateral edge of epimeron one smooth. . . . . *T. bilobus* (Lewis, in press)

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I wish to thank those of my colleagues who read and commented on this paper.

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A new southern Australian subgenus of *Temognatha* Solier (Coleoptera: Buprestidae: Buprestinae), with nomenclatural notes on Solier's generic name.

Magnus Peterson*

Abstract

Temognatha (Calotemognatha) subgen. nov. is described for three species: *T. (C.) yarelli* (Gory & Laporte, 1837); *T. (C.) laevicollis* (Saunders, 1868); *T. (C.) varicollis* (Carter, 1913). *Stigmodera laevicollis* Saunders is designated type species of *Calotemognatha*, and is illustrated. Lectotypes are designated for *Stigmodera bonvouloirii* Saunders, 1868, *S. laevicollis, S. varicollis*. Possible location of syntypes of *Buprestis variabilis* Donovan, 1805 and *Stigmodera (Temognatha) yarelli* is discussed. *Stigmodera (Stigmoderoides)* Thery, 1937, recently synonymized with *Temognatha* Solier, 1833, is shown to be nomenclaturally unavailable. Ovipositors (in dorsal view) of *T. (C.) laevicollis, Temognatha (Temognatha) variabilis* (Donovan) (type species of *Temognatha*) and *T. (T.) bonvouloirii* are figured. Distribution of the new subgenus is mapped. Correct spelling/citation of *Temognatha* is discussed.

Introduction

Bellamy (1988:416) and Gardner (1990:313-315,325) have shown how useful ovipositor morphology is in distinguishing supraspecific taxa within the externally uniform family Buprestidae.

After examining ovipositor morphology of all nominal species-level taxa currently assigned to *Temognatha* Solier, 1833, for an eventual revision of this stigmoderine genus, it became apparent that three of its species were clearly separable from the others on the basis of divergent structural modification to their ovipositors. Closer study revealed that these three taxa were very closely allied because this discrete structural modification was homologous and identical. This synapomorphy is significant enough to necessitate description of a new subgenus to accommodate the three species. This is the second in a series of papers describing new *Temognatha* taxa, which began with Peterson (1982).

Methods and Terminology

Specimen measurements linear, measured to the nearest 0.05 mm using a Zeisls stereomicroscope eyepiece graticule (cephalic, thoracic, leg measurements) or calipers (body measurements). Morphological measurement definitions and their text abbreviations (capitalized in brackets) as follows: total length (TL) — from front of head (between antennae) to elytral apex; total width (TW) — at widest point of body (elytra);

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head width (HW) — to outer margins of eyes in frontal view; minimum interocular distance at vertex (MIDAV).

Drawings were made with the aid of a Zeiss stereomicroscope camera lucida.

The following collection codens are used in the text: ANIC — Australian National Insect Collection, Canberra; BMNH — British Museum of Natural History, London; MMUS — Macleay Museum, University of Sydney; MNHN — Museum National d'Histoire Naturelle, Paris; MVMA — Museum of Victoria, Melbourne; SAMA —South Australian Museum, Adelaide; WAMP — Western Australian Museum, Perth.

Type specimen label data: a slash mark (/) separates data from individual labels; curved brackets enclose my notations for handwritten (h) or printed (p) label data, where noted; square brackets enclose inferred label data.

Correct spelling/citation of *Temognatha/Themognatha* Solier?

Examination of Solier (1833) revealed that this author used two different spellings (*Temognatha*/*Themognatha*) in his original descriptions/diagnoses of this Australian genus. Interpretation of the current International Code of Zoological Nomenclature provides two different methods for establishing which spelling is correct.

If both spellings are considered to constitute valid generic descriptions and available names (under Article 12a; b: 5-7), because they are introduced on separate pages and are accompanied by definitions/illustrations purporting to diagnose them, then precedence is determined by the First Reviser Principle (Article 24). I consider that Gory & Laporte (1837: 11, in *Stigmodera* livraison), who were the first to use both spellings in a subsequent work, clearly selected/validated *Temognatha* over *Themognatha*. They use the spelling *Temognatha* (in large bold print) as the heading under "Seconde Division" (p. 11), and also use it in the "division" (= subgeneric) key (p. 4), while the spelling *Themognatha* (in small fine print) is listed only once in their work, as a synonym under the genus *Stigmodera* (p. 3).

Alternatively, if one of the two original spellings is considered a lapsus (and therefore an incorrect original spelling under Article 32c) then the correct spelling should be ascertained by establishing the original author's intent, if possible, through studying the wording of the original description, potential origins of both spellings and their frequency of appearance in the original work. Solier (1833) mentions *Temognatha* on three occasions (once on p. 263; twice on p. 281, once in combination with the species name *variabilis*), but mentions *Themognatha* only once (p. 291). The names *Temognatha*/*Themognatha* are based on classical Greek, with half of each name having the common suffix stem *gnatha* (Greek for jaw). Adoption of the correct spelling thus partially depends on which, or whether the, prefix makes descriptive sense when used in combination with *gnatha*. A translation of the relevant section of Solier's original description reads: "Mandibles medium-sized, *knife-edged* interiorly above; the one on the right slightly obtuse, the one on the left pointed; *internal edge forming a tooth towards the extremity, only above.*" This is compelling evidence that Solier's intended choice was the prefix *temo*-(= *temno*-) (Greek for carved, cut, to cut, divided), alluding to the cutting ("knife-edged") and/or divided (subapically toothed) mandibles. The prefix *themon* (Greek for heap) was most unlikely as Solier's choice, since he did not mention heaped (conical) mouthparts (also note Solier's descriptive differentiation between left and right mandibles) and he illustrated (plate XI, figure 18) the mandibles as curved/elongate "knife blades" with a distinct subapical notch, which certainly could not be considered "heaped".

While it is sometimes impossible to determine a deceased author's intent, on this occasion the alternative methods both support *Temognatha* Solier as the correct spelling for this genus. Correct spelling of *Temognatha* only recently became an issue, because all works (including popular) subsequent to Solier (1833) (except four minor papers: Murray, 1852, 1873; Gehin, 1855; Boheman, 1858) completely synonymized this genus under *Stigmodera* Eschscholtz or treated it as its subgenus, until Matthews (1985) and Gardner (1990) resurrected *Themognatha* (sic) to generic status. Four different spellings of *Temognatha* (as a genus, or *Stigmodera* subgenus) have been deliberately used, since Solier's description of this taxon: *Temognatha* Solier, 1833; *Themognatha* Solier, 1833; *Temnognatha* Agassiz, 1845; *Themnognatha* Obenberger, 1922. I believe retention of the more frequently used incorrect spelling (*Themognatha*), on the basis of supposed "stability", is not justified in view of all the above evidence.

Systematics

Temognatha (Calotemognatha) subgen. nov.

Figures 1,2,5.

Type Species

Stigmodera laevicollis Saunders, 1868: 466. (Figure 1)

Diagnosis

Small to moderately large size; scutellum small; dorsal surface of ovipositor dorsal valve with complex, strongly sclerotized and carinate, apically bifurcate, reinforcing structure which extends slightly beyond lateroapical corner of dorsal valve margin (Figure 2); MIDAV 31-47% of HW, slightly to strongly sexually dimorphic; elytral pattern (when present) composed of four dark transverse fasciae, including apical and excluding basal margin; epipleuron entire (non-serrate), without apically directed ventral spur at level of hind-coxae, and only moderately expanded anterior to this level; elytral apices rounded to sub-truncate.

Description

Body: TL 10-39 mm, variable within and between species; elongate-oval in dorsal view, subparallel in lateral view; with silver-white setae on anterior half of venter (anterior to sternite 4), longer and more dense in males than females; with a mostly matt pale-coloured undersurface.

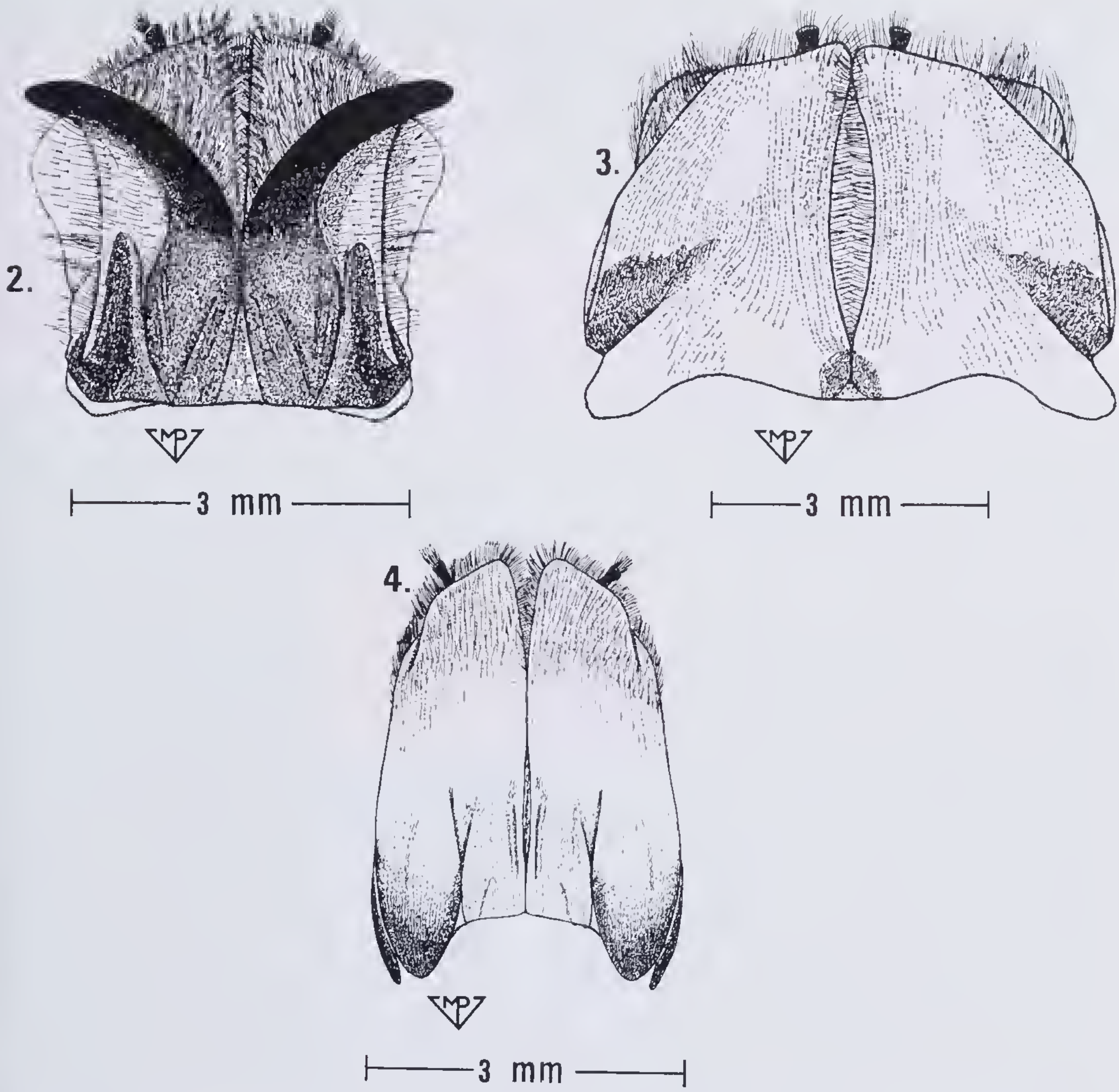
Head: frons with silver-white setae, longer and more dense in males than females; eyes large, with posterior margins touching pronotum and inner margins slightly to moderately converging dorsally; MIDAV 31-47% of HW, ♂ < ♀, interspecifically

Figure 1. Dorsal view of female *Temognatha (Calotemognatha) laevicollis* (Saunders).

slightly to strongly sexually dimorphic; frontoclypeus slightly to moderately prolonged; labrum subtriangular with curved outer margin, apically with weak median notch; prementum attached to postmentum dorsally; postmentum subhexagonal (length 65-85% of width), anterior margin sometimes with slight median emargination; antennal length equal to or slightly greater than head width; antennomeres 4 or 5-11 (inclusive) serrate (occasionally antennomere 4 subserrate).

Thorax: sides of pronotum non-explanate, with lateral margin complete and weakly carinate; pronotum with very slightly bisinuate basal margin; pronotum with matt pale-coloured lateral margins; sternal cavity formed by metasternum and divided mesosternum; meso-metasternal suture oblique and halfway along sternal cavity; scutellum very small, less than or equal to 0.1x width of elytron, shape scutiform.

Elytra: non setose; interneurs numbering ten, completely separate, punctate-striate; apices rounded to occasionally sub-truncate, non-denticulate; epipleuron non-serrate for entire length, dorsoventrally moderately expanded anterior to level of hind-coxae, and never with apically directed ventral spur at latter level; elytral length roughly equal to length of abdomen; elytral pattern (when present) composed of four dark transverse fasciae (including apical and excluding basal margin), anterior three sometimes reduced to transverse rows of spots, alternating with pale interspaces.



Figures 2-4. Dorsal view of ovipositor dorsal valves: 2 — *Temognatha (Calotemognatha) laevicollis* (Saunders); 3 — *T. (T.) variabilis* (Donovan); 4 — *T. (T.) bonvouloirii* (Saunders).

Metathoracic wing (terminology based on Good, 1925): as for Stigmoderini; membranous, with apex of all posteriorly directed veins nearly reaching hind margin; radial cell closed, moderately large and elongate, with radial sector forming short recurrent spur; radiomedial crossvein complete and contacting radial cell slightly distad of first radial crossvein; medial recurrent vein same length as fused medial-cubital, reaching back to level of first radial crossvein; cubitus strongly developed; cubito-anal crossvein complete, with well developed recurrent 1stA spur; first anal vein same length as $2dA_1$, slightly curved in basal 1/4, not basally connected to other veins (especially $2dA_1$); $2dA_1$ basally connected to $2dA_2$ slightly distad of cubito-anal crossvein; "wedge cell" (2d-2dA) open; $2dA_3$ sub-basally connected to $2dA_2$, via crossvein contacting latter slightly distad of $2dA_1$-$2dA_2$ junction; $2dA_3$ same length as 2dA; $3dA_2$ connected to $3dA_1$, via crossvein contacting latter 1/3 distance from $2dA_3$-$3dA_1$ junction to apex; fourth anal vein present, well developed.

Abdomen: sternite 7 sexually dimorphic, in male with moderately arcuate apical emargination, in female apically rounded and more elongate; female proctiger (length 1.5x width) comprised of completely fused epiproct and paraprocts, without discernible suture between both; male proctiger comprised of incompletely fused epiproct and paraprocts, with suture visible between both.

Legs: tarsomeres 1 to 4 with large well developed pulvilli; basal hind-tarsomere length 1-1.5x that of following hind-tarsomere; tarsal claw with pronounced to absent basal lobe (morphology subgenerically variable, intraspecifically constant).

Female reproductive system: ovipositor with three testaceous membranous/semi-sclerotized valves, vulva opening ventral; dorsal valve deeply divided medially/longitudinally; two black-brown bilaterally symmetrical heavily sclerotized cornute structures attached to, and part of, dorsal surface of dorsal valve (Figure 2), with each resembling (in two dimensional dorsal view) a bovine horn, with the red-brown "boss" located at base of dorsal valve immediately adjacent to the median longitudinal division; "horns" arcuately curved away from each other apically (bifurcate), extending beyond dorsal valve apex for short distance at latero-apical corner; each "horn" (beyond the "boss") forming a strongly carinate ridge above dorsal surface that is vertically concave to the lateral margins of the ovipositor, and vertically rounded (almost spatulate) at apex; dorsal surface of dorsal valve, apicomedial to bifurcate "horns", densely covered in long semi-erect apically-directed hairlike setae; dorsal surface of dorsal valve, basolateral to "horns", sparsely covered in short erect hairlike setae; lateral margin of dorsal surface of dorsal valve with long erect laterally-directed hairlike setae; ventral surface of dorsal valve, apicomedial to "horns", with moderately long sparse semi-erect hairlike setae; style bearing valve without setae on dorsal or ventral surfaces, except at apical margin; recumbent apically-directed spatulate setae, on dorsal surface of style bearing valve, cover width of valve to slightly laterad of apex of dorsal valve "horns"; ventral surface of style bearing valve with moderately long sparse erect hairlike setae; dorsal surface of ventral valve without setae; ventral surface of ventral valve basally and medially with red-brown sclerotization, and covered in long sparse semi-erect hairlike setae (less densely than apicomedial area of dorsal valve); ovipositor setae testaceous.

Male reproductive system: aedeagal width 36-41% of length (from basal apophysis apex to paramere apex); basal apophysis 20-25% of aedeagal length; paramere apex dorsally and ventrally with erect hairlike setae; paramere blades (in dorsal view) acutely produced at apex with inner margins roundly angled to junction of both blades, junction occurring at 69-75% of aedeagal length from base (apex of basal apophysis); outer margin of penis curved to penile apex, which is slightly more produced to form a small 'nipple'; penis width 36-43% of length; penis ventrally without membranous flap covering ostium, ostium at 80-83% of penis length from base.

Included Species

T. (Calotemognatha) yarelli (Gory & Laporte, 1837); *T. (C.) laevicollis* (Saunders, 1868); *T. (C.) varicollis* (Carter, 1913).

Distribution

The southern Australian mallee zone and adjacent forest/coastal habitats in the west. Currently known from the Carnarvon/Shark Bay region of midwest Western Australia across to the Euabalong/ Lake Cargelligo district of central New South Wales (Figure 5).

Etymology

Derived from *calos,* Greek for beautiful, and *Temognatha* Solier, 1833 (the 'parent' genus); gender to be treated as feminine.

Remarks

The single autapomorphy of a sclerotized, strongly carinate, apically bifurcate and cornute reinforcing structure on the ovipositor dorsal valve (Figure 2) easily distinguishes *Temognatha (Calotemognatha)* from the other 10 genera/subgenera in the tribe Stigmoderini, and supports its monophyly. The ovipositor dorsal valves of these other stigmoderine genera/subgenera, and the remaining *Temognatha* species, are morphologically similar to that of *Temognatha variabilis* (Donovan, 1805) (Figure 3), type species of the nominotypical subgenus of *Temognatha.* Despite *Calotemognatha* diverging from the rest of the tribe in ovipositor dorsal valve structure, the greater similarities to *Temognatha* (in other aspects of ovipositor, internal and external morphology) indicate *Calotemognatha* is best treated as its subgenus. An intermediate condition between the ovipositor dorsal valve structure of *Calotemognatha* and nominotypical *Temognatha* is unknown.

Gardner (1990) indicated that 12 tubules per testis was probably the primitive condition, in the Stigmoderini, for this character. *Temognatha (Calotemognatha) yarelli* (G. & L.) was the only one of the 23 nominal taxa, that she listed under *Temognatha* (as *Themognatha*) and examined for this character, to exhibit this condition. All other listed species had the derived condition of much higher numbers of tubules per testis, and are members of the nominotypical subgenus of *Temognatha.* I consider this possible evidence that *T. (Calotemognatha)* diverged at an early stage from the *Temognatha* lineage.

Thery (1937) described *Stigmoderoides* as a subgenus of *Stigmodera* Eschscholtz, for the reception of six species, and this constitutes the only previous attempt to formally subdivide the traditional concept of *Temognatha.* Gardner (1990) synonymized *Stigmoderoides* under *Temognatha,* when she re-elevated the latter to generic level. However, Bellamy (1985, 1986) and Gardner (1990) obviously did not realize that

Stigmoderoides Thery, 1937 is unavailable for the purposes of nomenclature because it does not conform to Article 13b (see Art. 67h, 68b-e) of the current International Code of Zoological Nomenclature. Comparison of ovipositor dorsal valves of the two valid subgenera with those of a "*Stigmoderoides*" species (*Stigmodera bonvouloirii* Saunders, 1868) (see Figures 2-4) indicate this name would have been a direct synonym of the nominotypical subgenus of *Temognatha* Solier, had it been available. The taxon "*Stigmoderoides*" is currently referred to as the informal *Temognatha reichei* (G. & L.) species-group.

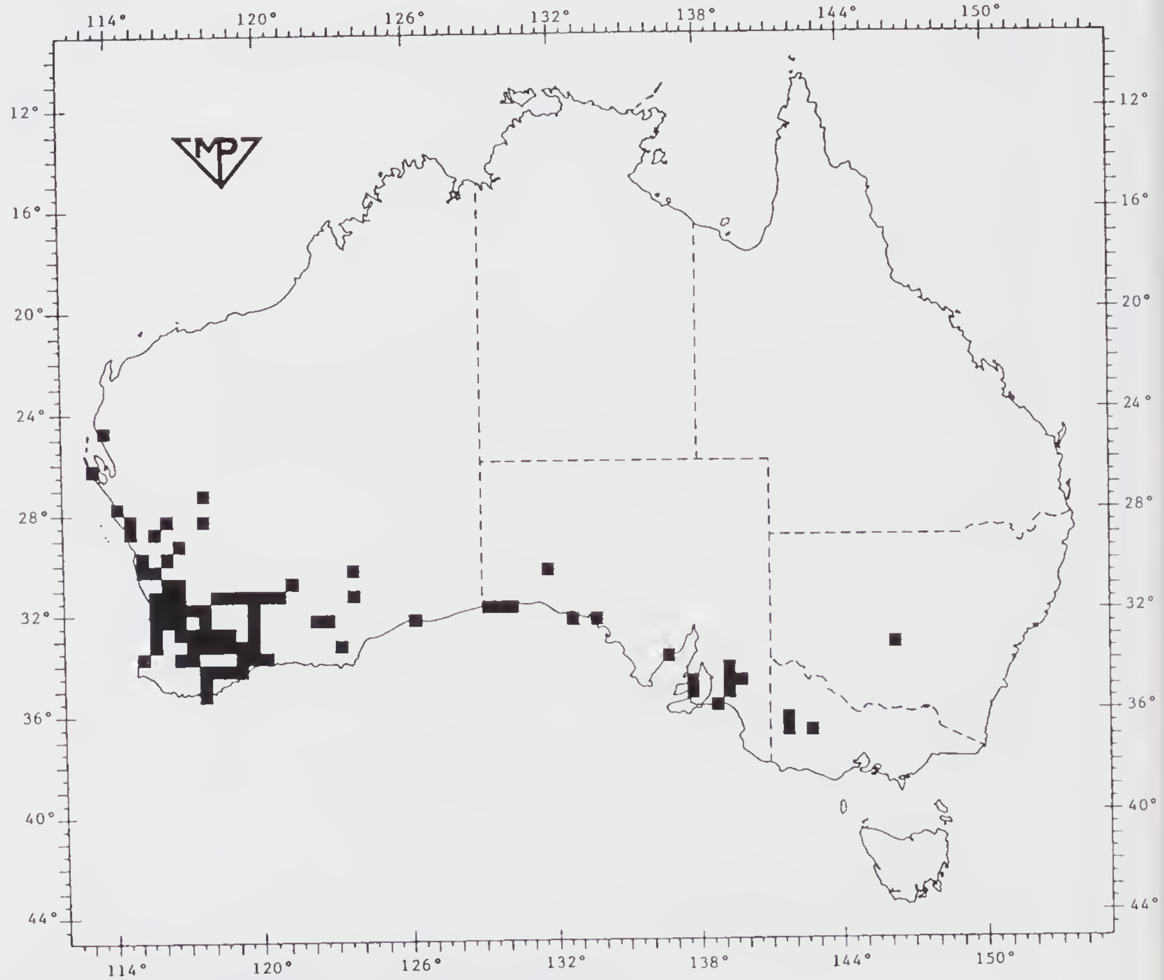


Figure 5. Temognatha (Calotemognatha) distribution.

Type Specimens Examined

***Temognatha (Calotemognatha) laevicollis* (Saunders):** Lectotype of *Stigmodera laevicollis* Saunders, 1868 (here designated): female; label data: laevicollis (Type) Saund.[ers]/ HT/ Saunders 74.18/ Type; lectotype measurements: TL — 33.6 mm, TW — 12.5 mm (in BMNH).

Temognatha (Calotemognatha) varicollis **(Carter):** Lectotype of *Stigmodera varicollis* Carter, 1913 (here designated): male; label data: Wanneroo (W.[estern]A[ustralia]) (h)/ S.[tigmodera] yarelli L&G var. varicollis C[ar]t[e]r, W.[estern] Australia, Cotype (h); lectotype measurements: TL — 16.7 mm, TW — 6.0 mm (in SAMA).

Temognatha (Temognatha) bonvouloirii **(Saunders):** Lectotype of *Stigmodera bonvouloirii* Saunders, 1868 (here designated): female; label data: bonvouloiri (type) Saund.[ers]/ HT/ Saunders 74.18/ Type; lectotype measurements: TL — 34.0 mm, TW — 12.9 mm (in BMNH).

Temognatha (Calotemognatha) yarelli **(Gory & Laporte):** Syntype/s not located. Gory & Laporte (1837:14-15), in *Stigmodera (Temognatha) yarelli* description, provided a type locality ("Swan River, Nouv.-Holl."), listed specimen measurements ("Long. 12 lig. Larg. 4 lig. ½." = TL: 27.0 mm; TW: 10.1 mm), illustrated a specimen of the species in colour (Plate 3, figure 11), noted their description was based on specimen/s in their own collection ("Du cabinet des auteurs"), but did not designate types; their measurements and description/illustration respectively suggest a single specimen was used for description, and that it was female; Horn & Kahle (1935:38-39,93) indicate Gory's buprestid collection and Laporte's buprestids from his second collection (which had suffered greatly) were eventually procured by Rene Oberthur (Oberthur's collection now housed in MNHN), and that Laporte's first collection (private) went to MVMA; primary type possibly among numerous unlabelled specimens (?syntypes), in MNHN, identified by Dr R.P. Dechambre as pinned with Gory & Laporte pins. I prefer not to designate a neotype, until it is certain syntype/s are lost/destroyed, since Gory & Laporte's excellent description/colour illustration is sufficent to diagnose the taxon and ascertain its nomenclature.

Temognatha (Temognatha) variabilis **(Donovan):** Syntypes not located. Donovan (1805:21), in *Buprestis variabilis* description, provided a generalized type locality ("New South Wales"), illustrated three specimens of the species in colour (plate 7, *), briefly described these, but did not list specimen measurements or designate types; Donovan's illustrations/description indicate a minimum of three syntypes were used and that two of these (with fewer dark spots on elytra) were males; Horn & Kahle (1935:60) indicate Donovan's collection of insects of the world went to J.C. Stevens (London), in 1818, and was subsequently auctioned; Anderson (1965:48) notes a large section of Donovan's collection was purchased by Sir Alexander Macleay before the latter left England for Australia in 1825 (Macleay's collection now housed in MMUS); Anderson (1965:50) also notes part of MMUS collection was destroyed or lost during the decade after the First World War; Britton & Stanbury (1981) did not locate/identify in MMUS, or transfer to ANIC on permanent loan, types of Australian buprestid species described by Donovan (1805); MMUS possesses eight poorly labelled (locality only, without attached type status indication) *variabilis* specimens (which may include missing syntypes, if still extant) with locality labels that generally agree with the description, but it is not certain if Macleay procured and brought all of Donovan's types to Australia or, if Macleay did bring them here, that they were not later destroyed after the First World War. I prefer not to designate a neotype, until it is certain all syntypes are lost/destroyed, since Donovan's excellent colour illustrations/ meagre description are sufficient to diagnose the taxon and ascertain its nomenclature.

Acknowledgements

I would like to thank Ms B.M. Coulson (Perth) and Mr G.M. Shea (Sydney) for assistance with numerous aspects of the preparation of this manuscript; the following for loans of and access to specimens in their care: Mr P. Hammond and Mr M. Kerley (BMNH), Dr D.S. Horning (MMUS), Dr R.P. Dechambre (MNHN), Dr E.G. Matthews (SAMA); Dr T.F. Houston and Mr B. Hanich (WAMP) for handling of loans and use of equipment.

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A new *Temognatha* species (Coleoptera: Buprestidae: Buprestinae) from north-eastern Australia.

Magnus Peterson*

Abstract

Temognatha (Temognatha) aquilonia sp. nov., from north-east Queensland, is described and figured. It is placed with *T. gigas* (Carter, 1916) and *T. parvicollis* (Saunders, 1869) (including the subspecies *T. parvicollis andromeda* (Peterson, 1988) stat. nov.), in the *T. parvicollis* species-group. These species are diagnosed and keyed and the coloration of *T. gigas* is redescribed, based on live and freshly dead material. Lectotypes are designated for *Stigmodera parvicollis* Saunders, *Stigmodera picea* Kerremans, 1890, *Stigmodera andromeda* Peterson/*Stigmodera princeps* Blackburn, 1891. The zoogeographic significance of *T. aquilonia* is discussed.

Introduction

Temognatha Solier, 1833 is a speciose genus of conspicuous, often spectacular, moderately small to very large Buprestidae/Coleoptera. Only three new, small to medium sized, *Temognatha* species have been described since Obenberger's (1934) catalogue, suggesting that the alpha taxonomy of this genus, especially of its larger members, is almost complete. Most of the larger described taxa have their distributions centred over southern Australia, and it was therefore surprising to find two specimens of a very large apparently undescribed *Temognatha* taxon, from north-east Queensland, in the Queensland Museum, Brisbane. Both specimens are female and only one specimen bears locality data. Comparison with descriptions and identified type material of all described *Temognatha* confirms that this taxon is undescribed and, despite the small series, sufficiently distinct to warrant description as a new species. Ovipositor morphology places this taxon in the nominotypical *Temognatha* subgenus. This species is especially interesting because of its direct taxonomic links to south-west Western Australia. This is the third in a series of papers describing new *Temognatha* taxa. The format is modified from that of Peterson (1982).

Methods and Terminology

Specimen measurements linear, measured to the nearest 0.05 mm using a Zeiss stereomicroscope eyepiece graticule (cephalic, thoracic, leg measurements) or calipers (body measurements). Morphological measurement definitions and their text abbreviations (capitalized in brackets) as follows: total length (TL) — from front of head (between antennae) to elytral apex; total width (TW) — at widest point of body (elytra); head width (HW) — to outer margins of eyes in frontal view; minimum interocular

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distance at vertex (MIDAV); eye length (EL); antennal length (AL) — from basal condyle of basal antennomere to apex; pronotal width (PW) — at widest point.

Drawings were made with the aid of a Zeiss stereomicroscope camera lucida.

The following collection codens are used in the text: BMNH — British Museum of Natural History, London; MMUS — Macleay Museum, University of Sydney; QMBA — Queensland Museum, Brisbane; SAMA — South Australian Museum, Adelaide; WAMP — Western Australian Museum, Perth.

Type specimen label data: a slash mark (/) separates data from individual labels; curved brackets enclose my notations for handwritten (h) or printed (p) label data, where noted; square brackets enclose inferred label data.

Systematics

Temognatha (Temognatha) aquilonia sp. nov.

Figures 1-10.

Holotype

In QMBA (T9129), female: Mt. Molloy, F. Little, May 1970 (h).

Paratype

In QMBA (T9130), female: *Stigmodera parvicollis* Saund. ♀, DuB[oulay] det. (h). ('No locality or collection data provided').

Condition of Types

T. aquilonia holotype complete and in good condition; paratype discolored (darker than holotype) from preservation and (in dorsal view) is missing all tarsomeres on right fore-leg, two tarsomeres on left fore-leg, one tarsal claw on right hind-leg, all tarsomeres and tibia on left hind-leg, seven distal antennomeres on left antenna.

Diagnosis

Size: 46.5 — 48.8 mm (TL) x 19.6 — 19.7 mm (TW), (n=2); frons, pronotum and elytra orange-brown, underside and legs red-brown; postmentum subhexagonal; pronotal base same width as elytral base; elytra striate, epipleuron without apically directed ventral spur at level of hind-coxae, elytral apex bidentate/tridentate-truncate and angled anteromedially; basal hind-tarsomere same length as following hind-tarsomere, tarsal claw not strongly curved or basally lobed. The only character unique to *T. aquilonia,* within *Temognatha,* is the non-metallic orange-brown frons.

Holotype Description

Size: TL: 46.5 mm; TW: 19.6 mm.

Shape/Sculpture: *Body* elongate-oval (Figure 1), TW 42.2% of TL. *Head* (Figure 2) finely and densely punctate, with a strong longitudinal median sulcus on dorsal half of frons; HW 17.0% of TL, HW 48.6% of PW; eyes large, not projecting beyond outline of head, EL 73.1% of HW; inner margins of eyes slightly concave, not strongly converging dorsally, MIDAV 45.6% of HW; distal margin of frontoclypeus shallowly arcuately emarginate between antennal sockets; labrum weakly bilobed, with longitudinal median

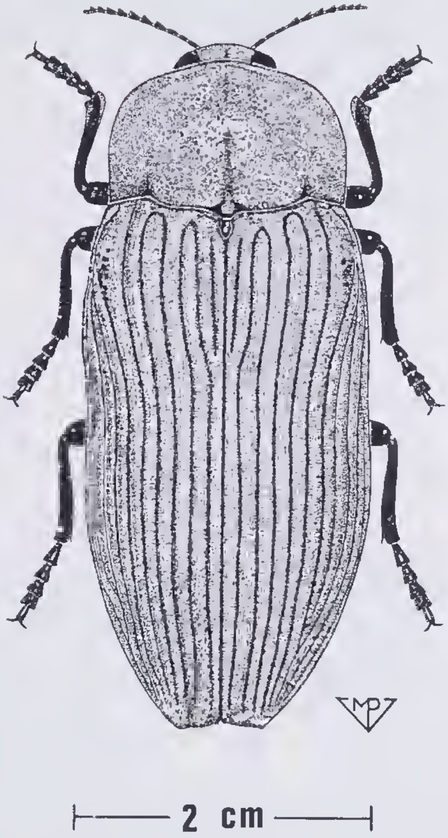
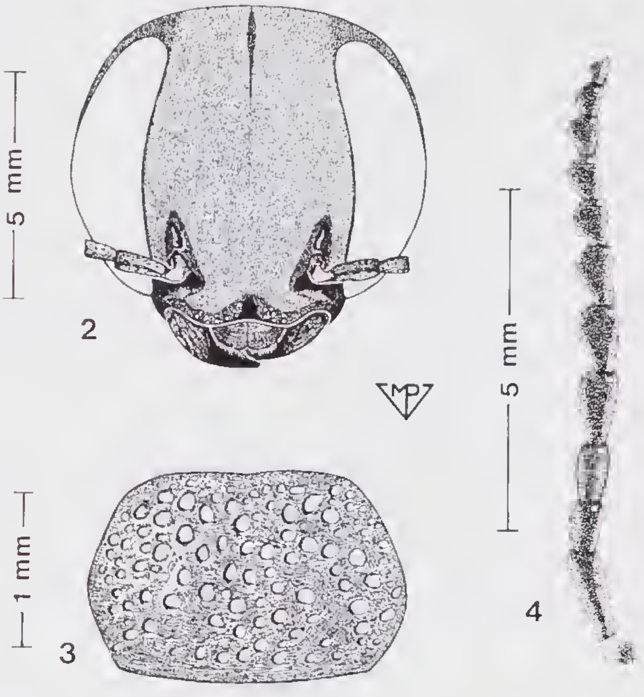
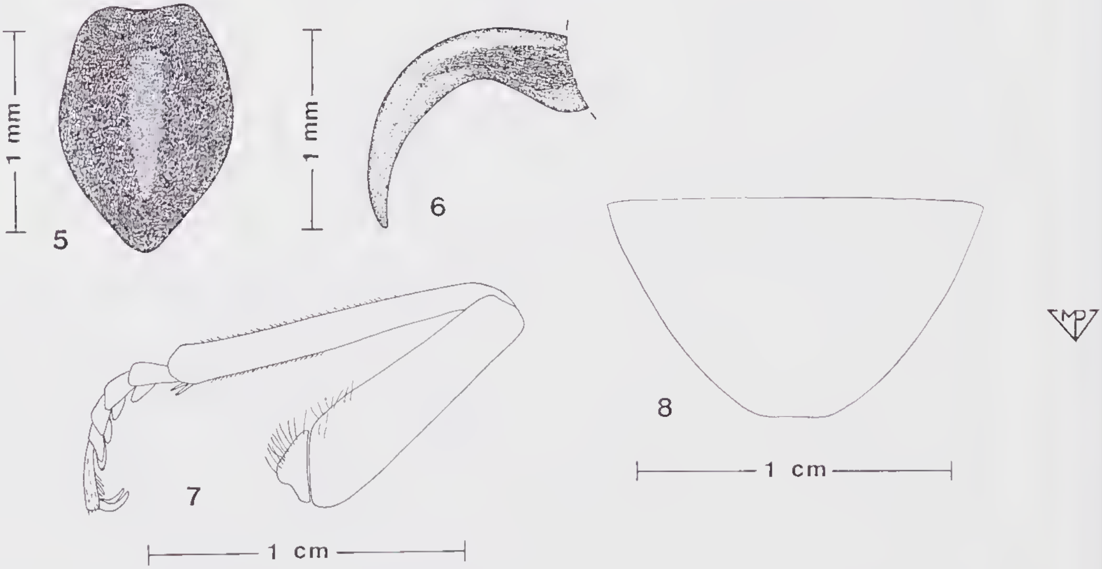


Figure 1. Dorsal view of female *Temognatha aquilonia.*

sulcus, setose distally; postmentum (Figure 3) subhexagonal (with rounded lateral and anterior corners), 1.49x wider than long and widest at middle, very slightly indented anteromedially, punctate-foveolate with long semi-erect setae (one per foveole); narrow supra-antennal pits ventromedially oblique, length equal to antennal socket diameter; antennae (Figure 4) serrate from segment 4; AL 19.0% of TL; antennomere lengths (1-11), expressed as percentage of AL: 20.3, 7.9, 9.1, 11.3, 10.7, 9.6, 7.9, 7.4, 6.2, 5.1, 4.5. *Pronotum* 1.5x wider than long, widest at middle; disc moderately convex, subrectangular from above, narrowly explanate in anterior half when viewed dorsally, and lateral margins sinuate in lateral view (angled higher basally), surface with moderately fine, deep and dense (though irregularly spaced) punctures and a smooth longitudinal median line for length of pronotum (more pronounced in basal half); anterior margin mostly forming straight line but slightly produced in median third, and narrowly explanate for entire width; lateral margins (from above) with basal third forming straight line, angled very slightly anterolaterad, middle third straight, angled slightly mediad, and anterior third weakly convex; basal margin moderately bisinuate, strongly excised on both sides of wide median lobe. *Scutellum* small, nitid, impunctate with shape as in Figure 5. *Elytra* widening laterally from base, narrowing at junction of



Figures 2-4. *Temognatha aquilonia* (holotype) head and associated structures (setae omitted). 2 — head, frontal view; 3 — postmentum; 4 — antenna.



Figures 5-8. *Temognatha aquilonia* (holotype) body and leg structures: 5 — scutellum; 6 — tarsal claw; 7 — hind-leg; 8 — fifth visible sternite.

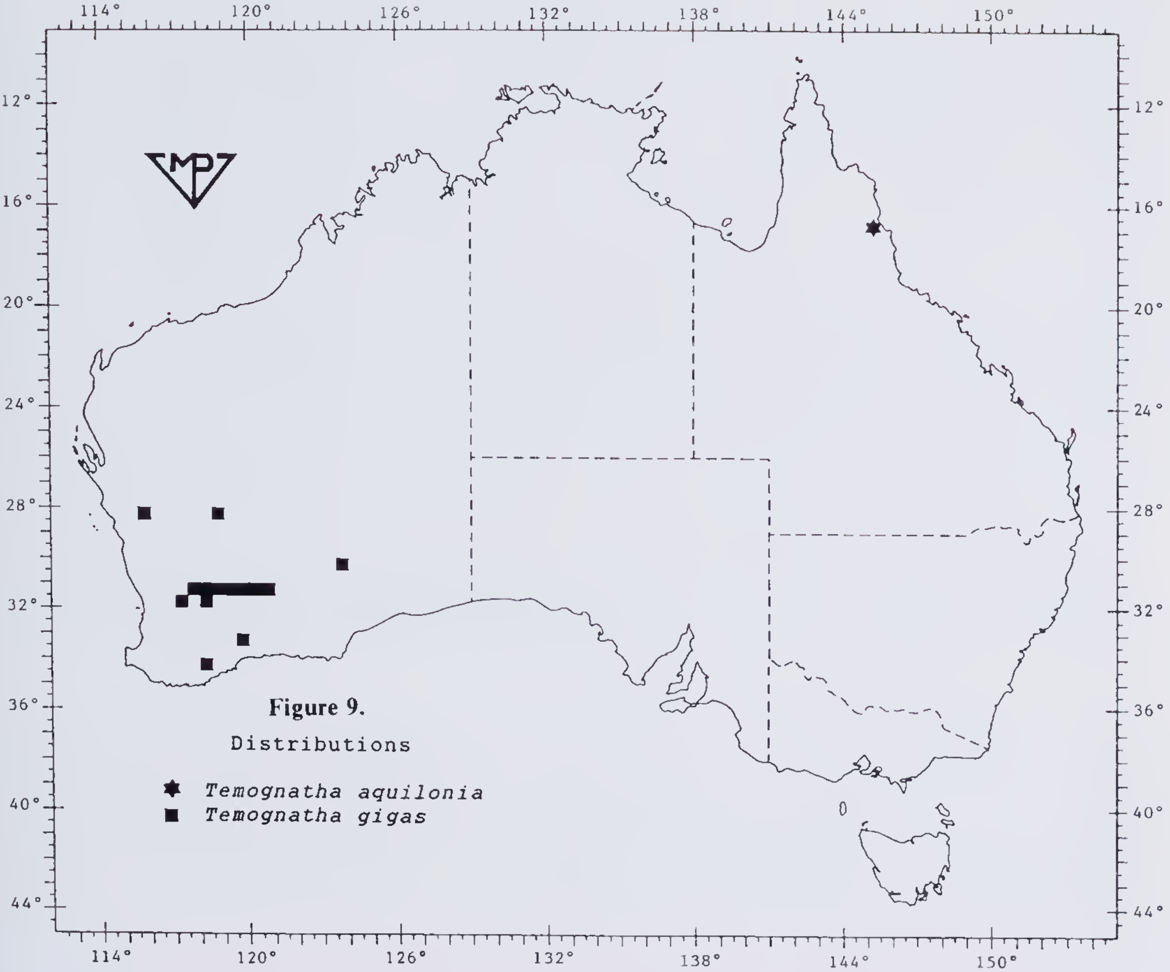
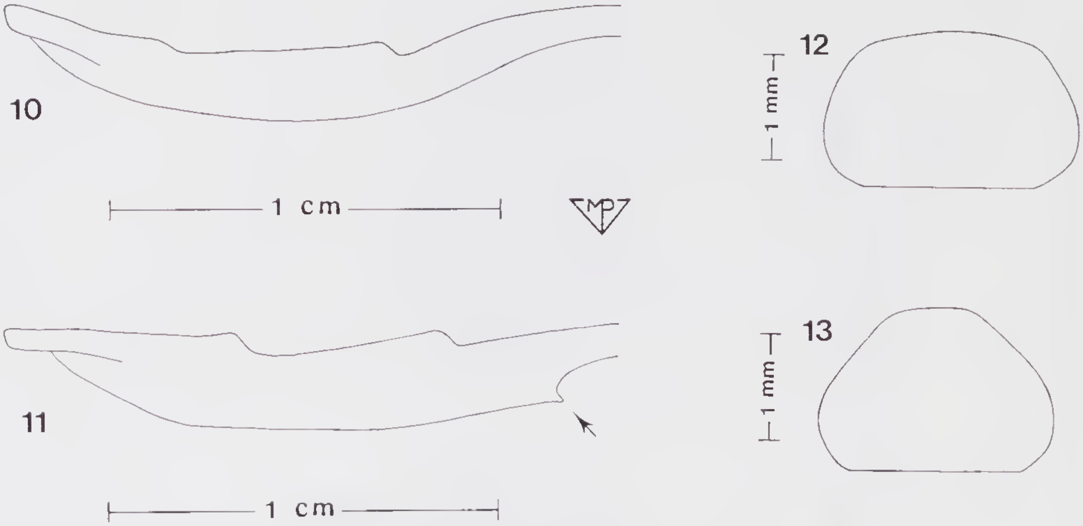


Figure 9.
Distributions

anterior and middle thirds, slightly expanding in middle third, angled caudomedially to apex in apical third; elytral disc striate, intervals strongly convex basally, medially and laterally, less convex near elytral apices; all intervals finely and sparsely punctate for entire length particularly immediately adjacent to striae; a small area with several deep punctures at expanded base of sixth interval near junction of sixth and seventh intervals; elytral base same width as pronotal base; basal margin slightly undulating transversely; epipleuron entire, moderately expanded and strongly inflexed between level of elytral basal margin and hind-coxae, without apically directed ventral spur at level of hind-coxae (see Figures 10, 11); elytral apices bidentate, truncate, slightly angled anteromedially from level of stria four. *Undersurface* moderately finely but sparsely punctate on prosternum, more densely punctate at lateral and anterior margins of prosternum; anterior margin of prosternum very shallowly emarginate for middle third; hypomera moderately finely, deeply and densely (though irregularly) punctate; metasternum finely and closely punctate except for median area between meso-coxae which is finely but sparsely punctate; visible sternites finely, moderately densely and



Figures 10-13. Outline diagrams of elytral and head structures of *Temognatha parvicollis* group species: 10 — *T. aquilonia* epipleuron; 11 — *T. gigas* epipleuron (arrow indicates apically directed ventral spur); 12 — *T. gigas* postmentum; 13 — *T. parvicollis* postmentum.

evenly punctate; fifth visible sternite (sternite 7) moderately elongate, sides tapering to moderately narrow sub-truncate apex (Figure 8). *Legs* with a few fine, moderately short hairs at proximal extremity of femora; hind-coxae finely and sparsely punctate for medial third becoming gradually more deeply and densely punctate over lateral two thirds, caudal margin slightly sinuate; fore-femora not swollen; fore-tibial brush 46% of fore-tibial length; basal hind-tarsomere not elongate, same length as following hind-tarsomere (Figure 7); pulvilli present on basal four tarsomeres, trapezoidal, slightly bilobed and widest apically, covering distal half of basal hind-tarsomere; tarsal claws simple, moderately curved, basally very slightly expanded but not lobed (Figure 6). *Ovipositor* moderately broad; dorsal surface of dorsal valve longitudinally striated and without sclerotized, apically bifurcate, cornute structures.

Colour/Pattern: *Head* with immaculate, uniform orange-brown frons margined with translucent red along inner margins of eyes; median impressed line on vertex dorsally bronze-black, gradually becoming red-brown ventrally; both sides of vertex, above eyes, red-brown; labrum bronze-black with median apical area red-brown; mandibles bronze-black with red-brown area between cusp and pitted region; postmentum uniformly bronze-black; antennal sockets, supra-antennal pits and distal clypeal margin bronze-black; antennomeres bronze-black except for orange-brown basal elbow and ventral surface (nearly to apex) of antennomere 1. *Pronotum* orange-brown with narrow medial red-brown anterior margin and dark anterior sub-marginal line; basal margin narrowly bronze-black with a median translucent reddish triangular marking (apex directed anteriorly). *Scutellum* black with translucent dark red centre. *Elytra* entirely orange-brown except for narrowly translucent reddish basal margin and median suture.

Undersurface dark red-brown with narrow slightly darker margins to all segments except hypomera, which are orange-brown with narrow translucent reddish inner margins adjacent to prosternum. *Legs* dark red-brown to reddish, basal half of tarsal claw tarsomere bronze-black; coxae dark red-brown with darker margins, fore-coxae slightly brighter (red-orange); tarsal claws translucent reddish to red-brown, base and margins of culmen darker. *Sternal hairs* silvery white.

Paratype Variation

TW 40.4% of TL; HW 16.3% of TL, HW 48.9% of PW; MIDAV 43.4% of HW; postmentum 1.53x wider than long; AL 19.5% of TL; pronotum widest at base, 1.45x wider than long; elytral apices with tridentate truncature; postmentum red-brown with bronze-black basal margin; all antennomeres orange-brown with slightly darker apices.

Distribution

At present, known only from Mt. Molloy, Queensland (16°41′S, 145°20′E) (Figure 9).

Etymology

The specific epithet derives from *aquilonius,* Latin for northerly, and alludes to the northern distribution of this taxon compared to that of its closest relatives (see ‘relationships’).

Discussion

Relationships

Within the nominotypical *Temognatha* subgenus, I consider *T. aquilonia* most closely allied to *T. gigas* (Carter, 1916) and *T. parvicollis* (Saunders, 1869). These three species form the informal *T. parvicollis* species-group, which is diagnosed by the following combination of characters: large size and robust build; MIDAV >31% of HW; pronotum moderately deeply punctate, without vermiculations and long dense setae; pronotal base same width as elytral base; elytra striate; female tergite 9 broad and caudally convex; undersurface almost nitid, without long dense setae; basal hind-tarsomere same length as following hind-tarsomere; tarsal claws not strongly curved or basally lobed; lateral margins of pronotum (dorsally or ventrally) without narrow paler markings over entire length; elytral color pattern constant, non-fasciated; undersurface coloration red-brown or bronze-black (never metallic bronze). The *T. parvicollis* group species key out as follows:

1. Epipleuron without apically directed ventral spur at level of hind-coxae (Figure 10); frons orange-brown .... *aquilonia*
   Epipleuron with apically directed ventral spur at level of hind-coxae (Figure 11); frons bronze-black with or without pale spots 2
2. Postmentum subhexagonal (Figure 12); elytral apices truncate; frons with pale spots; pronotum bicolored .... *gigas*
   Postmentum subtriangular (Figure 13); elytral apices rounded; frons without pale spots; pronotum unicolored .... *parvicollis*

Within the *T. parvicollis* species-group, I consider *T. aquilonia* more closely related to *T. gigas* (Carter). These two taxa share the following characters: subhexagonal postmentum (Figures 3, 12); a wide subrectangular pronotum; truncate elytral apices (though not as extreme in *T. gigas*); pale matt colored markings on frons. Apart from the key characters, *T. gigas* differs from *T. aquilonia* by possessing a proportionately narrower frons (MIDAV <40% of HW, in females), proportionately narrower head (HW <43% of PW, in females), proportionately shorter antennae (AL <18% of TL, in females (n=10)), black frons with two or three pale yellow spots, black and pale yellow mottled pronotum, dark red-brown elytra with pale yellow to white apicolateral margins, bronze-black venter. Carter's (1916) description of coloration in *T. gigas* was based on discolored dead material, which differs quite markedly from the coloration of live material as described above.

Temognatha parvicollis is more distantly allied to the other members of the *T. parvicollis* species-group, differing from them by possessing a more slender form, subtriangular postmentum, rounded elytral apices, uniformly dark (bronze-black) frons. *Temognatha parvicollis* is divisible into two subspecies: the nominate subspecies, occurring from south-east Western Australia eastwards to central New South Wales and characterized by orange-brown elytra; a western subspecies, restricted to south-west Western Australia and characterized by black elytra with a red or orange narrow apicolateral margin. The available name for the latter race is *T. parvicollis andromeda* (Peterson, 1988) stat. nov.. *Temognatha aquilonia* is most similar in dorsal coloration to the more proximate, nominate *T. parvicollis* subspecies.

Zoogeography

The direct taxonomic connection between the geographically isolated extant faunas of south-west Western Australia and north-east Queensland (Figure 9) has been rarely documented. I am aware of two comparable taxonomic (species-pairs) alliances between the more mesically adapted components of the two respective regional faunas (e.g. (Odonata: Corduliidae): *Lathrocordulia metallica* Tillyard and an undescribed *Lathrocordulia* species (Theischinger, *in litt.*); (Coleoptera: Buprestidae): *Cyria vittigera* (Laporte & Gory) and *C. cincta* Carter). The species-pair relationship of *T. aquilonia* and *T. gigas* is of interest because it stems from the more xeric faunal components, adds further support to the tenuous zoogeographic links between the two faunal regions and suggests the two taxa are relics of an earlier epoch. Interestingly, the four mesic taxa are also relictual, to a similar extent, and the three species-pairs appear to share Gondwanan (South American) connections at generic level. The only other examples, known to me, of possible parallel taxonomic alliances amongst the more xeric faunas of the two regions are those of *Delma fraseri* Gray and *D. mitella* Shea (Lacertilia: Pygopodidae), and *Acantholophus hystrix* (Bohemann) and *A. krefftii* Macleay/*A. doddi* Ferguson (Coleoptera: Curculionidae). However, the closeness of their relationships is uncertain and there are no apparent Gondwanan allies of these, at or below family or subfamily level, respectively. Nevertheless, it is possible that the two latter examples may help to establish the timing of the speciation of *T. aquilonia* and *T. gigas*.

Type Specimens Examined

***Temognatha (Temognatha) aquilonia* sp. nov.:** Holotype: female (QMBA T9129). Paratype: female (QMBA T9130).

***Temognatha (Temognatha) gigas* (Carter):** Holotype of *Stigmodera gigas* Carter, 1916: male; label data: Southern Cross W.[estern] A.[ustralia], Victor (h)/ W.[estern] Austral[ia] (p)/ Type ♀ (p)/ Stigmodera gigas Carter (h), Id by H.J. Carter (p)/ Stigmodera gigas Carter (h); holotype measurements: TL — 44.1 mm, TW — 19.1 mm; holotype has large median triangular hole near apex of sternite 7 (in MMUS).

***Temognatha (Temognatha) parvicollis parvicollis* (Saunders):** Lectotype of *Stigmodera parvicollis* Saunders, 1869 (here designated): male; label data: parvicollis E.[dward] S.[aunders]/ HT/ Saunders 74.18/ type/ Adel.[aide]; lectotype measurements: TL —33.0 mm, TW — 13.3 mm (in BMNH). Lectotype of *Stigmodera picea* Kerremans, 1890 (here designated): female; label data: Picea Kerrem.[ans] Type/ Kerremans 1903-59/ HT/ Australie Deyrolle; lectotype measurements: TL — 46.2 mm, TW — 18.3 mm (in BMNH).

***Temognatha (Temognatha) parvicollis andromeda* (Peterson):** Lectotype of *Stigmodera andromeda* Peterson, 1988/*Stigmodera princeps* Blackburn, 1891 (here designated): female; label data: W.[estern] Australia, Tammin Scrub, J.C.F. Johnson, 26.3.[18]91 (h); lectotype measurements: TL — 49.5 mm, TW — 17.8 mm (in SAMA).

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Four new members of the *Lerista nichollsi* complex (Lacertilia: Scincidae)

G.M. Storr*

Abstract

Lerista kendricki sp. nov. and *L. yuna* sp. nov. are separated from '*L. nichollsi petersoni*' (*L. petersoni* and *L. nichollsi* are now regarded as full species). *L. talpina* sp. nov. is based on a unique patternless specimen, and *L. maculosa* sp. nov. is based on two spotted specimens. The four new species are confined to the vicinity of the upper west coast of Western Australia. An *L. nichollsi* subgroup is diagnosed, and *L. petersoni* is redescribed.

Introduction

The *Lerista nichollsi* complex is endemic to the Carnarvon Basin and adjacent Precambrian Shield of Western Australia. When I revised the complex in 1984 my small samples of the isolated southern populations seemed too similar to the northern nominate population of '*L. nichollsi petersoni*' to warrant their formal separation. Recently G. Harold urged me to re-open the question; he believed that the southern skinks differed from the northern considerably in colour and pattern. I was able to confirm this and find additional differences after examining the large series recently collected by P.G. Kendrick in the Hamelin area. Moreover, the southern populations were found to consist of two distinct taxa: one from near the coast between Shark Bay and Kalbarri, and one from further inland (Yuna district).

The question then arose, were these taxa subspecies of *L. nichollsi?* I therefore re-examined *L. nichollsi* and its closest relatives *L. gascoynensis* and *L. petersoni,* which replace each other from south-east to north-west in the arid interior. For the reasons given below these three taxa are now treated as species rather than subspecies. Hence the new taxa are described as full species, including the unpatterned specimen from Bullara (Storr 1984: 113) and a new taxon from the Hamelin area.

This study is based on specimens in the Western Australian Museum (R prefix omitted from register numbers) and colour slides kindly loaned by G. Harold, M. Peterson, P. Griffin and R.E. Johnstone.

Systematics

The *Lerista nichollsi* subgroup

Composition

L. nichollsi (Loveridge, 1933); *L. petersoni* Storr, 1976; *L. gascoynensis* Storr, 1986.

Diagnosis

Medium-sized members of the *L. nichollsi* complex (up to 131 mm long) with

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* C/o Western Australian Museum, Francis Street, Perth WA 6000.

Figure 1 Map of mid-western Western Australia showing location of specimens of *Lerista nichollsi* subgroup.

moderately long tail (80-109% of SVL), immovable eyelids, second loreal much smaller than first and occasionally fused to prefrontal, presuboculars very small, second occasionally fused to first or to a labial, colour pattern strongly developed and including a wide pale or narrow dark vertebral stripe and a wide dark upper lateral stripe (usually one and a half scales wide on body), and yellow ventral and/or ventrolateral surfaces.

Distribution

Arid north-western and mid-western interior of Western Australia. See map, Figure 1.

Habitat

Leaf litter beneath acacias growing on a wide variety of soils including loose-surfaced clayey or stony loams.

Remarks

The differences between these taxa (width and intensity of vertebral stripe and number of supraciliaries) are of the order that separate sympatric species within the complex. Moreover the ranges of two of them (*L. petersoni* and *L. gascoynensis*) abut without

Figure 2 Map of mid-western Western Australia showing location of specimens of *Lerista talpina, L. kendricki, L. maculosa* and *L. yuna.*

evidence of hybridization. Hence they seem to be more than subspecies. On the other hand their sharing of so many and such diverse characters indicates a closer relationship than between sympatric members of the complex. Their nearest relative appears to be *L. uniduo,* which also has ventral yellow and very small second loreal and presuboculars.

Lerista petersoni Storr, 1976

Diagnosis

A member of the *L. nichollsi* subgroup, distinguishable from others by its much wider and paler vertebral stripe. Further distinguishable from *L. gascoynensis* by 4 (rather than 1 + 2) supraciliaries.

Description

Snout-vent length (mm): 39-71 (N 45, mean 58.3). Tail (% SVL): 83-109 (N 8, mean 91.2).

Nasals in very short to moderately long contact. Supraoculars 3, first two in contact with frontal. Supraciliaries normally 4, last much the smallest (3 and 1 + 3 in one specimen). Loreals 2, second much smaller than first (fused to prefrontal in three of 30 specimens). Presuboculars very small, 1 (N 4) or 2 (26). Upper labials 5 (N 1, when third and fourth fused) or 6 (28). Nuchals 1 (N 3), 2 (21) or 3 (5). Midbody scale rows 18 (N 1), 20 (27) or 22 (1). Lamellae under longer toe 10-14 (N 36, mean 11.4). Forelimb represented by a small groove or pit and usually a very small stump (up to 0.5 mm long).

Upper surface brownish white or very pale brown. Head, especially sutures, irregularly marked with dark brown. Back with 4 (occasionally 2) longitudinal rows of small angular dark brown or blackish brown spots, the space between them pale greyish brown, the resultant stripe extending irregularly on to tail. Wide dark brown or blackish brown upper lateral stripe from nasal to end of tail, on body usually occupying a longitudinal row of scales and lower half of row immediately above it, and continuous with vertical bars on lips (mostly located on sutures between upper labials). Upper surface of hindlegs mottled with greyish brown or blackish brown. Lower lateral surface and sometimes ventral surface yellow in life.

Distribution

Arid north-western interior of Western Australia, from Barradale south to the Kennedy Range and Yinnetharra. See map, Figure 1.

Material

North-West Division (WA): 17 km NE Barradale (80251) and 1 km W (84187) and 2 km S (80155-7, 98146-7) and 50 km WSW (81828-9); 25 km NW Maroonah (98187) and 30 km S (98180); Williambury (98178-9) and 3 km S (98185-6); 1 km N Mangaroon (98144-5) and 6 km SSE (84185-6); 10 km W Manberry (76842) and 14 km WSW (88889-95); Mt Augustus (84087); 4 km NE Mt Phillips HS (87760); near Merlinleigh Outstation (98136, 98141, 98188, 99637, 99641); 2 km E Mt Sandiman (99629-35); Yinnetharra (46197, 51738) and 12 km NNE (87610-2).

Lerista kendricki **sp. nov.**
Figure 3

Holotype

93887 in Western Australian Museum, collected by P.G. Kendrick on 28 February 1986 at 15 km SW Hamelin HS, Western Australia, in 26°32′S, 114°05′E.

Paratypes

The 270 specimens listed under Material.

Diagnosis

A moderately small, strongly patterned member of the *L. nichollsi* complex (up to 118 mm long) with immovable eyelids, 4 supraciliaries, wide vertebral stripe, two toes and forelimb represented by a small pit or groove (occasionally with a minute stump up to 0.2 mm long). Distinguishable from the *L. nichollsi* subgroup by lesser size, relatively shorter tail, larger second loreal, larger presuboculars, darker head, wider vertebral stripe and narrower upper lateral stripe.

Description

Snout-vent length (mm): 28-67 (N 265, mean 48.1). Tail (% SVL): 68-95 (N 105, mean 81.7).

Nasals in very short to long contact. Prefrontals widely separated. Frontoparietals

Figure 3 A *Lerista kendricki* from 16 km SSW Hamelin, photographed in life by M. Peterson.

and interparietal fused. Supraoculars 3, first two in contact with frontal. Supraciliaries normally 4, last much the smallest (in one specimen second and third fused to each other, in another third and fourth fused to third supraocular, in another fourth divided). Loreals 2, second not fused to prefrontal. Presuboculars 2. Upper labials 6. Nuchals 1 (N 11), 2 (19) or 3 (1). Midbody scale rows 20 (N 5). Lamellae under longer toe 11-15 (N 25, mean 11.6), rarely with a weak keel.

Broad medium to dark brown vertebral stripe from snout to tail, very rarely covering whole width of back but usually leaving a narrow brownish white dorsolateral stripe; enclosing 4 rows of small angular brown to blackish brown spots on back. Narrow blackish brown upper lateral stripe from nasal to end of tail, on body usually occupying two adjacent half-scales, and continuous with dark upper and lateral edges of upper labials. Upper surface of hindlegs mottled with dark greyish brown.

Distribution

Sandy country near mid-west coast of Western Australia, from base of Peron Peninsula south to the mouth of the Murchison. See map, Figure 2.

Derivation of name

After zoologist Peter Graeme Kendrick in appreciation of his research into *Lerista*, notably the *L. nichollsi* complex.

Material

North-West Division (WA): 6 km SSE Nilemah Outstation (92728-31, 94162, 94164, 94166-7, 94169, 94171) and 7 km S (92698-9, 92702-4, 93910-1, 93915-8, 93922, 94152) and 9 km S 92427, 92429, 92432-3, 92439, 92441-3, 92446-7, 92449-50, 92452, 92460, 92509, 92511-3, 92514-6, 92519-21, 92523, 92541, 92544-5, 92547, 92786-95, 92797, 92799-801, 92812-3, 93946-52) and 10 km SSE (96875-82) and 11 km SE (92199, 93970, 93973-6) and 17 km SE (92740-1, 92748, 92752-4, 92831-3, 92835-7) and 17 km SSE (92857-8, 92863, 92865, 92869-73); 11 km SSW Hamelin (88773) and 13 km SW (95818-9) and 14 km SW (88717-21, 89677-83, 92205, 92207, 92209, 92214-7, 92219, 92225-6, 92234, 92737, 92904, 92906, 92908-10, 92912, 92915-6) and 15 km SW (92411-2, 92419, 92424-5, 92581, 92585, 92589-90, 92592-6, 92665, 92874, 92877-80, 92883-4, 92886, 92888-95, 93873-6, 93880-2, 93884-5) and 15 km S (95827-9) and 17 km SW (88941-51) and 17 km SSW (95830) and 18 km WSW (88969-75) and 18 km SSW (92391-2. 92396, 92401-3, 92407, 92510, 92514, 92526-35, 92537-40, 92817) and 18 km S (89314) and 20 km SW (89563-72) and 25 km SSW (89871); 42 km NE Tamala (64363) and 41 km NE (89860-6) and 30 km NE (88767) and 40 km SE (96152); 23 km NW Cooloomia (66357) and 14 km W (69543) and 15 km WSW (66372) and 18 km SW (69557) and 23 km SW (66357).

South-West Division (WA): Gee Gie Outcamp (34046); Kalbarri (37640-1).

Lerista yuna sp. nov.

Figure 4

Holotype

97214 in Western Australian Museum, collected by G. Harold on 9 July 1987 on the East Yuna Reserve, Western Australia, in 28°28′S, 115°13′E.

Paratypes

South-West Division (WA): 40 km ENE Yuna (57528); East Yuna Reserve (97213,100846).

Diagnosis

A strongly patterned member of the *L. nichollsi* complex with immovable eyelids, 4 supraciliaries, wide vertebral stripe, 2 toes and forelimb represented by a small groove or pit (and occasionally a minute stump). Distinguishable from *L. petersoni* by larger second loreal, larger presuboculars and lack of yellow on flanks and venter, and from *L. kendricki* by paler head and vertebral stripe and wider upper lateral stripe.

Description

Snout-vent length (mm): 29-66 (N4). Tail (% SVL): 88 (N 1).

Nasals in short to long contact. Prefrontals widely separated. Frontoparietals and interparietal fused. Supraoculars 3, first two in contact with frontal. Supraciliaries 4, last much the smallest. Loreals 2, second not fused to prefrontal. Presuboculars 2. Upper labials 6. Nuchals 2 (occasionally 3). Midbody scale rows 20. Lamellae under longer toe 10-12.

Head pale greyish brown, irregularly marked with dark brown or blackish brown (especially along sutures). Four series of angular dark brown or blackish brown spots on back (outer series continuing on to tail), space between them greyish brown, flecked darker. Dorsolateral stripe brownish white (pale coppery brown in life). Wide dark brown or blackish brown upper lateral stripe from nasal to end of tail, occupying on body a row of scales and lower half of row immediately above. Upper surface of hindlegs mottled with greyish brown. Lower lateral and ventral surfaces whitish in life.

Figure 4 Holotype of *Lerista yuna* photographed in life by R.E. Johnstone.

Distribution

Semiarid northern interior of South-West Division of Western Australia (north-east and south-east of Yuna). See map, Figure 2.

Lerista talpina sp. nov.

Holotype

74947 in Western Australian Museum, collected by G. Harold on 28 June 1981 at 2 km W Bullara, Western Australia, in 22°41′S, 114°01′E.

Diagnosis

A small slender short-tailed member of the *L. nichollsi* complex with small deep-set eyes and immovable eyelids, distinguishable from all others by lack of colour pattern and lack of ear aperture (only a small depression).

Description (of single available specimen)

Snout-vent length (mm): 36. Tail (% SVL): 66.

Nasals in short contact. Prefrontals widely separated. Frontoparietals and interparietal fused. Supraoculars 3, first two in contact with frontal. Supraciliaries 4, last much the smallest. Loreals 2. Presuboculars 2. Upper labials 6. Nuchals 1-2. Midbody scale rows 20. Lamellae under longer toe 10-12. Forelimb represented by a small pit.

Dorsal and lateral surfaces buffy white, without pattern. Hindlegs and lower surfaces white.

Distribution

Only known from one locality a little south of Exmouth Gulf, Western Australia.

Remarks

The holotype was collected (along with an *Aprasia fusca*) on a red *Triodia*-covered sandridge.

Derivation of name

From Latin *talpa* (mole).

Lerista maculosa sp. nov.

Holotype

95921 in Western Australian Museum, collected by P.G. Kendrick on 22 November 1987 at 5 km W Overlander, Western Australia, in 26°24'S, 114°25'E.

Paratype

North-West Division (WA): 16 km S Hamelin (92182).

Diagnosis

A member of the *L. nichollsi* complex with immovable eyelids, distinguishable from all others by heavily spotted pattern.

Description

Snout-vent length (mm): 39-41 (N 2). Tail (% SVL): 90 (N 1).

Nasals in contact. Prefrontals widely separated. Frontoparietals and interparietal fused. Supraoculars 3, first two in contact with frontal. Supraciliarics 1 + 2 (second fused to first supraocular). Loreal 1 (second fused to prefrontal). Presuboculars 2. Upper labials 6. Nuchals 2. Midbody scale rows 18. Lamellae under longer toe 10-11. Forelimb represented by a minute pit.

Top of head pale greyish brown stippled with dark brown. Back and tail pale brown with 4 longitudinal rows of small dark brown spots (outer series darker). Side of head barred and blotched with blackish brown (all but last upper labial almost wholly dark). Side of body and tail brownish white with 5 rows of dark brown to blackish brown spots (largest, darkest and tending to be transversely elongate on upper flanks). Hindlegs and lower surfaces brownish white to pale brown, stippled or indistinctly spotted or barred with pale brown, except for white mental and pre-anal scales.

Distribution

Only known from two localities a little south of Shark Bay (one of them a small area of mallee/*Triodia* shared with the endemic skink *Ctenotus zastictus* and the isolated southern population of the agamid *Ctenophorus rubens*). See map, Figure 2.

Derivation of name

Latin for covered in spots.

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Partial revision of the *Lerista macropisthopus* group (Lacertilia: Scincidae)

G.M. Storr*

Abstract

Three new species are described, namely *L. bunglebungle* from east Kimberley, *L. puncticauda* from the Great Victoria Desert and *L. axillaris* from the west coast. *L. macropisthopus* is divided into four subspecies. *L. neander* and *L. desertorum* are redescribed.

Introduction

Few specimens of *L. macropisthopus* and *L. desertorum* and very few of *L. neander* were available for my revision of *Lerista* (Storr 1972). Since then the Western Australian Museum has received many more specimens of these lizards, enabling me to re-assess their taxonomic status. Although *L. macropisthopus*, *L. neander* and *L. desertorum* are very closely related and replace each other geographically, I prefer to treat them as species rather than subspecies. Despite the proximity of their ranges (Figure 1), there is no evidence of intergradation or hybridization between them. Moreover *L. macropisthopus* itself has broken up into four subspecies. A new species of *Lerista* is described from the Kalbarri area, where it coexists with *L. macropisthopus galea;* a new species is described from the far north-east of Western Australia, and a new species is described from the Queen Victoria Spring area, where it is probably sympatric (but not syntopic) with *L. desertorum.*

Systematics

Lerista macropisthopus macropisthopus (Werner, 1903)

Figure 2

Diagnosis

A dark robust subspecies of *L. macropisthopus* with 2 fingers, 3 toes and little or no colour pattern.

Description

Snout-vent length (mm): 37-96 (N 58, mean 79.3). Length of appendages (% SVL): foreleg 2.3-4.6 (N 40, mean 3.4); hindleg 12.8-17.3 (N 40, mean 15.1); tail 81-112 (N 24, mean 94.1); snout to foreleg 22.0-31.0 (N 39, mean 24.8).

Nasals narrowly to moderately separated (N 38) or in short contact (3). Prefrontals widely separated. Frontoparietals narrowly to moderately separated (N 39) or fused to parietals (1), slightly to much smaller than interparietal. Nuchals 1-4 (N 40, mean 2.6). Supraoculars 3, first two in contact with frontal. Supraciliaries 1 + 3 (N 53), 1 + 2 (1) or 5 (1). Upper labials 5 (N 2) or 6 (46). Midbody scale rows 20 (N 31), 21 (2) or 22 (3). Lamellae under longest toe 9-13 (N 43, mean 11.6).

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* C/o Western Australian Museum, Francis Street, Perth, WA 6000.

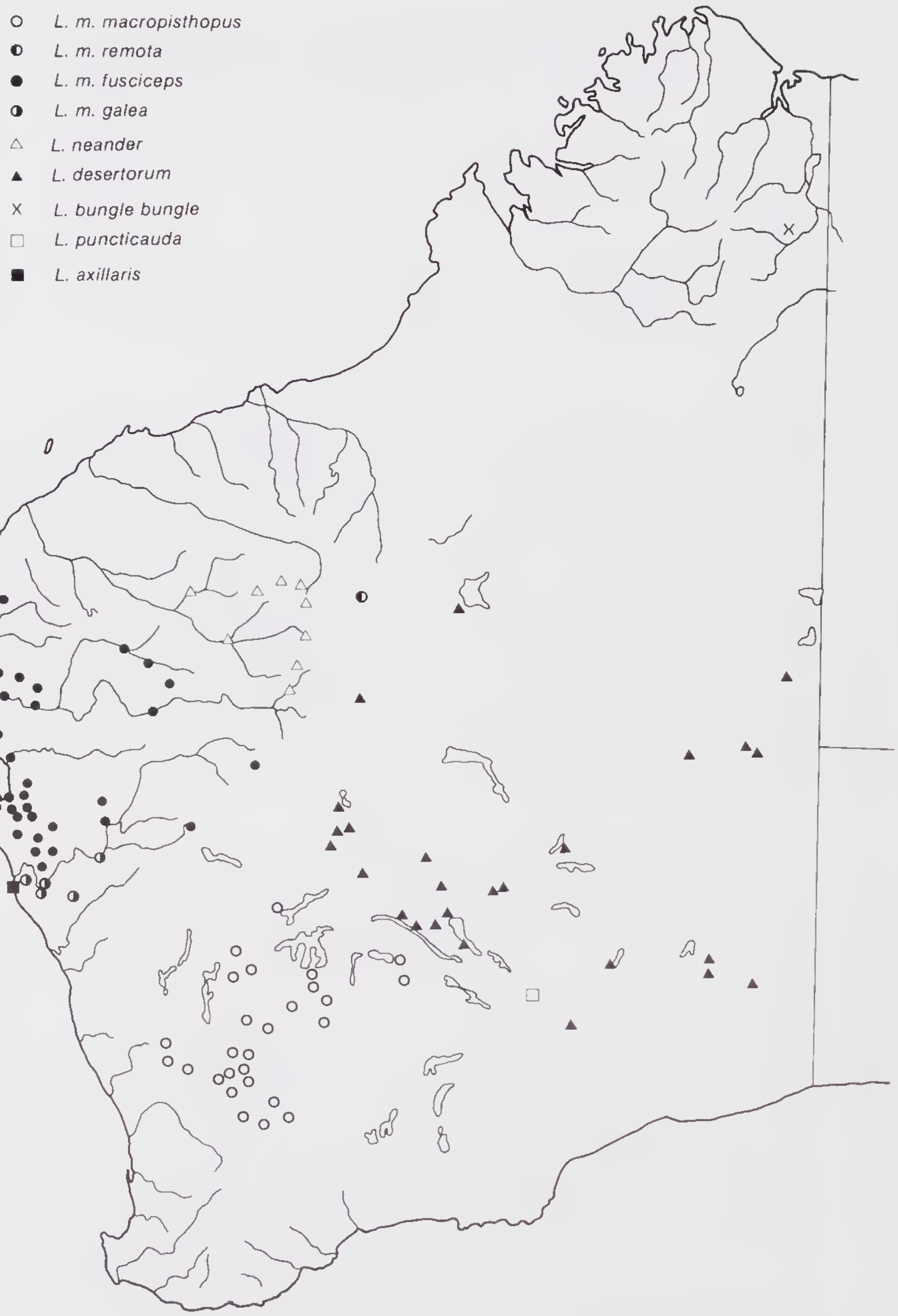

Figure 1 Map of Western Australia, showing location of specimens of *Lerista macropisthopus remota, L. m. fusciceps, L. m. galea, L. m. macropisthopus, L. neander, L. desertorum, L. bunglebungle, L. puncticauda* and *L. axillaris.*

Dorsal and upper lateral surfaces chocolate brown to greyish brown, without pattern except for slight darkening in loreal region and occasionally a slight paling across occiput. Ventral and lower lateral surfaces whitish except for brownish grey under hands and feet.

Distribution

Semiarid and arid south-western interior of Western Australia, from the eastern wheat belt north nearly to Atley, west to Wongan Hills and east to Jeedamya.

Material

North-West Division (WA): 20 km NNE Pindabunna (93104); near Earoo Rock (90279, 90282-3, 90290).

South-West Division (WA): Bimbijy (96594-6); 45 km ESE Karroun Hill (96568); Wialki (24881) and 23 km NE (18187); Ballidu (13931, 101499); Wongan Hills (4237); Ejanding (9833); Bencubbin (2759); Mukinbudin (32048); Billyacatting Hill (45978); Nembudding (7393); 8 km E Kununoppin (22343); Nukarni (4991); North Baandee (26159, 97475); Bruce Rock (1113); East Muntadgin (68280-1); Narembeen (12371) and 64 km E (25827).

Eastern Division (WA): Dead Horse Rocks (85260-4); 3 km N Jeedamya (24043); 14 km ENE Comet Vale (65824, 72716) and 3 km NE (72744); Blue Hill (64816); Evanston (64817); Mt Manning Range (64764-5, 64788-9); 25 km NE Pittosporum Rockhole (67158, 67168-70); near Mt Jackson (67027, 67046, 72086, 76107, 76111, 76129); 15 km NE Bungalbin Hill (76188) and 12 km NNE (72134); 3 km S Walyahmoning Rock (95866, 95938).

Figure 2 A *Lerista m. macropisthopus* from Bungalbin Hill, photographed in life by G. Harold.

Lerista macropisthopus remota subsp. nov.

Holotype

42282 in Western Australian Museum, collected by W.H. Butler on 22 September 1972 at Coondra Coondra Spring, Robertson Range, Western Australia, in 23°06′S, 121°02′S.

Diagnosis

Most like *L. m. macropisthopus* but having paler coloration and some pattern (head stippled and back dotted with dark brown).

Description (of single available specimen)

Snout-vent length (mm): 80. Length of appendages (% SVL): foreleg 4.0; hindleg 15.5; snout to foreleg 22.5.

Nasals narrowly separated. Prefrontals widely separated. Frontoparietals narrowly separated, smaller than interparietal. Nuchals 3-4. Supraoculars 3, first two in contact with frontal. Supraciliaries 1 + 3. Upper labials 6. Midbody scale rows 20. Lamellae under longest toe 11-12.

Dorsal and upper lateral surfaces brown. Head and upper lips heavily stippled with dark brown. On body 10 rows of indistinct dark brown dots, each passing through a dorsal or upper lateral scale. Ventral and lower lateral surfaces whitish, except for pale grey under hands and toes.

Distribution

Only known from one locality in arid central interior of Western Australia (40 km NE Jiggalong).

Lerista macropisthopus fusciceps subsp. nov.

Figure 3

Holotype

71118 in Western Australian Museum, collected by P. Griffin on 27 August 1980 at 2 km SSW Carnarvon, Western Australia, in 24°54′S, 113°39′E.

Paralypes

The 305 specimens listed under material.

Diagnosis

A subspecies of *L. macropisthopus* with 2 fingers, 3 toes and dark head contrasting with pale body and tail.

Description

Snout-vent length (mm): 36-100 (N 306, mean 69.2). Length of appendages (% SVL): foreleg 2.1-6.3 (N 58, mean 3.5); hindleg 11.8-18.7 (N 56, mean 14.9); tail 86-122 (N 68, mean 103.0); snout to foreleg 19.9-28.0 (N 57, mean 23.7).

Nasals narrowly to moderately separated (N 38) or in short contact (8). Prefrontals widely separated. Frontoparietals narrowly to moderately separated (N 42) or in point contact (3), slightly to much smaller than interparietal. Nuchals 1-7 (only one with more than 4, N 44, mean 2.8). Supraoculars 3, first two in contact with frontal. Supraciliaries 0 + 3 (N 19), 1 + 3 (102), 4 (3) or 5 (165). Upper labials 6. Midbody scale rows 18 (N 2), 19 (2) or 20 (41). Lamellae under longest toe 9-13 (N 46, mean 11.7).

Figure 3 A *Lerista macropisthopus fusciceps* from Hamelin, photographed in life by R.E. Johnstone.

Dorsal and upper lateral surfaces pale to medium brown, greyish brown or brownish yellow, except for blackish or grey head (back to a little beyond eyes and down to top of upper labials) and occasionally dark dots on back. Ventral and lower lateral surfaces whitish except for brownish grey under hands and feet.

Distribution

Arid and semiarid mid-west of Western Australia from Yardie Creek south nearly to the lower Murchison (Eurardy and Meeberrie) and east to Waldburg, Karalundi and Poona.

Geographic variation

In the extreme north-west (Yardie Creek) the head is paler and the foreleg relatively longer than elsewhere, and here alone the predominant supraciliary formula is 0 + 3. Immediately north and east of Lake MacLeod (Minilya, Manberry and Cooralya) the tail is pinkish, especially on the under side and in juveniles. Specimens from Waldburg in the far north-east have unusually long fingers.

Derivation of name

From Latin *fuscus* (dark) and *-ceps* (head).

Material

North-West Division (WA): Yardie Creek (51028) and 5 km N (6142) and 4 km E (89798-805); 1 km W Bullara (89605-8, 98125-6); 25 km SW Winning (81834); 20 km ESE Warroora (98133); 9 km NNW Minilya

Roadhouse (76595-8, 76646-55, 89929-32); 18 km E Gnaraloo (76574) and 5 km SE (71540, 71595) and 9 km SE (76716) and 15 km SE (76759); 10 km W Manberry (76845-7) and 14 km WSW (89597-9, 89791-4); 5 km ENE Cobra (87663-4); 14 km SSE Mt Augustus (85270); 12 km S Waldburg (81210-1); 10 km N Boologooro (71370-1); 3 km NW Mardathuna (71490); 8 km W Cooralya (76861-8) and 27 km E (71384) and 15 km ESE (89944) and 30 km SSE (89619-23); 10 km N Boolathana (89641-3); 22 km NNE Carnarvon (71079-80) and 12 km NE (71498) and 48 km E (71527-30) and 2 km SSW (71074-8, 71119); 12 km WNW Binthalya (95462) and 11 km W (71508-9); Mooka (39069); Landor (2708); 21 km SW Edaggee (89725-36); Wooramel (54605, 54742-5, 54956-62, 54972-81, 55016); 18 km N Yaringa (71129) and 14 km S (89705-9); Woodleigh (48007, 57388); 'presumahly Karalundi' (42661); near Monkey Mia (91186-91, 94188); Denham (88701, 89375) and 8 km NE (89374); near Nilemah (92210, 92223, 92238, 92695, 92697, 92796, 92815, 92830, 92847-8, 92851, 92855, 92860, 92862, 92867, 92913, 93968, 94155); 40 km ENE Tamala (89694); near Hamelin (54925, 55204, 56478-80, 87911, 88584-5, 88670-2, 88687-8, 88713-4, 88723, 88738-42, 88749-51, 89573, 89587-8, 89637-8, 89647, 89650, 89668-70, 89688, 89780-3, 89829-30. 89842, 89888-9, 89919-23, 89940-1, 92183, 92201-2, 92298-300, 92340, 92390, 92394, 92475, 92491, 92583, 92600, 92634, 92637, 92667, 92669, 92676-7, 92680, 92689-90, 92721, 92774, 92783, 92913, 93872, 93886, 93894, 93906, 93937-8, 93940, 93964, 94146); Overlander (44528) and 6 km E (88725-31) and 24 km SSE (71060); Coburn (64392-3) and 17 km N (64430); 60 km ESE Meadow (95526); Wannoo (71064-6, 81411) and 7 km N (64335, 64398) and 6 km NNW (71136-41) and 6 km S (64310-1); Meeberrie (59686) and 40 km W (66196); Cooloomia (64370, 64386-7, 64435); 3 km SSW Nerren Nerren (71114) and 31 km SE (60645) and 38 km SE (60626) and 34 km SSE (59623); Poona (28944); Meka (29723).

South-West Division (WA): 60 km N Galena (61401) and 46 km N (59018-9, 61361) and 40 km N (58787) and 32 km N (69847); 5 km E Eurardy (86860).

Lerista macropisthopus galea subsp. nov.

Figure 4

Holotype

83228 in Western Australian Museum, collected by G. Harold on 7 March 1983 at 8 km S Galena, Western Australia, in 27°53′S, 114°42′E.

Paratypes

North-West Division (WA): Murchison crossing, 122 km N Mullewa (60484).

South-West Division (WA): 23 km ESE Kalbarri (33800); Galena (71050-1, 101242) and 8 km S (80726); Ajana (25220); 46 km NE Yuna (26505).

Diagnosis

Most like *L. m. fusciceps* but having 1 finger (occasionally 2), 2 toes and less contrast between colour of head and body.

Description

Snout-vent length (mm): 49-86 (N 10, mean 68.8). Length of appendages (% SVL): foreleg 2.5-3.8 (N 10, mean 3.4); hindleg 12.5-17.1 (N 10, mean 15.5); tail 95-107 (N 5, mean 101.5); snout to foreleg 23.0-26.6 (N 10, mean 24.2).

Nasals narrowly separated (N 8) or in short contact (1). Prefrontals widely separated. Frontoparietals narrowly to moderately separated, slightly to much smaller than interparietal. Nuchals 2-3 (N 10, mean 2.6). Supraoculars 3, first two in contact with frontal. Supraciliaries 1 + 3 (N 10). Upper labials 6. Midbody scale rows 20 (N 7), 21 (1) or 22 (2). Lamellae under longer toe 10-14 (N 10, mean 11.7).

Dorsal and upper lateral surfaces medium to dark greyish brown, darkest on snout and in loreal region. Ventral and lower lateral surfaces whitish except for grey under hands and feet.

Figure 4 A *Lerista macropisthopus galea* from Galena, photographed in life by M. Peterson.

Distribution

Semiarid and arid upper south-west of Western Australia, about the lower Murchison upstream to the Mullewa-Gascoyne Junction road.

Remarks

In coloration it shows some tendency towards the nominate race, with which it shares a predominant supraciliary formula of 1 + 3 (in southern *L. m. fusciceps* 5 supraciliaries is almost as frequent as 1 + 3). Only the westernmost specimen of *L. m. galea* (33800) has two fingers.

Derivation of name

Latin for helmet, in allusion to dark top of head.

Lerista neander Storr, 1972

Figure 5

Diagnosis

Very like *L. macropisthopus* but having 2 fingers, 2 toes and strongly spotted dorsum.

Description

Snout-vent length (mm): 36-88 (N 25, mean 72.7). Length of appendages (% SVL): foreleg 2.5-5.7 (N 20, mean 3.7); hindleg 11.4-16.1 (N 21, mean 12.8); tail 99-117 (N 7, mean 107.7); snout to foreleg 22.1-31.4 (N 21, mean 24.0).

Nasals narrowly to moderately separated (N 25) or in very short contact (1). Prefrontals widely separated. Frontoparietals narrowly to moderately separated (N 23) or in point contact (1), smaller than interparietal. Nuchals 1-5 (N 23, mean 2.4). Supraoculars 3, first two in contact with frontal. Supraciliaries 0 + 3 (N 13) or 1 + 3 (13). Upper labials 6. Midbody scale rows 18 (N 1) or 20 (9). Lamellae under longer toe 8-12 (N 20, mean 10.4).

Dorsal and upper lateral surfaces pale to medium greyish brown (darkest on lores and top of upper labials) with dark brown stippling on head and tail and 8 (occasionally 10) rows of dark brown spots on body. Ventral and lower lateral surfaces whitish except for brownish dots or vermiculations on tail and pale grey under hands and feet and sometimes chin and throat.

Distribution

Arid western plateau of Western Australia from the eastern Hamersley and Ophthalmia Ranges south to the head of the Gascoyne.

Figure 5 A *Lerista neander* from 21 km SE Bulloo Downs, photographed in life by R.E. Johnstone.

Geographic variation

Specimens from the extreme south of range (96917-21) are darker than the others.

Material

North-West Division (WA): 4 km ENE Mt Maguire (94870); 31 km SE Mt Meharry (67924) and 36 km SE (67900-1); 6 km E Rhodes Ridge (88819-20); Newman (23988-9, 26528-9) and 38 km W (96922-3); 2 km S Capricorn Roadhouse (81321); 26 km SSW Tangadee (95638); 16 km SE Bulloo Downs (88813-7) and 21 km SE (81509); 6 km N Kumarina (87730) and 30 km S (96917-21).

Lerista desertorum (Sternfeld, 1919)

Figure 6

Diagnosis

A member of the *L. macropisthopus* group with 2 fingers, 3 toes, dark upper lateral stripe and 2 (occasionally 4) rows of small dark spots on back and tail.

Description

Snout-vent length (mm): 39-93 (N 113, mean 73.4). Length of appendages (% SVL): foreleg 2.1-5.8 (N 53, mean 3.9); hindleg 13.0-18.9 (N 55, mean 15.7); tail 85-119 (N 33, mean 103.2); snout to foreleg 22.0-28.7 (N 54, mean 24.6).

Nasals narrowly to moderately separated (N 61) or in point contact (1). Prefrontals widely separated (fused to frontal on one side of one specimen). Frontoparietals narrowly to moderately separated (N 72), in point contact (9) or in short to moderate contact (10), slightly to considerably smaller than interparietal. Nuchals 1-4 (N 78, mean 2.8). Supraoculars 3, first two in contact with frontal. Supraciliaries 0 + 3 (N 105), 1 + 3 (4), 0 + 2 (2), 1 + 1 (1), 1 + 2 (1), 3 (1), 5 (1). Midbody scale rows 18 (N 6), 19 (1), 20 (50), 21 (3) or 22 (5). Lamellae under longest toe 9-14 (N 77, mean 11.4).

Dorsal and upper lateral surfaces greyish brown to pale reddish brown. Head stippled with dark brown. A paravertebral series of brown dots or small spots on back and tail, sometimes coalescing into a narrow stripe; occasionally an additional series of dots or small spots on back. Dark brown to blackish brown upper lateral stripe from lore to base of tail, 1-2 scales wide on body. Ventral and lower lateral surfaces whitish (often yellow in life), except for greyish brown under hands and feet and often brown dots under tail.

Distribution

Arid eastern interior of Western Australia, from Lake Disappointment and the Rawlinson Range south nearly to Kitchener and north edge of Nullarbor Plain. Also south of Northern Territory and north-western South Australia.

Material

Eastern Division (WA): Durba Spring 54401-2; Carnarvon Range (51872); 5 km N Giles (34155); Winburn Rocks (20726); Barrow Range (20724); near Warburton (15146, 15176, 18224, 22000, 22060, 22089-90); Lake Wells (1607); 18 km NW Nuendah (82572-3); Yeelirrie (82574-80); Altona (87456); near Albion Downs (8787, 30596, 30963); Wanjarri (16903, 19766, 27229, 40739-41); Lake Throssell (15709); 8-9 km SE Banjawarn (69335, 74746, 74790) and 12-13 km SE (66016-7, 66037-8, 74754-5, 74762, 74767, 74787); 7-8 km WNW Point Salvation (85627-31); White Cliffs (20662) and 15 km ENE (85284-5); 21 km NNW Mt Windarra (78566); 13 km ENE Laverton (85320-1); Burtville (86755-7); Mt Morgans (85293-4, 86715-20) and 8 km SW (25953); 10 km N Leonora (86657); Glenorn (3785); Linden (46625); 3 km NE Mt Linden

Figure 6 A *Lerista desertorum* from Big Shot Bore, photographed in life by G. Harold.

(65930-4, 72874) and 8 km SSE (72770, 72884) and 10 km SSE (65941-3, 72785-7); 67 km SE Blue Robin Hill (91461, 92030) and 70 km SE (92034, 92037; 45 km ENE Lake Colville (92032) and 39 km E (91910), 92031, 92035, 92050) and 40 km E (91912, 92036) and 42 km ESE (92027); 102 km NNW Forrest (91294-5, 92033, 92053) and 95 km NNW (92038) and 94 km NNW (91293, 92929); 48 km NNE Kitchener (96744) and 36 km NNE (96745).

Northern Territory: 20 km S Alice Springs (74065-6); Kulgera (24472).

Lerista bunglebungle sp. nov.

Holotype

103484 in Western Australian Museum, collected by N.J. Gambold on 8 December 1989 in Bungle Bungle National Park, Western Australia, in 17°29′S, 128°22′E.

Diagnosis

A member of the *L. macropisthopus* group with 2 fingers, 3 toes and dark dorsal spots and upper lateral stripe, most like *L. desertorum* but having contiguous nasals, 4 supraciliaries and 6 rows of dorsal spots.

Description (of single available specimen)

Snout-vent length (mm): 59. Length of appendages (% of SVL): foreleg 5.1; hindleg 14.5; snout to foreleg 25.1.

Nasals in short contact. Prefrontals widely separated. Frontoparietals narrowly separated, smaller than interparietal. Nuchals 1-2. Supraoculars 3, first two in contact with frontal. Supraciliaries 4, first largest, last much the smallest. Midbody scale rows 22. Lamellae under longest toe 11.

Dorsal and upper lateral surfaces pale brown. Head stippled with dark brown. Six series of dark brown dots on back, becoming larger and less regular on tail. Dark brown upper lateral stripe from nasal to base of tail, diffuse and ragged-edged on head, slightly more than one scale wide on body, and replaced by two series of small irregular spots on tail. Ventral and lower lateral surfaces of body brownish white, scales faintly edged with brown. Ventral and lower lateral surfaces of tail brownish white, irregularly spotted with blackish brown. Limbs brownish white, their upper surface smudged with brown.

Distribution

Bungle Bungle Range in semiarid east Kimberley.

Remarks

The discovery of this species in the far north-east of Western Australia constitutes a large northward extension of known range in the *Lerista macropisthopus* group. It joins other central and southern skinks that have an outlying population in east Kimberley, viz. *Ctenotus alacer, C. schomburgkii* and *Egernia slateri.*

Lerista puncticauda sp. nov.

Holotype

100809 in Western Australian Museum, collected by D. Pearson on 15 December 1988 at 25 km NNE Queen Victoria Spring, Western Australia, in 30°14′S, 123°41′E.

Paratypes

Eastern Division (WA): 25 km NNE Queen Victoria Spring (100808, 100810, 100883).

Diagnosis

A member of the *L. macropisthopus* group with 2 fingers, 3 toes and little pattern apart from brown-dotted whitish tail.

Description

Snout-vent length (mm): 63-86 (N4, mean 76.2). Length of appendages (% SVL): foreleg 3.6-4.6 (N4, mean 4.0); hindleg 17.2-19.0 (N4, mean 17.8); tail 94-100 (N3, mean 96); snout to foreleg 23.0-27.6 (N4, mean 24.4).

Nasals narrowly to moderately separated. Prefrontals widely separated. Frontoparietals narrowly separated, smaller than interparietal. Nuchals 2-4. Supraoculars 3, first two in contact with frontal. Supraciliaries 0 + 3 (0 + 1 on one side of one specimen). Upper labials 6. Midbody scale rows 20. Lamellae under longest toe 11-13.

Head greyish brown, except for spotty dark brown loreal streak. Neck and back greyish brown, with or without a series of narrowly to widely separated dark brown upper lateral spots. Tail brownish white, heavily dotted with brown. Chin pale greyish brown. Under tail brownish white, with or without brown dots. Remaining under surfaces and limbs greyish white.

Distribution

Only known from extreme south-west of Great Victoria Desert.

Remarks

Its supraciliary formula, subcaudal pattern and incipient upper lateral stripe indicate a closer relationship to *L. desertorum* than to *L. macropisthopus.*

Derivation of name

From Latin *punctum* (dot) and *cauda* (tail).

Lerista axillaris sp. nov.

Figure 7

Holotype

97212 in Western Australian Museum, collected by G. Harold on 11 July 1987 at 21 km S Kalbarri, Western Australia, in 27°52′S, 114°10′E.

Diagnosis

A member of the *L. macropisthopus* group with 2 fingers, 3 toes and movable eyelids, most like *L. macropisthopus* but having a dark upper lateral stripe, yellow venter, more elongate body, shorter limbs and a much longer and deeper forelimb groove.

Figure 7 Holotype of *Lerista axillaris,* photographed in life by R.E. Johnstone.

Description (of single available specimen)

Snout-vent length (mm): 87. Length of appendages (% SVL): foreleg 2.9; hindleg 10.9; tail 83; snout to foreleg 20.7.

Nasals narrowly separated. Prefrontals widely separated. Frontoparietals separated, much smaller than interparietal. Supraoculars 3, first two in contact with frontal. Supraciliaries 1 + 3. Upper labials 6. Nuchals 2. Midbody scale rows 20. Lamellae under longest toe 11.

Upper surface greyish brown, becoming darker on head (especially in loreotemporal region and on top of upper labials), back and tail finely flecked with blackish brown. Narrow blackish brown upper lateral stripe from ear to base of tail. Upper surface of limbs blotched with dark greyish brown. Lower surfaces whitish (yellow in life), except for dark brownish grey under hands and feet.

Distribution

Only known from one locality south of the mouth of the Murchison.

Derviation of name

From Latin *axilla* (armpit), in allusion to the peculiar forelimb groove.

Reference

Storr, G.M. (1972). The genus *Lerista* (Lacertilia, Scincidae) in Western Australia. *J. Proc. R. Soc. West. Aust.* **54**: 59-75.

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Seasonal variations of spermatogenesis and of the sexual segment of the kidney in the Carpet Python, *Morelia spilota imbricata* (Serpentes: Boidae)

Gerald Kuchling

Abstract

Testes, vasa deferentia and kidneys of museum specimens of *Morelia spilota imbricata* from south-western Australia have been histologically studies. *Morelia spilota imbricata* shows a prenuptial spermatogenetic pattern. During summer the germial epithelium is quiescent; multiplication of spermatogonia begins in late summer/autumn, spermatocytogenesis and spermiogenesis progress quickly, the culmination phase of spermiogenesis and spermiation occuring in November. Only during this time of the year is the sexual segment of the kidney hypertrophied; during summer, autumn and winter it is completely regressed, corresponding to the period of sexual quiescence. The male reproductive cycle of the Carpet Phthon in south-western Australia corresponds to patterns found in some snakes of other families in the temperate and subtropical zone.

Introduction

Although several species of boas and phythons (Boidae) are regularly bred in captivity, data on male gonadal cycles of these snakes are still scarce. The most complete description of the reproductive cycle in any species of Boidae is that given by Slip and Shine (1988) for *Morelia spilota spilota* (Pythoninae) in eastern Australia. But data on the histology of the male reproductive organs in this species are entirely lacking; Slip and Shine (1988) based their conclusions regarding the male reproductive cycle on behaviour of wild animals and on observations of turgid or flaccid testes in museum specimens. Saint Girons (1972) described histologically the sexual segment of the kidney of one specimen of the north-american boa *Charina bottae* (Boinae), without giving details of the testicular state or of the time of the year when this animal was sacrificed.

The major patterns of reproductive cycles in male snakes have been discussed by Saint Girons (1982) and Seigel and Ford (1987). The limited data for *Morelia spilota spilota* suggest a prenuptial spermatogenetic pattern (Slip and Shine, 1988), a pattern which is commonly found in tropical and subtropical snakes (Saint Girons 1982). *Morelia spilota* is widely distributed in Australia and New Guinea, covering an enormous variety of climatic conditions, from tropical rainforests to deserts and to temperate regions (Cogger 1988). This paper describes histologically the annual cycle of the testis and of the sexual segment of the kidney of *Morelia spilota imbricata,* a subspecies which inhabits temperate climate with good winter rains and dry summers in south-western Australia (Smith 1981). This snake is declared as rare by the Western Australian Wildlife Conservation Act and fully protected by law. Therefore this study was restricted to preserved specimens in the collection of the Western Australian Museum.

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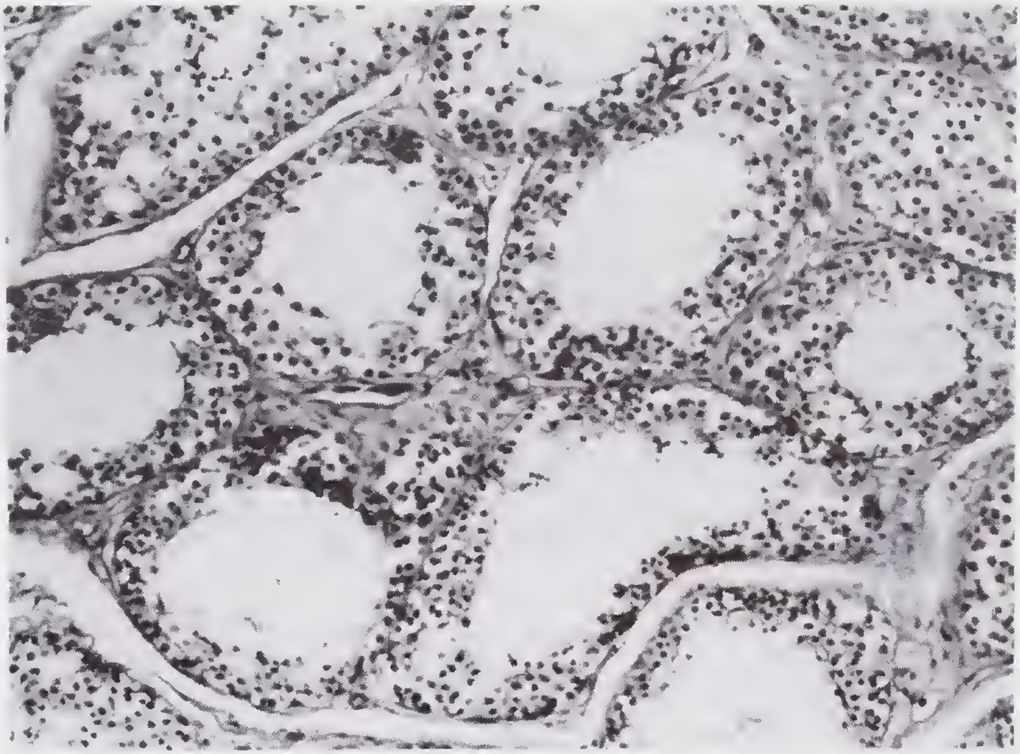

Figure 1. Testis, 28. April (X 250): The tubuli seminiferi have a large lumen, the germinal epithelium is thin, the only germ cells are spermatogonia which start to multiply.

Materials and Methods

All specimens of *Morelia spilota imbricata* in the collection of the Western Australian Museum were examined. The urogenital organs of 11 mature males with known date of collection and preservation were used in this study. Pieces of one testis and of the mid part of one kidney, together with the vas deferens, were paraffin embedded, sectioned (nominally 6μm) and stained with Haematoxilin and Eosin. Nine specimens of adult males which were well enough preserved for histology were available for the months January, April, May, July, October, November and December. Measurements of transversally sectioned parts of tubules were performed with an ocular micrometer. The mean of 15 measurements per structure and animal is presented, smoothed to the nearest unit of measurement (μm). Spermatogenetic stages and the development of the sexual segment of the kidney were determined according to the criteria of Saint Girons (1972, 1982).

Results

The spermatogenetic cycle of *M. s. imbricata* commences in late summer when spermatogonia begin to multiply (Figure 1). Few spermatocytes of I. order appear during April and May and spermatocytogenesis proceeds slowly until winter (July). During spring, spermatocytogenesis and spermiogenesis progress quickly, and by the end of October spermiogenesis and spermatids of all stages are abundant. By late October most spermatozoa are clustered at the distal end of Sertoli cells and the vas deferens contains no sperm. The culmination phase of spermiogenesis is reached during November (Figure 2), with massive spermiation and discharge of spermatozoa into the efferent ducts; the vas deferens is enlarged and filled with a dense mass of spermatozoa (Figure 3a). By the beginning of December the testes regress; during summer the only germ cells in the germinal epithelium are inactive spermatogonia; the lumen of the seminiferous tubules is filled with cell debris of spermatocytes and spermatids. The vas deferens becomes more-or-less devoid of spermatozoa and its diameter decreases markedly until next spring (Figure 3b, c, Tab. 1). The annual variations of the diameter of the tubuli seminiferi reflect the changes in the germinal epithelium, with the largest diameter being reached in November at the height of spermiogenesis and spermiation (Table 1).

The sexual segment of the kidney is involuted during summer, autumn and winter and has similar diameters to adjacent tubular regions. With the onset of spermiogenesis in

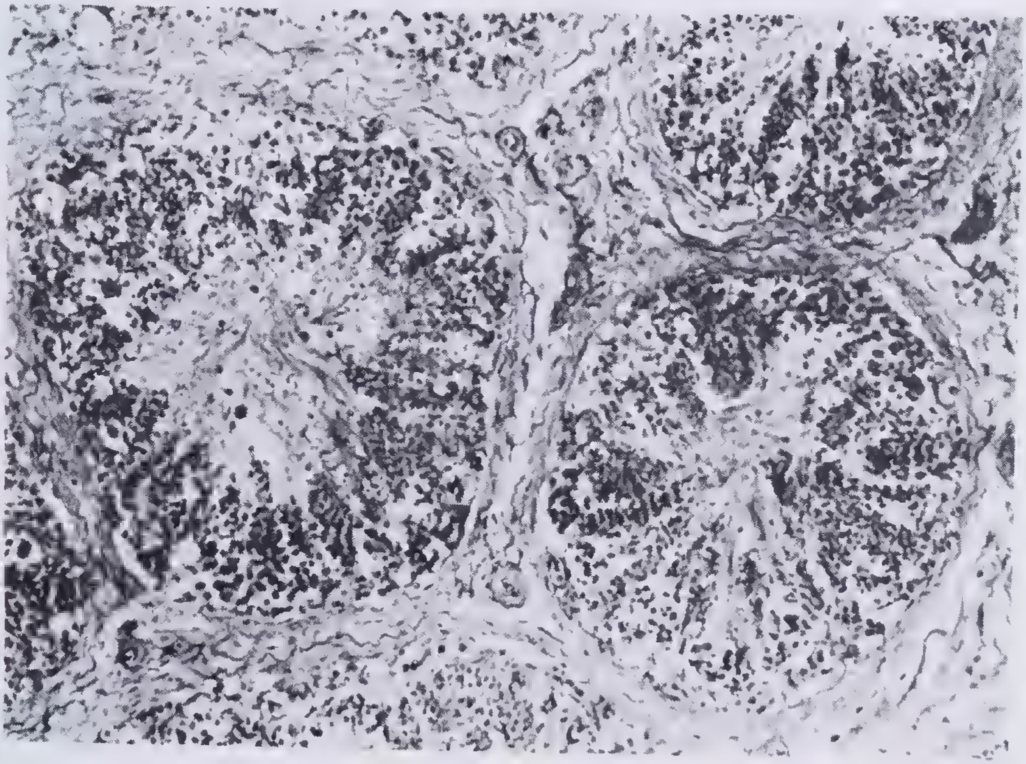

Figure 2. Testis, 13. November (X 250): Culmination phase of spermiogenesis; all types of germ cells are present in the germinal epithelium: spermatogonia, spermatocytes, spermatids in all stages of differentiation, and spermatozoa which are partly clustred at the distal end of Sertoli cells and partly free in the lumen.

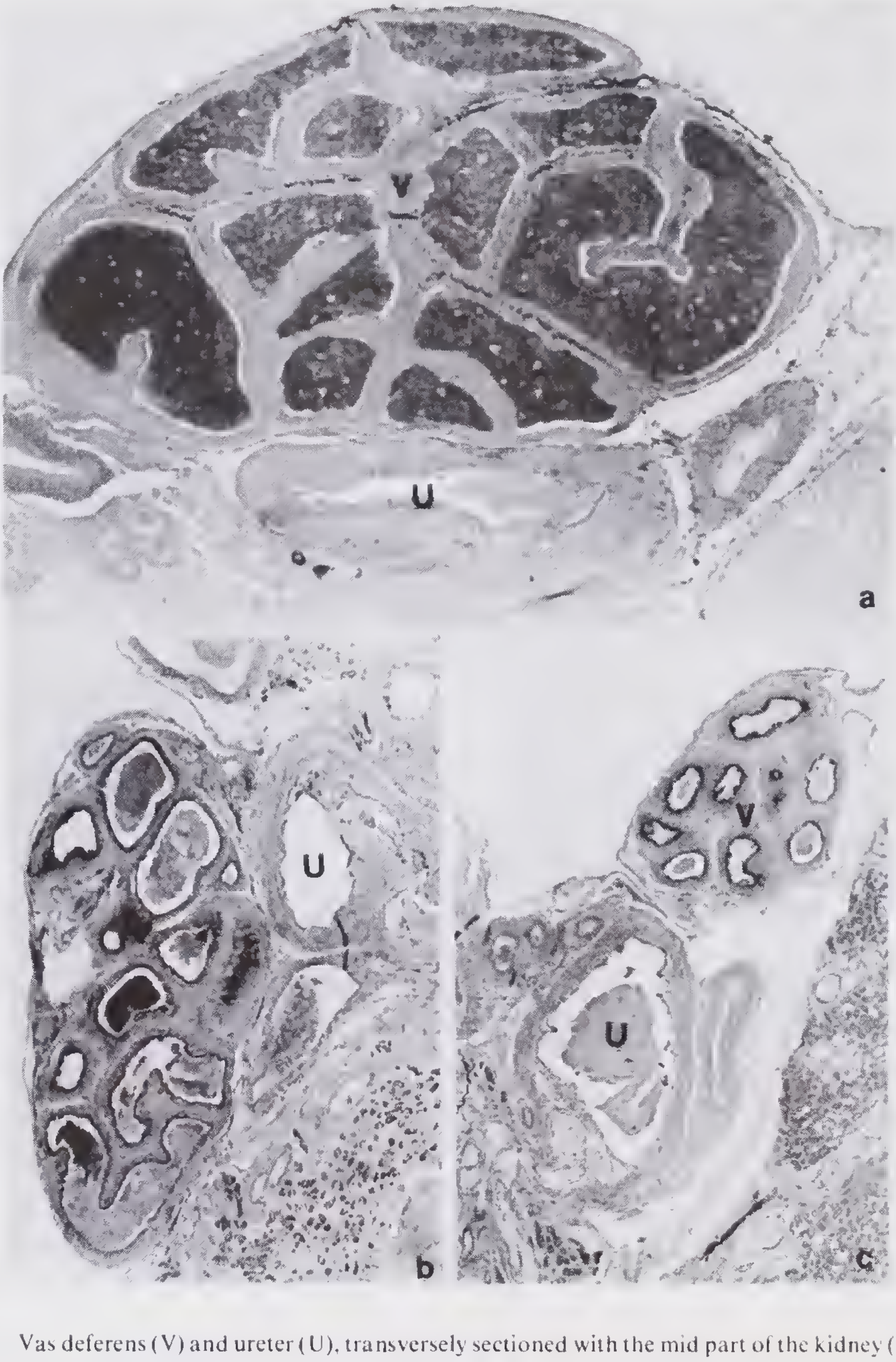

Figure 3. Vas deferens (V) and ureter (U), transversely sectioned with the mid part of the kidney (X 40); a: 11. November, lumen of vas deferens filled with a dense mass of spermatozoa; b: 12. December, only few spermatozoa in vas deferens; c: 12. May, vas defererns has a small diameter and is devoid of spermatozoa.

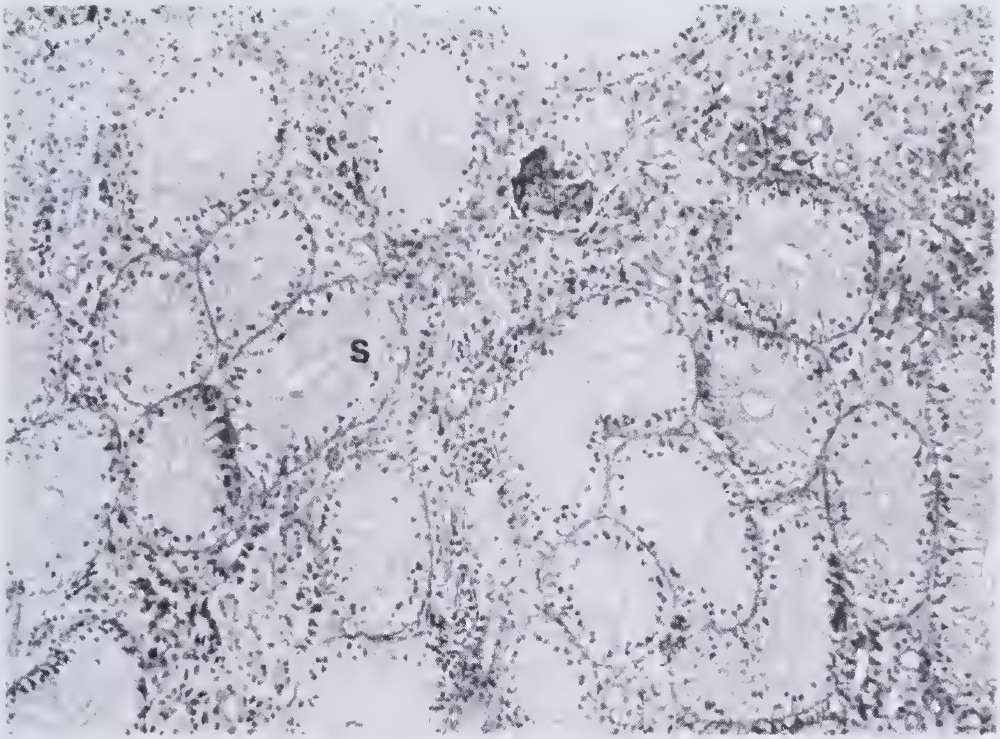

Figure 4. Kidney, 13. November (X 150): The sexual segment (S) is hypertrophied and shows high, columnar epithelial cells with basal nuclei.

spring, the diameter increases and the epithelium consists of high columnar cells with basal nuclei; the maximal tubular diameter is reached in November at the culmination of spermiation (Figure 4; Table 1).

Discussion

The hypertrophied and secretorily active sexual segment of the kidney and the masses of spermatozoa found in the vas deferens during November indicate that this is the mating time of *M. a. imbricata*. Spermatogenesis is of the prenuptial type, the reproductive pattern seems to be similar to that of *M. s. spilota* in coastal New South Wales (Slip and Shine 1988) where seasonal temperature conditions are comparable with those in south-western Australia. However, no direct observations of reproductive activity are available for *M. s. imbricata* in the wild. In *M. s. spilota* in coastal eastern Australia near Sydney, copulations have been observed during late October and November; females oviposited in late December or early January (Slip and Shine 1988). In tropical northern Queensland (Townsville), however, several captive *M. s. variegata* mated during August and eggs were laid in November (Charles *et al.* 1985). This indicates that timing of reproduction in *Morelia spilota* varies with the climatic conditions. In general, Australia snakes which live in relatively cool (temperate zone) climates seem to be remarkably

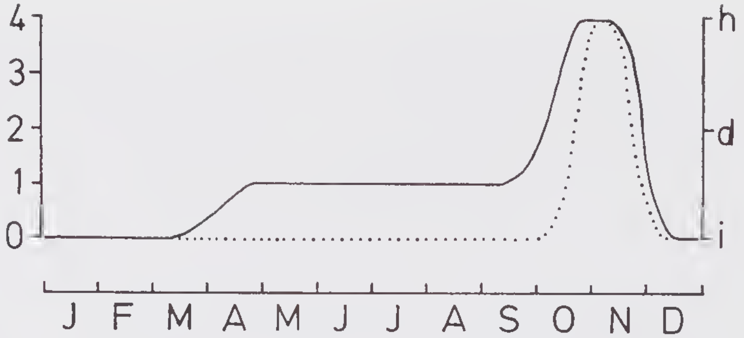

Figure 5. Diagrammatic representation of the annual cycle of spermatogenesis (left ordinate and solid line), where 0-1 = multiplication of spermatogonia (with the first spermatocytes appearing at 1); 1-2 = spermatocytogenesis; 2-2 = early spermiogenesis; 3-4 = continuation of spermiogenesis; the plateau at 4 = culmination phase of spermiogenesis, spermiation; 4-0 = end of spermiogenesis and spermiation. Right ordinate and dotted line give the relative development of the sexual segment of the kidney, where i = sexual segment regressed and mucous; d = sexual segment differentiated but not hypertrophied; h = sexual segment hypertrophied and serous.

consistent in their seasonal timing of reproduction: ovulation occurs in late spring, eggs are laid in early summer and offspring hatch (or are born) in late summer (Shine 1985). A prenuptial spermatogenetic pattern has been found in several Australian elapids (Shine 1977).

During most of the year, the sexual segment of the kidney of *M. s. imbricata* is completely regressed and mucous, corresponding to the period of sexual rest (Figure 5). A comparable pattern has been found in two Mediterranean Colubridae and in the Saharan Viperidae *Cerastes cerastes* (Saint Girons 1982). As in *M. spilota*, females of these species have a single ovulation in late spring or early summer. In many other snakes of temperate or subtropical regions, the sexual segment of the kidney shows only one brief period of partial regression in summer and remains secretory over most of the year (Saint Girons 1982).

Pythons inhabit mainly tropical regions where the climatic conditions allow spermatogenesis to proceed at any time during the year. In tropical snakes, spermatogenesis is always prenuptial when not continuous (Saint Girons 1982). The prenuptial spermatogenetic pattern of *M. s. imbricata* reflects the tropical origin of this snake which has been able to extend its range into temperate regions. In general, the temperate climate constrains female rather than male reproduction, which demands much less energy. But, despite being prenuptial, the testicular cycle of *M. s. imbricata* is not purely vernal, since spermatogenia start to multiply in late summer and spermatocytogensis proceeds slowly during autumn and winter (Figure 5). This pattern is common in most snakes of temperate and subtropical zones which show prenuptial spermatogenesis in spring (Saint Girons 1982). In temperate and subtropical zones purely vernal, prenuptial spermatogenesis occurs only in some lizards from arid regions (Bradshaw 1986).

Acknowledgements

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Table 1. Seasonal variations in male reproductive organs of *Morelia spilota imbricata*.

Date	mean diameter of tubuli seminiferi (μm)	abundance of spermatozoa in vas deferens[a]	mean diameter of the sexual segment (μm)
? Jan.	73	±	41
19. Apr.	91		41
28 Apr.	119	±	51
12 May	114		40
26 July	102		41
27 Oct.	190	—	98
11 Nov.	192	++	107
13 Nov.	223	++	133
12 Dec.	80	+	42

[a] ++: dense mass of spermatozol; +: spermatozoa abundant; ±: sporadic few spermatozoa; —: no spermatozoa

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Paulamys sp. cf. *P. naso* (Musser, 1981) (Rodentia: Muridae) from Flores Island, Nusa Tenggara, Indonesia — description from a modern specimen and a consideration of its phylogenetic affinities.

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Abstract

Paulamys naso was described from Holocene and Pleistocene fragments of dentary and lower teeth from western Flores I. by Musser (1981b) and Musser *et al.* (1986).

A single specimen of a distinctive murid live-trapped in 1989 at Kelimutu, central southern Flores, appears to be closely related to *P. naso*. This specimen is described in detail and its phylogenetic relationships are discussed.

Introduction

Musser (1981b) described the genus *Floresomys,* to accommodate a distinctively long-nosed murid (*F. naso*) from fossils represented by dentaries and lower teeth from sediment in Liang Toge cave, near Warukia, 1 km south of Lepa, Menggarai District, West Flores. The deposit was dated at 3550 ± 525 yr BP. The holotype is a "piece of right dentary with a complete molar row and part of the incisor ... from an adult." *Floresomys,* however, is a preoccupied generic name so Musser in Musser *et al.* (1986) proposed the replacement name of *Paulamys* for it. Musser *et al.* (1986) also provide additional observations on fossil dentaries and lower teeth of *P. naso,* younger than 4000 yr BP, collected in two caves in Manggarai District: Liang Soki, 15 km north of Ruteng and Liang Bua, 10-12 km northwest of Ruteng.

In October 1989 an expedition comprising staff from the Western Australian Museum and Museum Zoologicum Bogoriense, trapped a murid rodent with a long snout and short tail at Kelimutu, central south Flores. This specimen has dentaries and lower dentition that are very similar to *P. naso* and is herein tentatively referred to that taxon. It appears to be the first modern representative of the genus *Paulamys.* This paper provides a description of the Kelimutu specimen, and examines its taxonomic status.

Methodology

Measurement and descriptions

External measurements were recorded from the Kelimutu specimen, WAM M32000, following its preservation in 70% ethanol. Weight was taken in the field prior to fixation. Cranial and dental measurements were taken with dial calipers to the nearest one-hundreth millimetre. Measurement points are illustrated in Musser (1970a) and

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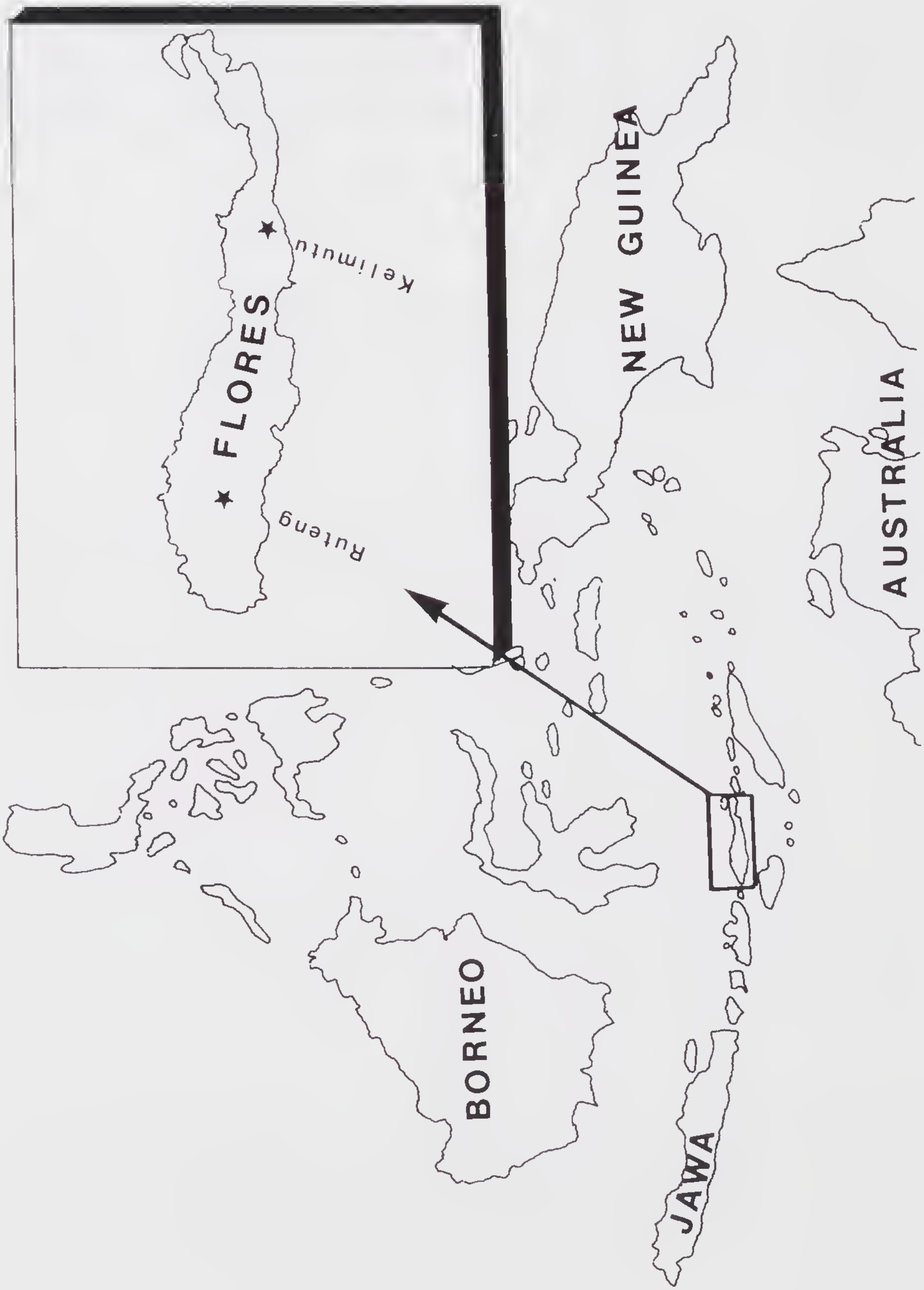

Figure 1. Map of Nusa Tenggara showing the collection locality of WAM M32000.

described in Musser and Newcomb (1983). Description of occlusal structure of teeth follows Musser and Newcomb's (1983: 333) modifications of the numbering system of Miller (1912) for upper molars, and of the nomenclature of Van de Weerd (1976) for lower molars. The terminology of cranial bones and foramina is that employed and illustrated by Musser (1981a, b).

Phylogenetic analysis

Phylogenetic relationships were examined between *Paulamys* sp. cf. *P. naso* and 13 genera — including *Rattus* and some other closely related genera — listed in Table 11 of Musser (1981a: 324), as well as *Bunomys* [described and illustrated in Musser and Newcomb (1983)].

Cladograms were constructed using the tree-building phylogenetic computer package HENNIG 86 (Farris, 1988). The search for the most parsimonious tree was conducted using a branch and bound routine, based on the WAGNER algorithm.

The polarity of the 29 character traits used in this analysis for most genera was taken from Musser (1981a, Table 11); character states for *Paulamys* sp. cf. *naso* and *Bunomys* were derived from the descriptions provided in Musser (1981a) to determine polarity of traits, checked against specimens of taxa he too had examined.

The tree was rooted using a hypothetical ancestor that was plesiomorphic for all 29 characters.

Colour: Pelage and skin colour where they follow Ridgway (1912) are capitalised.

Systematics

Paulamys sp. cf. *P. naso* (Musser, 1981)

The Kelimutu specimen

Western Australian Museum No. WAM M32000; juvenile or young adult male, body fixed in 10% formalin, preserved in 70% ethanol; skull and dentaries separate; collected in 'Break Back' commercial rat trap on 25 October 1989.

Collection Locality and Habitat

Near Kampong Woloara, *c.* 3 km from summit of Gunung Kelimutu, south-central Flores I. (8°42′, 121°54′), at *c.* 1600 m (Figure 1). Collected in dry creek bed (the entrance of which is shown in Figure 2) in dense tall rainforest dominated by large *Ficus* spp., *Zizyphus* sp., *Garuga* sp., *Erythrina, Albizzia* and *Myristica* sp. to 20-35 m in height. There was a scattered layer of *Rhododendron* sp. shrubs and a dense layer of ferns (one species with fronds up to 7 m long from a base almost at ground level). Vines were abundant throughout. Leaf litter in the dry creek was dense and from 30-50 cm deep. The road to the summit from the forestry department office (*c.* 7 km from the summit) went through 2-3 km of mixed kebun of coffee, pineapple, banana, and maize; then a narrow zone of *c.* 1 km of open rough grey barked *Eucalyptus urophylla* to a height of *c.* 15 m, over a dense low *Lantana*-like vegetation on black soil; before reaching the rainforest zone in which specimen WAM M32000 was collected. Above this zone were patches of *Casuarina junghuhniana* on open stony ground with patches of heath-like vegetation to 0.5 m in height.

Figure 2. Photograph of vegetation close to the place where WAM M32000 was collected.

Diagnosis

Paulamys sp. cf. *naso* is similar to the genus *Rattus* but differs from all other species of *Rattus* (*sensu* Musser and Newcomb (1983)) by having a combination of the following characteristics: body moderately large; tail much shorter than body length; rostrum exceptionally long; dorsolateral margins of braincase without prominent ridges; dorsolateral margin of interorbital region with only a slight beading; incisive foramina terminating posteriorly before anterior alveoli of first upper molar; posterior margin of palatal bridge terminates level with posterior edge of third upper molars and does not extend behind them to form a wide platform; mesopterygoid fossa wide, almost as wide as back of palatal bridge, its walls with moderately large, short, sphenopalatine vacuities; and cusp t_3 absent from second and third upper molars.

Apart from its body size, it may be distinguished readily by any one of the above characters from *Rattus* on Flores (*R. rattus, R. argentiventer, R. exulans* and *R. norvegicus*). (The skulls of these are illustrated in Musser and Newcomb (1983: 574-575.)

It is readily distinguished from other non-*Rattus* murids on Flores (two genera of which are known only from fossils) which are described and illustrated in detail in Musser (1981b). It differs from *Papagomys* in the following ways: it is much smaller in all measurements; the cranium of WAM M32000 is considerably more inflated; rostrum longer relative to greatest skull length; ridges on dorsolateral sides of braincase and posterorbital region absent; molar cusp morphology considerably simpler — lingual cusps on M^1 and M^2 less discrete; cusp t_3 absent on M^{1-2}; primary cusps on M_1 and M_2 not a tear-drop shape in cross section and cusps less discrete.

It differs from the fossil taxon *Hooijeromys* spp. (known only from its dentition) in the following ways: it is considerably smaller; cusp t_2 on M^1 is not 'gourd-shaped'; incisive foramina do not extend posterior to anterior margins of M^1; zygomatic plate arises from maxilla at a point near the middle of M^1 rather than near posterior edge of M^2.

It differs from *Spelaeomys florensis* (described from fossil maxillary fragments and mandibles, all with teeth) in having much smaller teeth with a simple rather than elaborate occlusal pattern. In *S. florensis* upper molars are high crowned and individual cusps are discrete and remain separate even after appreciable wear; molars overlap considerably rather than only very slightly.

It differs from *Komodomys rintjanus* in that the dorsal fur is not spinous; the rostrum flattened such that dorsal profile of cranium not strongly arched from nasal tip to occiput; rostrum much longer relative to cranium; top of skull much more inflated (not nearly flat); zygomatic plate narrower, without anterior spines; interparietal wider anteroposteriorly; incisive foramina shorter, terminates posteriorly before M^1 anterior edge; mesopterygoid fossa wider relative to posterior palate width; molar teeth simple, not high coned; labial cusps on second row of M^1 closely applied to adjacent medial cusp and not set apart; M_2 not appreciably wider than M_1.

Description of *Paulamys* sp. cf. *P. naso* specimen WAM M32000

Measurements (in mm) are as follows

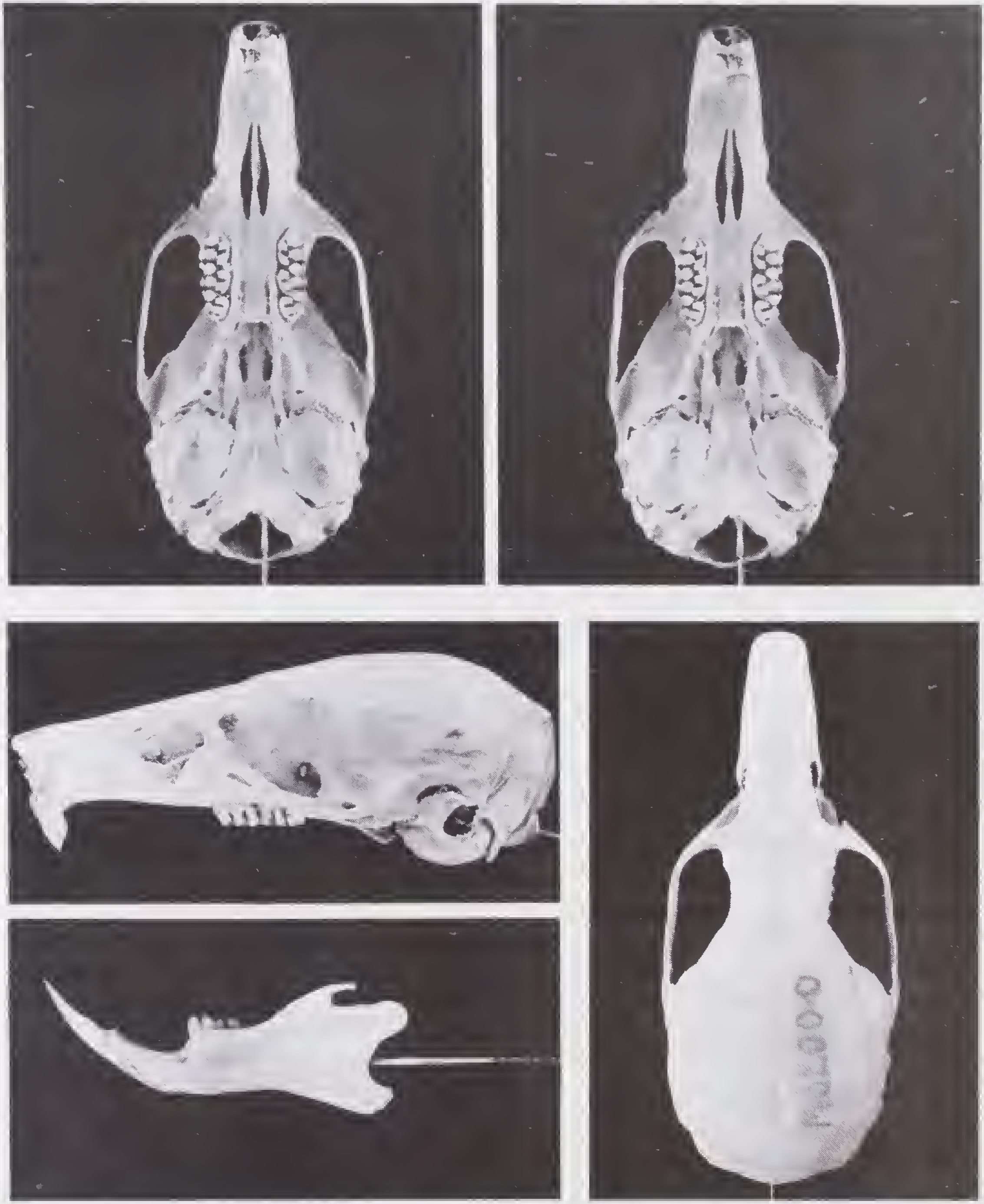

Figure 3. Photographs of skull, dentary and teeth of WAM M32000, ventral aspect of cranium as stereopairs.

Tip of rhinarium to vent length 164; distal tip of tail to vent length 117; hind foot length 39.3; ear length 24.2; greatest skull length 41.88; zygomatic breadth 18.66; interorbital breadth 6.74; braincase breadth 16.74; braincase height 13.03; nasal length 15.94; rostrum length 14.90; rostrum breadth 6.50; rostral tube length anterior to I^1 1.90; zygomatic plate breadth 3.97; breadth across upper incisor tips 1.85; diastema length 11.77; palatal length 21.46; postpalatal length 14.34; incisive foramen length 7.37; incisive foramina breadth 2.22; incisive foramen posterior to anterior edge M^1 cusp 0.49; palatal bridge length 7.82; palatal bridge breadth at M^3 3.86; mesopterygoid fossa breadth 2.88; bulla length 7.04; bulla height 6.93; M^{1-3} crown length 7.11; M^{1-3} alveolar length 7.30; M^1 length 3.58; M^1 breadth 2.35; dentary and incisor length 26.64; dentary length 23.40; dentary height 10.44; M_{1-3} crown length 7.15; M_{1-3} alveoli length 7.14; M_1 breadth 1.97; M_2 breadth 2.09; M_3 breath 1.83; incisor breadth at point emergent from ramus 0.87. Also weight 122 gm, and rows of scales on tail per cm (at one-third tail length from base) 13.

Skull

Cranium of moderate size. Its distinctive features (Figures 3) are: elongate rostrum with dorsal profile in lateral view straight and moderately sharply inflected at interorbital region immediately behind nasal-frontal sutures (where frontal is inflated as two low globose structures); rostrum distal end slightly inflated and elevated dorsally to form narrow rostral tube that extends 1.9 mm anterior to canines; braincase oval; interparietal moderately long anteroposteriorly, anterior margin abuts with slight intrusion between parietals; orbit dorsolateral margins with weak beading but such margins of postorbital region and braincase smooth; braincase lateral surface almost vertical from dorsolateral margin of cranium to squamosal root of zygomatic arch; interorbital region moderately wide; narrow zygomatic plate, slope forward gently from zygomatic arch anterodorsal root, anterior marginal projection absent; incisive foramen moderately long, spindle-shaped, posteriorly terminate 0.49 mm anterior to M^1 anterior cusp; palatal bridge moderately wide, terminating posteriorly at M^3 posterior edge; mesopterygoid fossa moderately wide, its walls penetrated by an oval-shaped sphenopalatine vacuity about 3 mm long; pterygoid fossa concave, tilted towards skull midline, penetrated by moderately large interpterygoid foramen; bulla large but because of elongate rostrum only *c.* 17 percent of greatest skull length, eustachian tube short, jagged distally; alisphenoid canal open, not concealed by strut of alisphenoid bone; zygomatic arch squamosal root set halfway down braincase; squamosal root with low horizontal posterior ridge extending about 3mm, but terminating well short of occiput; parietal-squamosal suture strongly sinusoidal-shaped above squamosal root; postglenoid foramen moderately large, lateral margin posterior to foramen ovale with definite ridge.

Dentary

Dentary (Figure 3) with coronoid process slender and low; ramus slender and moderately long; posterior margin between condyloid and angular process concave, shallow; angular process ventral surface tilted to form a moderately wide internal shelf; capsular projection on outside surface at end of incisor smooth; mental foramen moderately large, immediately anterior to junction of masseteric ridges; dorsal masseteric ridge weak, low; ventral masseteric ridge strong; shelf-like ridge extends from behind M_3 in gentle arc below alveolar line of molars to base of condylar process; large oval mandibular foramen at base of condylar process close but dorsal to above shelf-like ridge.

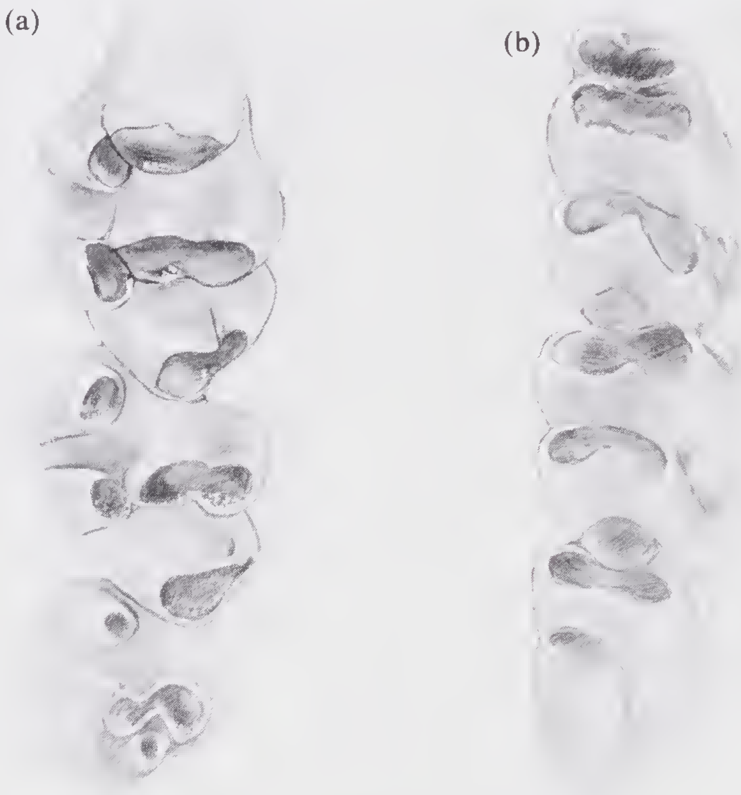

Figure 4. Drawings of occlusal surface of molar rows WAM M32000, (a) upper and (b) lower.

Dentition

WAM M32000 has moderately large brachydont molars, simple occlusal patterns, cusps broadly united to form rows of laminae; laminae gently sloping such that teeth are slightly overlapped by immediate anterior teeth (Figures 3 and 4); M^1 apparently with five roots (anterior, posterior, labial and two lingual); the first three of these roots are obvious externally and through x-ray photographs — the lingual roots are less clear but appear to be separate rather than a single bi-lobed root. M^2 apparently with four roots, the anterior, posterior and labial roots are clear on x-ray photographs; a lingual root is less clear but an alveoli is seen to take this root. M^1 oval-shaped, anterior lamina formed from a small cusp t1 loosely fused with a large cusp t2 (cusp t3 absent); middle lamina weakly chevron-shaped, cusp t4 moderately large and weakly merged to cusp t5, cusp t6 strongly fused to cusp t5 (cusp t7 absent), cusp t8 large and fused with small cusp t9; cusp t9 squarish, with trace of ridge on anterior face. M^2 broad, consists primarily of large cusp t1 (weakly pressed against M^1 cusp t8) and t8 (merged with very small cusp t9); cusp t9 with small low ridge on anterior face; middle lamina composed of merged cusps t4, t5 and t6, almost straight, cusp t4 more distinct than cusp t6 from central cusp. M^3 with cusp t1 moderately large, discrete, loosely against M^2 cusp t8; middle lamina slightly chevron-shaped; small posterior (cusp t8?). Upper incisors opisthodont, enamel orange.

Occlusal surface of lower molars with oblong outline, surface area decreases evenly from M_1 to M_3. M_1 anterior lamina from fusion of approximately equal sized anterior lingual and labial cusps; broadly adpressed with similar lamina formed from fusion of metaconid and protoconid; posterior lamina more chevron-shaped, formed from fusion of entoconid and hypoconid — the latter cusp with a moderately large posterior labial cusplet; posterior cingulum distinct. M_2 anterior lamina almost straight, formed from metaconid and protoconid, closely adpressed to protoconid is a moderately large anterior labial cusp; second lamina weakly chevron-shaped, has a small posterior labial cusplet; posterior cingulum distinct; M_2 slightly broader than M_1. M_3 anterior lamina straight; small low anterolabial cusp (not visible from occlusal view); and small low posterior labial cusplet on right side only.

Pelage and skin

Fur long and soft; dominant colour of dorsum Brownish Olive flecked with Isabella Color (light brown) and Bister (deep brown); venter, chest and throat a lighter grey. Dorsum hairs with basal two-thirds Pale Quaker Drab (light lilac-grey), middle section Brownish Olive tipped variously with: Isabella Color on back — hairs moderately long (15 mm); Cinnamon on shoulders and head; Chamois on flanks (hairs up to 10 mm long); and Bister on rump. Guard hairs long, particularly on rump where they are Sepia and up to 35 mm long; on flank shorter (up to 20 mm), grey.

On venter, chest and throat, hairs moderately long (up to 13 mm), Pale Quaker Drab. Immediately behind mouth and on cheek light dense hairs of Tilleul-Buff (light pink-cream), contrasts sharply with darker hairs of face and head.

Tail with moderately dense hairs, up to 3 mm long, on dorsal surface Chaetura Drab (black-brown), on ventral surface Light Drab (lilac-grey); scales bicoloured, background Pale Vinaceous Fawn (light pink-cream) with central square of Black.

Skin of lips, dorsal surface of hands and feet Vinaceous Buff (pink-cream); on manus main dorsal surface lightly covered with Olive Brown hair but fingers with sparse White hair; hair on pes dorsal surface and toes Olive Brown; pes plantar surface Deep Brownish Drab (dark lilac-brown), ears Chaetura Drab.

Pes and manus

Typically *Rattus*-like. Manus claws moderately long (4 mm), pollex with nail, all pads prominent; three interdigital pads: outer and inner kidney-shaped, central pad triangular-shaped, thenar pad approximately one-half area of hypothenar — both moderately large (Figure 5). Pes with moderate pads, all raised, smooth, without lamellae or ridges — although with a lamellae-like pattern to skin pigmentation; inner

Figure 5. Photograph of plantar surface of pes of WAM M32000.

plantar pad long, 5.5 mm, outer plantar pad 2.4 mm behind nearest interdigital pad and approximately three-quarters size of this front pad; outer interdigital pad broadly kidney-shaped with smaller posterolateral subcircular accessory pad.

Tail

Tail very short (Figure 6), 71 percent of tip of rhinarium to vent length; approximately 13 scale rows per cm and 19 scales around circumference at a position of one-third length of tail from its base; hair length at this position approximately equal to two and one-half times the length of a scale.

Vibrissae

On each side of face approximately 10 very long (up to 60 mm) mystacial vibrissae, dark coloured above lips, lighter closer to lips; three moderately long (up to 40 mm) dark supraciliary vibrissae; two dark genal vibrissae (up to 15 mm long); numerous short (up to 10 mm) white interramal and submental vibrissae; six short (up to 11 mm), white, ulnar carpal vibrissae; four short (up to 11 mm), white, medial antebrachial vibrissae; approximately four short (up to 13 mm), white anconeal vibrissae; and two short (*c*. 4 mm), white calcaneal vibrissae.

Figure 6. Photographs of carcase of WAM M32000.

Diet and Habits

Musser (1981b: 130) speculated that *P. naso* was "likely terrestrial and could have included fungi, insects, snails, earthworms and possibly some fruit in its diet (by analogy with species of *Bunomys*)". The specimen WAM M32000 confirms in part this speculation. It had a full stomach when collected which contained: several oligochaete worms; two insect larva (possibly lepidopteran); a considerable quantity of unidentifiable plant matter (much of which is probably subterranean because it frequently had rootlets and root hairs attached); corms (probably immature) were abundant and may constitute much of the unidentified vegetable matter; several small seeds; several fragments thought to be fungal; and a few fragments of insects (including probable Hymenoptera, a beetle larva and a possible small centipede) the insects were in such small quantity that they may have been ingested incidentally.

The shape of the pads on the pes and manus and the absence of striations on these pads suggest the species is terrestrial. As it was collected in dense rainforest in an area with deep leaf-litter its diet would suggest that *Paulamys* sp. cf. *P. naso* feeds on the ground, using its long snout, and claws, to dig for a variety of food among leaf litter or just beneath the soil.

Identification of WAM M32000

The specimen WAM M32000 appears closely related to the taxon *Paulamys naso*. Its dentary is of a similar shape in that the ramus in front of M_1 is long, there is a prominent lingual shelf-like ridge extending from behind the molar row which slants gradually upwards to the base of the condylar process. Dorsal to this ridge and near the base of the condylar process is a large oval mandibular foramen. Further, the shape of the lower molars and the lamina, particularly the first lamina on M_1 and the slim incisors are all said by Musser (1981b) to be characteristic of *P. naso*.

The specific identity of WAM M32000 is difficult to determine, however, because even with a good series of specimens of modern murid taxa, some species are difficult to distinguish using mandibles alone. Further some diagnostic characters, such as presence or absence of lower molar cusplets are very variable within species (Musser and Newcomb 1983) and within individuals — for example, WAM M32000 has a small posterior labial cusplet on M_3 in the right dentary, but not on the left one. Our comparison is further complicated because we have only a single modern specimen and we are comparing it with fragmentary mandibular material which may be *c.* 4000 yr old. Altitudenal variation is not thought to be a factor as the earlier specimens from the Menggarai District were collected from a similar altitude as was WAM M32000.

Further, doubt as to whether WAM M32000 represents *P. naso* relates to its slightly smaller teeth. While the breadth of WAM M32000 are similar to values of *P. naso* given by Musser *et al.* (1986, Table 1), its M_{1-3} crown length of 7.15 is less than the range given for *P. naso* (7.3-7.6); its M_{1-3} alveolar length is smaller 7.14 versus 7.5-8.1, and its lower incisors at the point where they are emergent from the dentary sheath is narrower 0.87 versus 1.0-1.2. These lower values of WAM M32000 are unlikely to result from the specimen being younger than the *P. naso* specimens of Musser *et al.* (1986) because the wear on its teeth is approximately intermediate between that figured for two specimens (LB90 and LS9) by Musser *et al.* (1986) which are included in the above range of values for *P. naso*. Finally the dorsal masseteric ridge of WAM M32000 is weak and not "strong" as stated and figured by Musser *et al.* (1986: 4-6) for comparatively aged animals.

Given these uncertainties we hesitate to refer this modern specimen to *P. naso*. Confirmation will probably require discovery of maxillary dentition of *P. naso*.

The generic status of WAM M32000 is discussed later in this paper.

Relationships of *Paulamys*

Musser (1981b) proposed 29 characters which he used for primary analysis of systematic relationships of *Rattus* and other closely related genera. Because both Hooijer (1967) and Musser (1972b) originally determined the fossil fragments of *Paulamys naso* as *Rattus* we have used these 29 characters for our appraisal of the relationships of WAM M32000. In this analysis we include, in addition to genera considered by Musser (1981a) and Musser *et al.* (1986) to be close to both *Rattus* and *Paulamys, Apodemus* and *Arvicanthis.* Both these latter two genera are traditionally recognised as distinct from *Rattus* by Misonne (1969) and Ellerman (1941). While the largely African *Arvicanthis* is considered close to *Rattus* by Jacobs (1978) he places *Apodemus* in a different section of the murid radiation from both *Arvicanthis* and *Rattus.*

The phylogenetic tree constructed using WAM M32000, *Rattus* and 12 other genera was produced (Figure 7). This tree would appear to be reasonably stable: only one tree was produced by the exhaustive branch and bound analyses and the Consistency Index of 0.55 indicates a relatively low level of homoplasy. Characters used to create this tree include the number of roots on M^1 and M_1. These appear to be 5 and 4 respectively in WAM M32000. However if these two characters are left out or placed in the analysis as unknown characters, the topology of the tree remains as in Figure 7. This tree indicates that of the genera considered, *Paulamys* is closest to *Bunomys* but is also closely related to *Rattus* and *Arvicanthis.*

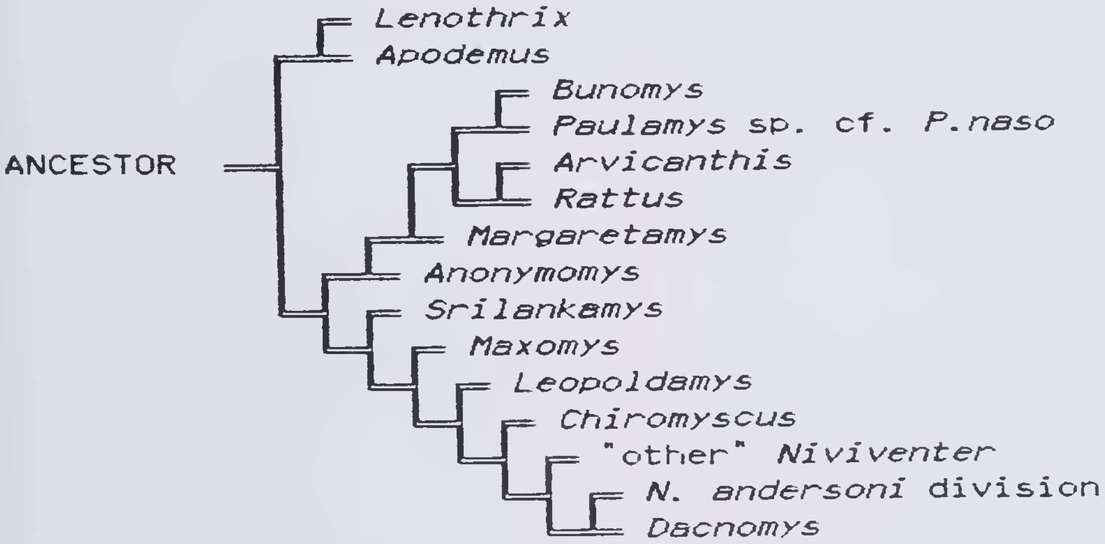

Figure 7. Cladogram of relationships between *Paulamys* sp. cf. *P. naso* and other genera, in part derived from data in Musser (1981a) and Musser and Newcomb (1983).

Paulamys and *Rattus*

The Kelimuta specimen WAM M32000 shares the same polarity for these characters states as *Rattus* for 24 of the 29 listed characters. It differs as follows: *Character 2* (plesiomorphic in WAM M32000) dorsolateral margins of the braincase proper of WAM M32000 is smooth, rather than medium to high ridges or shelves; *Character 8* (plesiomorphic in WAM M32000): incisive foramina are short in WAM M32000, terminating well before the maxillary toothrows, rather than projecting to the anterior edge of M^1 or posterior to this edge; *Character 9* (plesiomorphic in WAM M32000): posterior rim of the palatal bridge is situated level with the posterior margins of M^3 in WAM M32000 rather than projecting way beyond M^3 to form a wide platform behind the molar rows; *Character 10* (plesiomorphic in WAM M32000): mesopterygoid fossa is nearly as wide as the back of the palatal bridge and its wall is breached by a moderate, short sphenopalatine vacuity in WAM M32000 rather than having the mesopterygoid fossa one-third to one-half the width of the palatal bridge and the sphenopalatine vacuities huge so as the presphenoid and anterior part of the basisphenoid appear suspended in air; *Character 23* (plesiomorphic in WAM M32000): cusp t3 absent from M^2 and M^3 in WAM M32000 rather than almost always present on M^2 and often on M^3.

It should be noted, however, that the character states given to characters 2, 8, 9, 10 and 23 above for *Rattus* are not unequivocal for they appear to refer only to the Sundaic 'core' taxa. For example, Character 2: there are species of *Rattus* (e.g., *niobe* and *verecundus*) where the dorsolateral margins of the braincase proper are smooth; *Character 8:* some species of *Rattus* (e.g. *ceramicus*) have extremely short incisive foramen that terminate well in front of anterior edge of M^1; *Character 10:* some species of *Rattus* have sphenopalatine foramen similar to WAM M32000 and *Character 23:* as stated by Musser (1981b) cusp t3 is not always present on M^2 and M^3 in *Rattus.*

It appears that the only robust character separating WAM M32000 from other *Rattus* spp. is Character 9, which is the extremely long palatal bridge, such that it does not form a wide platform behind the molar rows. However, it has been pointed out to us (K. Aplin pers. comm.) that this may be a function of the steeply angled aspect of the long rostrum relative to basicranial axis of WAM M32000, which makes an extremely sharp angle and would by necessity create crowding at the posterior palatal region and lead to its shortened state.

Ellerman (1941) and Misonne (1969) made substantial and important attempts to clarify the members of the genus *Rattus.* Musser (1970b) discussed the scope of *Rattus* as proposed by these earlier workers and subsequently, with his co-workers, greatly contracted the membership of *Rattus* by establishing a series of new genera, some of which are only distantly related to *Rattus* (Musser *et al.* 1979; Musser 1981a, b; Musser and Newcomb 1983). In the meantime a number of new species have been described as belonging within *Rattus* and there has been a clarification of the status of a number of putative species of this genus (Musser 1970a, b; 1971; 1972a; 1973a, b; Musser and Boeadi 1980; Musser and Califia 1982; Taylor, Calaby and Van Deusen 1982; Musser and Heaney 1985; Musser 1986). As a consequence of these studies the number of native species of Indo-Australian *Rattus* was placed at 50 by Musser and Newcomb (1983), although several additional species have been added since that time (Musser and Heaney 1985; Musser 1986).

Despite the considerable attention given to revisionary studies on *Rattus* in recent years, the statement by Musser and Boeadi (1980) that there was no stable definition and diagnosis of *Rattus* still holds. For example, Musser and Newcomb (1983) state that "the monophyly of *Rattus* has yet to be determined. Some groups of species may eventually be disassociated from *Rattus,* such as the native species in the Australian and New Guinea region."

The zoogeography of *Rattus* in the Indo-Australian region has been discussed by Musser and Newcomb (1983). They draw attention to the absence of known endemic *Rattus* in the Lesser Sunda islands (Nusa Tenggara), an unusual situation given the presence of diverse *Rattus* faunas on the Sunda Shelf to the west and Australia and New Guinea to the east. The species of *Rattus* recorded from Nusa Tenggara are all considered by Musser (1981b) to be introduced to the region (*R. rattus, R. norvegicus, R. exulans* and *R. argentiventer*). Musser (1981b: 169) raised the possibility that the *Rattus*-like features characterising Australian and New Guinea species may have been independently derived from those that define Asian mainland *Rattus.* Most interestingly, he thought it possible that the Australian and New Guinea *Rattus* "evolved from a *Rattus*-like ancestral stock that was characterised by a suite of derived cranial and dental features similar to those found in some of the *Rattus*-like genera on Flores". If this possibility were correct then he continued by suggesting that native species of *Rattus* may not be found in Nusa Tenggara.

It is of interest that WAM M32000 appears to be closer in some ways to the New Guinea species *R. verecundus* and *R. niobe* and to the Seram species *R. ceramicus.* The species *verecundus* and *niobe* are examples of *Stenomys,* recognised as a genus by Thomas (1910), Tate (1936) and Rümmler (1938) and as a subgenus of *Rattus* by Ellerman (1941, 1949); Tate (1951); Misonne (1969). The distinctive species *ceramicus* was placed in the genus *Nesoromys* by Thomas (1922). *Nesoromys* is included in *Stenomys* by some authors (Rümmler, 1938; Musser, 1981b) but not by others (Tate 1936; Laurie and Hill, 1954; Misonne, 1969). Ellerman (1947-1948) separated the subgenus *Stenomys* from other subgenera of *Rattus* using the key character that their bulla was less than 15 percent of occipitonasal length (WAM M32000 is *c.* 17 percent). *Stenomys* was restricted to species that occur in New Guinea, western and southern Australia, Gaudalcanal, Bougainville and smaller islands in the New Guinea region by Misonne (1969). Musser and Newcomb (1983) would contract Missone's (1969) concept of *Stenomys* to exclude some species, and would positively place only *Rattus verecundus, R. niobe* and *R. richardsoni* in this subgenus — a situation they considered to be supported by Taylor, Calaby and Van Deusen (1982) as a cluster. Musser and Newcomb (1983) would restrict *Stenomys* to Seram and the New Guinea area (and Cape York if *R. leucopus* belongs to *Stenomys*). Ongoing studies by Baverstock, Aplin and others suggest that Australian-New Guinea *Rattus* represent a monophyletic grouping within *Rattus.* Based on a phylogenetic analysis of isozyme electrophoresis and microcomplement fixation of albumin data, Baverstock *et al.* (1986) have shown that *R. leucopus* and other Australian *Rattus* are monophyletic with respect to *R. rattus* and *R. norvegicus* — which are members of the 'core' *Rattus* group of Musser and Newcomb (1983). Furthermore, as yet unpublished electrophoretic data and morphological data (K. Aplin *pers. comm.*) show that *R. leucopus* is very close to members of other New Guinea species including *R. verecundus, R. niobe, R. steini* etc. The clear implication is that if *Stenomys* is a valid unit, it would have to include all Australian and probably all New Guinea *Rattus.*

The systematic status and relationship of *Paulamys* will be difficult to resolve fully without a clearer definition of the relationship of taxa still placed within *Rattus,* in particular the position of the Australian and New Guinea *Rattus* assemblage.

Paulamys and Bunomys

Musser (1981b: 117) considered that the occlusal configuration of the lower molars in *P. naso* is similar to that in *Bunomys,* a genus of rats, restricted to Sulawesi ranging from lowland to mountain forests including the central part and southwestern peninsula and associated islands. He states that the teeth of *B. fratrorum* are most like those of *F. naso* but differ in being "slightly larger ... the laminae are thicker and set closer, so they touch each other; ... anterolabial cusps are usually missing from the second molars ... all the cusplets and anterolabial cusps in *B. fratrorum* are low, small, and merge with the laminae at an early stage of wear to lose their definitions quickly, whereas the cusplets and anterolabial cusps remain discrete in *F.* (=*P.*) *naso,* the anterolingual and anterolabial cusps forming the anterior lamina of the first molar are dissimilar in size and after little wear coalesce into a high oblong surface that is narrower than the second lamina but flush with its anterior margin, a configuration unlike that in *F.* (=*P.*) *naso".*

The new material of *P. naso* described by Musser *et al.* (1986) — and the Kelimutu specimen WAM M32000 — blurs some of these distinctions between *Bunomys* and *Paulamys.* For example, Musser *et al.* (1986: Figure 3) and Figure 4, this paper, indicate that the anterior lamina of M_1 does not always contact the second lamina such that these two lamina are separated by a wide angular space on both the labial and lingual sides of the tooth. Further, the shape of the first lamina on M_1 is not so dissimilar between *P. naso* and species of *Bunomys* [compare Musser and Newcomb (1983: Figure 31D) and Musser *et al.* (1986, Figure 3B)]; the laminae of lower molars of *B. fratrorum* are also set further apart.

Musser and Newcomb (1983: 117) also states that *Bunomys* spp. have slender dentaries, with a low ramus and a short segment in front of the tooth row. The illustrations of the dentaries of four species of *Bunomys* in Musser and Newcomb (1983: Figure 29), and our examination of *B. chrysocomus* specimen WAM M27810, indicate that the dentaries are not particularly slender in comparison with WAM M32000, although they have a more erect coronoid process and a relatively shorter dentary ramus anterior to M_1. Musser and Newcomb (1983: 117) also state that *Bunomys* have a large toothrow set in a small dentary rather than the converse as in *P. naso.* The configuration in WAM M32000 indicates that the relationship of the toothrow to the size of the dentary is not dissimilar to that of *B. chrysocomus* (WAM M27810, Central Sulawesi) and this appears to be also the case in *B. fratrorum* which has similar length lower tooth row to WAM M32000 and a slightly larger dentary (see Musser and Newcomb 1983, Table 11 and Figure 29E).

The cusp morphology of the upper tooth row of WAM M32000 is also very similar to that illustrated in Musser and Newcomb (1983: Table 12 Figure 30) for *B. chrysocomus, B. andrewsi, B. penitus* and *B. fratrorum* and there are no consistent differences in cusps or cusplets.

The general configuration of the skull of WAM M32000 is similar to that of *Bunomys* [see description of *Bunomys* in Musser and Newcomb (1983: 393-395)]. For example, the incisive foramen is short, terminating in front of M^1, the palate terminates approximately level with the posterior margin of M^3; dorsolateral margin of braincase is without prominent ridges; zygomatic plate, mesopterygoid fossa, interparietal, and sphenopalatine vacuities in the sides of the mesopterygoid fossa are similar in shape. The rostrum of *Bunomys* and WAM M32000 are of similar length [see data in Musser and Newcomb (1983: Table 11)]. For example: the ratio of rostrum length to greatest skull length in WAM M32000 is 0.356 compared to 0.413 (*B. chrysocomus*), 0.360 (*B. andrewsi*), 0.380 (*B. penitus*) and 0.354 (*B. fratrorum*); bulla length to greatest skull length in WAM M32000 is 0.168 compared to 0.193 (*B. c.*), 0.154 (*B. a*), 0.156 (*B. p.*) and 0.138 (*B. f.*). The rostrum of WAM M32000 is, however, narrower than the rostrum of species of *Bunomys* figured in Musser and Newcomb (1983: Figure 29).

External appearance of WAM M32000 is not dissimilar to Bunomys which also have a short-tail (ranging in length from 83 to 87% of body length in *Bunomys chrysocomus, B. andrewsi, B. penitus*) or tail subequal to body length as in *B. fratrorum;* long hair, and moderately long face.

From Figure 7 it is seen that *Bunomys* and *Paulamys* sp. cf. *P. naso* are very closely related, and in fact share the same polarity for all 29 character states.

Conclusion

The distribution of *Bunomys* which includes the southwestern Peninsula of Sulawesi and offshore islands (Musser and Newcomb 1983) places it in reasonably close geographic proximity to *Paulamys.* On the basis of our rather limited material we can determine no reliable characters that enable us to distinguish *Paulamys* from *Bunomys.* Clearly members of these genera are very closely related as indicated by Musser and Newcomb (1983) and Musser *et al.* (1986). Additional modern specimens are required of *Paulamys* to further examine its systematic status and relationships, particularly with Australian and New Guinea *Rattus, Bunomys* and other closely related genera such as the essentially Indo-Chinese genus *Berylmys.*

Acknowledgements

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Pseudantechinus mimulus (Thomas, 1906) (Marsupialia, Dasyuridae): rediscovery and redescription.

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Abstract

Before the collection in 1967 of three specimens of *Pseudantechinus mimulus* from North I., Sir Edward Pellew Group, Northern Territory (*c.* 15°37′S, 136°53′E), the species was known only from the holotype collected 62 years earlier from Alexandria (*c.* 19°S, 137°E), approximately 300 km to the south of the Pellew Group. This paper redescribes *P. mimulus* and diagnoses it against other *Pseudantechinus* spp.

Introduction

In September 1988, Dr John Calaby, CSIRO, Division of Wildlife and Ecology, Canberra, forwarded to me three specimens of *Pseudantechinus* from North I., N.T., which differed from the forms of *Pseudantechinus* currently recognised: *P. ningbing* Kitchener, 1988; *P. bilarni* (Johnson, 1954); *P. macdonnellensis* (Spencer, 1896) and *P. woolleyae* Kitchener and Caputi, 1988.

These specimens from North I. closely accorded in skull, dental and external measurements and pelage colouration to the type description of *Phascogale mimulus* by Thomas (1906: 541-2) and to the additional notes on the holotype of *P. mimulus* by Tate (1947: 139) who recognised this form as a *Pseudantechinus* species. While most recent authors (e.g. Mahoney and Ride 1988) synonymise *Phascogale mimulus* with *P. macdonnellensis* (which they place in the genus *Parantechinus*), Kitchener and Caputi (1988: 46) indicated doubt on that taxonomic placement.

Regrettably, I am unable to directly compare the North I. *Pseudantechinus* specimens with the only other known specimen, the holotype, which is at the British Museum (Natural History) and is not available for loan. Fortunately, Mr Laurie Smith, Western Australian Museum, kindly compared one of these specimens (CM 3921) with the holotype and Ms Paula Jenkins, British Museum (Natural History) also kindly examined aspects of the skull of the holotype for me, and made available to me photographs of the skull for study.

Materials and methods

Measurements (all in mm)

Description of morphology follows Archer (1981). Tooth number follows Archer (1978). Cranial and external points used for measurements also follow Archer (1981) with the exception of three additional measurements, asterisked (*) below. Nineteen measurements of skull and dental characters, four of external body characters (in mm)

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and weight (in gms) were recorded from adult specimens and in the Description sections. Abbreviation for these measurements are as follows: MAXL, maximum skull length; BASCRANL, basicranial length; MSKH, maximum skull height; MSKW, width across zygoma; OBUL, outside bullae distance; INBUL, inside bullae distance; BULTOT*, length of tympanic wing of alisphenoid and periotic, from posterior lacerate foramen to anterior edge of alisphenoid wing; BULPER*, length of periotic tympanic wing from lacerate foramen to contact point with alisphenoid tympanic wing, measured in the same line as for BULTOT; C^1-M^5, M^2-M^5, I_1-M_5, M_2-M_5 crown lengths; RM^4-LM^4, width outside crowns; INORB, minimum interorbital width; MAXVAC*, maximum length of maxillary palatal vacuity; NASL, nasal length; DC-I_1 *dentary condyle to* I_1; ANGCON, tip of angular process to articular condyle; CONRAM, articular condyle to anterior border of ascending ramus; NV, tip of rhinarium to vent length; TV, tail tip to vent length; HF, hind foot length; EAR, ear height from notch; WT, weight.

Pelage and skin

Colour of pelage, when capitalised, follows Ridgway (1912). Specimens were regarded as adult if M^5 and P3 were fully erupted and basicranial sutures fully ossified. Only adults were included in the statistical comparison.

Taxonomy

Pseudantechinus mimulus (Thomas, 1906)

Table 1, Figures 1-4

Phascogale mimulus Thomas, 1906, Proc. Zool. Soc. Lond. 2: 536-43.

Holotype

British Museum Number (BM) 6.3.9.75, adult female, from near Alexandria (19°03′S, 136°42′E), Northern Territory, collected by Mr W. Stalker in 1905.

Diagnosis

Distinguished from other *Pseudantechinus* spp. by having a combination of: squamosal and frontal sutures of lateral cranium not in contact or close, P^3 more than 1/2 occlusal surface area of P^2, tail subequal to vent length and M^2 stylar cusp B low, fused with parastyle.

Pseudantechinus mimulus differs from *P. ningbing* in averaging smaller in skull, dental and external characters and having shorter: nasal (NASL) 8.9 (8.7-9.0) *v.* 10.2 (9.5-11.2) and I_1-M_5 11.0 (10.9-11.1) *v.* 12.2 (11.6-13.0); bulla length (BULTOT) shorter relative to maximum skull length; outside bulla length (OBUL) also shorter relative to MAXL (Figure 3); periotic tympanic wing larger compared to alisphenoid tympanic wing — periotic slightly more inflated, alisphenoid less inflated; small spike on lateral surface of alisphenoid tympanic bulla immediately anterior to postglenoid process present rather than usually absent or occasionally rudamentary; P^3 larger relative to P^2 usually 1/2 to 3/4 rather than <1/2 occlusal surface area of P^2; squamosal and frontal sutures of lateral cranium not close rather than usually in contact or close; tail more heavily furred.

Table 1: Measurements of *Pseudantechinus mimulus* holotype (externals from 'spirit') and specimens from North I. (externals when recently dead). Mean and range of measurements for other *Pseudantechinus* species are from Kitchener and Caputi (1988: Table 2). Explanation of character codes in Methods.

		North Island						
MUSEUM	BM	CM	CM	CM				
NUMBER	6.3.9.75	3921	2697	2894	*P. ningbing*	*P. bilarni*	*P. macdonnellensis*	*P. woolleyae*
SEX	♀	♂	♂	♀				
SKULL AND DENTARY CHARACTERS								
MAXL	24.7	24.8	25.5	25.4	27.1 (25.5-29.1)	28.3 (26.3-30.5)	27.5 (25.9-29.7)	29.9 (28.0-31.2)
BASCRANL	22	22.8	23.3	23.3	24.9 (23.3-27.1)	26.0 (24.0-28.2)	25.3 (23.4-27.0)	27.5 (25.6-28.7)
MSKH	5.6	6.3	6.6	6.4	6.7 (6.3- 7.1)	7.0 (6.4- 7.4)	6.7 (6.2- 7.2)	7.1 (6.8- 7.4)
MSKW	14.6	14.7	15.8	15.0	15.6 (14.6-17.0)	16.6 (15.0-18.4)	15.9 (14.9-17.0)	17.2 (15.9-18.7)
BULPER	2.0+	2.6	3.2	3.1	3.0 (2.5- 3.5)	2.7 (2.3- 2.9)	3.1 (2.7- 3.5)	3.8 (3.3- 4.3)
BULTOT	5.8	5.3	5.9	5.5	5.9 (5.5- 6.5)	5.9 (5.5- 6.3)	6.5 (6.0- 7.0)	7.6 (7.1- 8.2)
OBUL		10.8	11.6	11.0	11.1 (10.5-11.9)	11.6 (10.7-12.5)	11.6 (10.8-12.3)	12.9 (12.4-13.4)
INBUL		3.2	3.2	3.4	3.1 (2.8- 3.8)	3.5 (3.2- 3.9)	2.9 (2.1- 3.4)	2.8 (2.4- 3.3)
C^1-M^5		9.5	9.6	9.7	10.2 (9.0-10.9)	10.7 (10.0-11.4)	10.2 (9.3-10.7)	11.3 (10.8-11.6)
M^2-M^5		6.1	6.2	6.3	6.2 (5.8- 6.8)	6.5 (6.1- 7.2)	6.4 (5.8- 6.8)	6.7 (6.3- 7.1)
RM^4-LM^4	8.8	8.6	8.6	8.6	8.7 (8.2- 9.4)	9.1 (8.0- 9.7)	8.8 (8.3- 9.3)	9.6 (9.1-10.3)
INORB	5.3	5.1	5.2	5.3	5.5 (5.0- 6.2)	5.8 (5.4- 6.2)	5.2 (4.6- 5.7)	5.9 (5.5- 6.2)
MAXVAC		3.2	3.5	3.4	3.6 (2.4- 4.3)	2.8 (2.2- 3.8)	3.8 (2.8- 4.4)	3.9 (2.9- 4.7)
NASL	9	8.7	9.0	8.9	10.2 (9.5-11.2)	10.6 (9.3-11.6)	10.1 (8.6-11.4)	10.8 (9.0-11.4)
DC-I_1		18.0	18.9	18.6	19.6 (18.5-21.5)	20.6 (19.1-22.4)	20.1 (18.8-21.4)	21.7 (19.9-22.8)
I_1-M_5		11.0	11.1	10.9	12.2 (11.6-13.0)	12.8 (11.6-13.6)	12.2 (10.4-12.9)	13.4 (12.6-13.9)
M_2-M_5		6.8	6.8	6.9	7.0 (6.3- 7.4)	7.2 (6.8- 7.4)	7.2 (6.5- 7.6)	7.5 (6.9- 8.0)
ANGCON		4.9	5.4	5.0	5.1 (4.5- 6.0)	5.1 (4.0- 5.7)	5.4 (4.8- 5.8)	6.1 (5.6- 6.5)
CONRAM		4.7	4.9	4.6	4.9 (4.4- 5.5)	4.9 (4.2- 5.6)	5 4 (4.6- 5.9)	5.6 (4.6- 6.0)
EXTERNAL CHARACTERS								
NV	76	80.5	90	90	82.3 (72.5-93.0)	88.3 (80.0-96.2)	84.9 (80.1-90.5)	91.6 (84.3-101.0)
TV	74	69.5	68	69	84.8 (73.8-93.7)	105.4 (99.0-119.6)	76.3 (69.0-81.6)	82.0 (73.9-88.1)
HF	13.5	13.2	13.2	13.3	14.3 (13.0-15.4)	16.6 (14.8-18.4)	13.8 (12.8-15.0)	15.0 (13.5-15.9)
EAR	16++	16.7	17.5	16.9	18.0 (16.4-20.8)	19.4 (18.0-20.7)	17.1 (15.2-19.5)	20.0 (18.5-21.7)
WEIGHT		15	18	16.5	20.0 (10.0-33.0)	26.4 (21.0-30.0)	24.5 (17.5-33.0)	28.6 (18.0-43.0)

* Holotype, measurements from Thomas (1906)
\+ Calculated from Tate (1947)
++ from specimen label (fide' L. Smith)

It differs from *Pseudantechinus bilarni* in averaging smaller in skull, dental and external characters and in having shorter: MAXL 25.2 (24.7-25.5) *v.* 28.3 (26.3-30.5), C^1-M^5 9.6 (9.5-9.7) *v.* 10.7 (10.0-11.4), interorbital width (INORB) 5.2 (5.1-5.3) *v.* 5.8 (5.4-6.2), dentary condyle to I_1, (DC-I_1) 18.5 (18.1-18.9) *v.* 20.6 (19.1-22.4), I_1-M_5 11.0 (10.9-11.1) *v.* 12.8 (11.6-13.6), HF 13.2 (13.2-13.3) *v.* 16.6 (14.8-18.4), EAR 17.0 (16.7-17.5) *v.* 19.4 (18.0-20.7) and WT 16.5 (15-18) *v.* 26.4 (21-30); OBUL wider (and BULTOT longer) relative to MAXL (Figure 3); periotic tympanic wing more inflated; small spike on lateral surface of alisphenoid tympanic bulla immediately anterior to postglenoid process present rather than absent; P^3 smaller, 1/2 to 3/4 rather than >3/4 occlusal surface area of P^2; P^3 absent rather than always present; M^2 stylar cusp B low, fused with parastyle rather than separate from parastyle, moderate to occasionally tall;

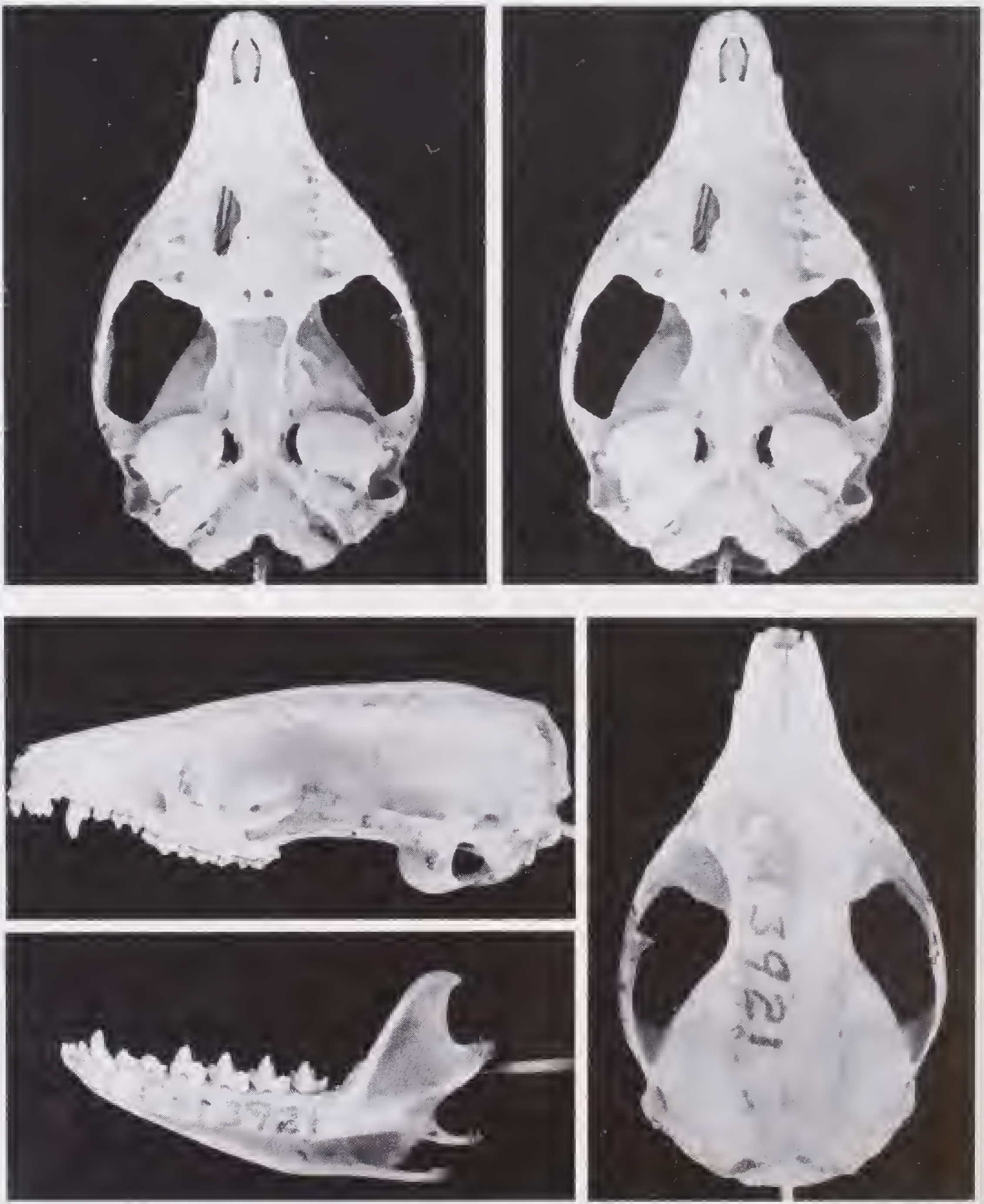


Figure 1: Skull and dentary, and ventral aspect of skull as stereopairs of *Pseudantechinus mimulus* CM 3921.

ectotympanic dorsolateral edge more expanded into postglenoid fossa; lateral squamosal wall of epitympanic sinus more pronounced; tail subequal or shorter (76-86%) rather than 109-144% length of tip of snout to vent, more heavily furred.

It differs from *P. macdonnellensis* in averaging smaller in most skull and external characters and in having smaller: MAXL 25.2 (24.7-25.5) *v.* 27.5 (25.9-29.7) and BULTOT 5.6 (5.3-5.9) *v.* 6.5 (6.0-7.0); OBUL wider relative to MAXL (Figure 3); periotic tympanic bulla less inflated; small spike on lateral surface of alisphenoid tympanic bulla immediately anterior to postglenoid process present rather than absent; P^3 much larger, 1/2 to 3/4 rather than <1/4 (or tiny or absent) occlusal surface area of P^2; M^2 stylar cusp B fused rather than not fused (when present) with parastyle; squamosal and frontal sutures of lateral cranium not close rather than close or in contact.

It differs from *P. woolleyae* in averaging smaller in most skull, dental and external characters: e.g., MAXL 25.2 (24.7-25.5) *v.* 29.9 (28.0-31.2), C^1-M^5 9.6 (9.5-9.7) *v.* 11.3 (10.8-11.6); bulla much smaller: periotic tympanic wing not as inflated; small spike on lateral surface of alisphenoid tympanic bulla immediately anterior to postglenoid process present rather than absent; P^3 smaller, 1/2 to 3/4 rather than >3/4surface area of P^2; P_3 absent rather than usually present; M^2 stylar cusp B low, fused with parastyle rather than moderately high and separate from parastyle; M_4 entoconid tiny to absent rather than moderate to large.

Description

Skull and dentary (Table 1, Figures 1 and 2)

Skull short, particularly rostrum as suggested by short nasals (slightly flared posteriorly), skull broad posteriorly, distance outside bullae (OBUL) broad; interorbital moderately wide; cranium not inflated, sagittal crest and postorbital swellings absent; lambdoidal crest low; squamosal and frontals separated laterally on cranium by from 0.96-1.02 mm (L.A.S. could not detect separation of the squamosal and frontal in the holotype because the situation was obscure. Paula Jenkins, Natural History Museum, London, kindly re-examined this aspect of the holotype skull for me. She also noted that "the degree of contact between frontal and squamosal on the holotype of *Phascogale mimulus* is unclear because of the obscuring by the internal shelving". However, the sketch she prepared shows that the internal shelving of the frontal and squamosal bones do not contact beneath the parietal. This is the situation occurring in the specimens from Sir Edward Pellew Is and strongly indicates a considerable separation between the squamosal and frontal bones. In *Pseudantechinus* where the frontal and squamosal bones are in contact or very close (e.g. *ningbing*), their internal shelving overlaps beneath the parietal. Maxillary palatal vacuities moderately long, located posterior to a line joining M^2 metacones and anterior of a line joining M^4 metacones; premaxillary palatal vacuities do not extend posterior to a line joining mid point of C^1 alveoli; palatine vacuities tiny to moderate: in CM 2894 and CM 2697 close to maxillary-palatine suture, in CM 3921 and holotype larger and closer to palate posterior margin; alisphenoid tympanic bulla moderate size, moderately inflated, ventrally covers ectotympanic wing

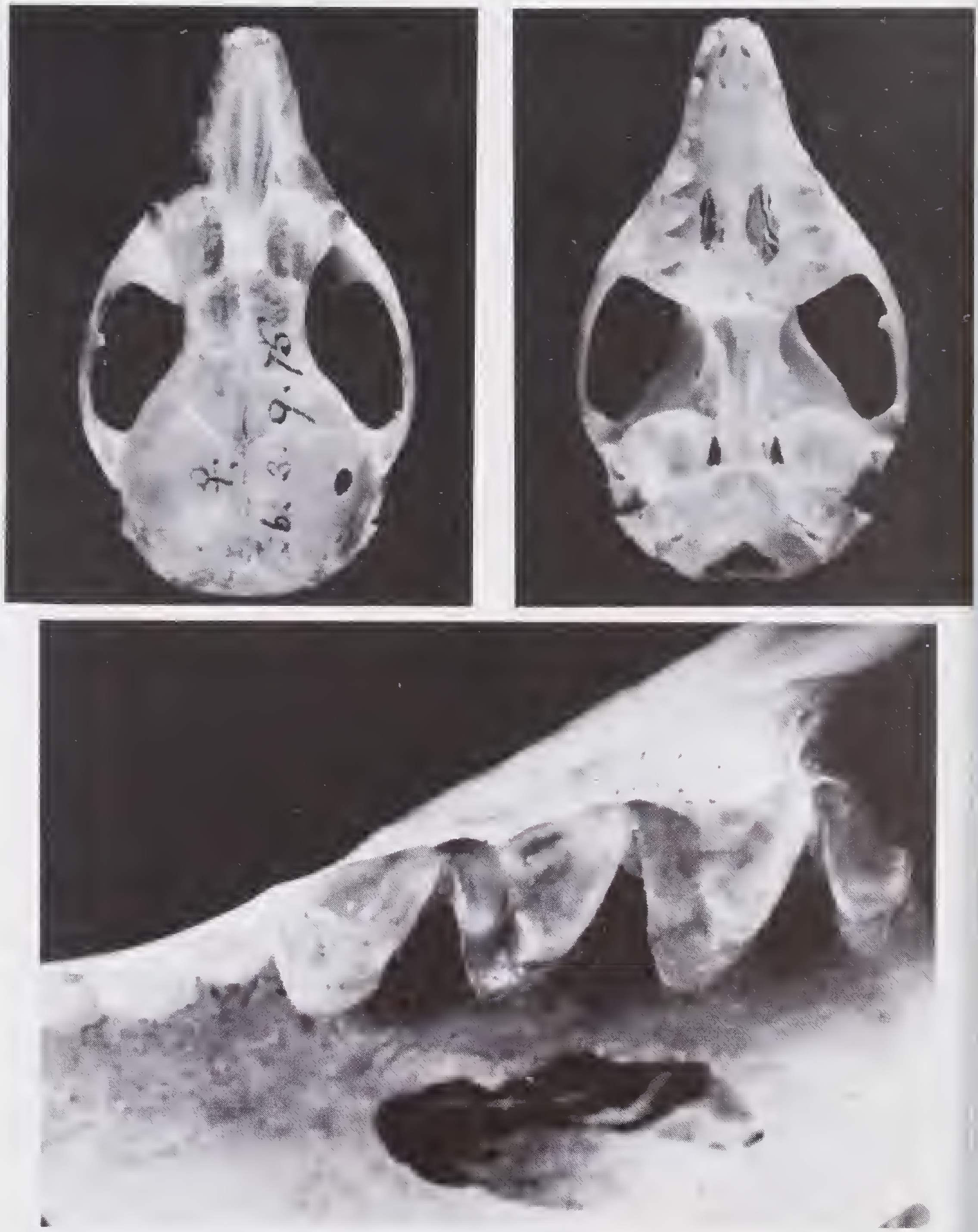
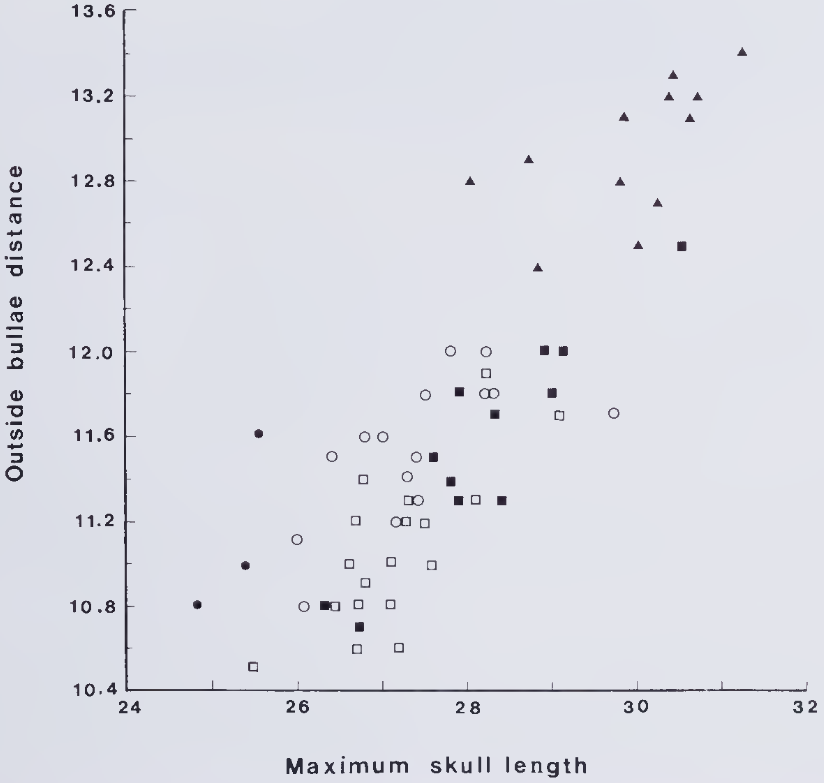


Figure 2: Dorsal and ventral aspect of the skull and oblique view of the left molar and premolar row of *Pseudantechinus mimulus* holotype.

Figure 3: Relationship between distance outside bullae (OBUL) and maximum skull length (MAXL) for *Pseudantechinus mimulus* (●), *P. ningbing* (□), *P. bilarni* (■), *P. macdonnellensis* (○) and *P. woolleyae* (▲).

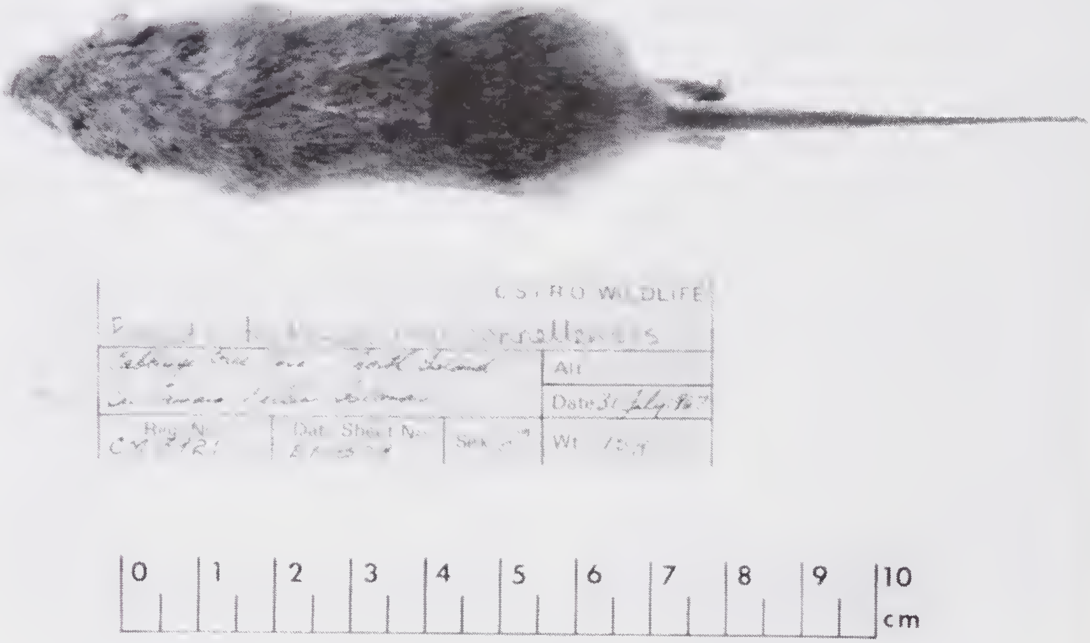


completely or almost so, in wide contact with periotic tympanic wing; small spike, up to 0.22 mm long, on lateral surface of alisphenoid tympanic bulla immediately anterior to postglenoid process (also in holotype fide' L.A.S. and Figure 2), wide apart; dorsolateral edge of ectotympanic expanded into 25-60% of glenoid fossa; lateral squamosal wall of ectotympanic sinus moderately expanded covering approximately 15-20% of opening of external auditory meatus; squamosal part of zygomata broader than jugal part — which has a 0.4 mm vertical spike at its apex; dentary with distance between tip of angular process and articular condyle (ANGCON) subequal to that between anterior condyle and tip of ascending ramus (CONRAM).

Dentition (Table 1, Figures 1 and 2)

I^1 tallest of upper incisors, separated from I^2 by diastema which approximates I^1 thickness; I^2, I^3 and I^4 approximately same height and crown area occasionally I^2 shorter than I^4; I^4 separated from C^1 by substantial diastema; C^1 width slight antero- and postero-lingual cingulum; C^1 crown height about x2 1/2 that of P^3, slight diastema between C^1 and P^1; P^1 and P^2 crown height subequal, taller than P^3; upper premolars with antero- and postero-basal cingular cuspules, encircled by moderate cingulum

Figure 4: Scientific skin of *P. mimulus* CM 3921.



except for lingual and buccal aspect where it narrows; occlusal crown area of P^3 from 1/2 to 3/4 that of P^2 (approximately 3/4 in holotype, fide' L.A.S. and Figure 2); P^3 with two roots, except left side of CM 2697 which appears to have a single root; on M^2 metacone subequal to stylar cusp (St D), St A fused with precingulum, St B fused with paracone (also in holotype, fide' L.A.S. and Figure 2), St E rudamentary; on M^3 St B shorter than St D which is shorter than metacone, St E rudamentary; on M^4 St B and St D subequal in height, St E absent, St D shorter than metacone; preprotocrista terminates at anterior base of M^2 to M^4 paracone, forms narrow contact with anterior cingular shelf on M^2; preparacrista absent on M^2, increases in length from M^2 to M^5; postprotocrista connects to posterolingual base of metacone; posterior lingual and buccal cingula absent on M^2 to M^5; on M^3 to M^5 preparacrista longer than postparacrista, which is approximately half length of premetacrista, which is approximately half length of postmetacrista; on M^5 metacone rudamentary, protocone and paracone very reduced, preparacrista about x 2 1/2 length of postparacrista; M^5 narrower than M^4.

I_1, taller crowned than I_2 which is subequal in length to I_3; I_1 to I_3 with posterior cingular cuspule; C_1 tall, twice height P_1, very slight lingual cingulum and tiny posterior cingular cuspule; P_1 and P_2 crown area subequal; P_3 absent; P_1 and P_2 with narrow encircling cingulum except for buccal aspect above P_1 and P_2 anterior root; P_2 and M_2 separated by short diastema; on M_2 protoconid much taller than metaconid, paraconid rudamentary, hypoconid much shorter than metaconid, hyopconulid small, entoconid rudamentary or absent; on M_3 to M_5 protoconid much taller than metaconid which is taller than paraconid; on M_3 entoconid, hypoconulid and hypoconid subequal in height; on M_4 entoconid much smaller than hypoconulid and hypoconid which are subequal in height; on M_5 hypocristid much shorter such that hypoconulid and hypoconid fuse, entoconid absent; cristid obliqua contacts metacrista at base of central notch in M_5 but is progressively closer to protoconid in M_4 to M_3; on M_2 paracristid slightly longer than metacristid which is subequal in length to cristid obliqua which is shorter than hypocristid; on M_3 paracristid longer than metacristid and hypocristid, which are much longer than cristid obliqua; on M_4 paracristid longer than metacristid, which is longer than hypocristid, which is longer than cristid obliqua; on M_5 paracristid slightly longer than metacristid; M_2 to M_5 have anterior cingula but no lingual or buccal cingula; M_2 to M_4 have posterior cingula which decrease in width posteriorly.

EXTERNALS (Table 1, Figure 4)

Pelage

Described from CM 2697, CM 2894 and CM 3921 study skins.

Overall dorsal fur colour Buffy Brown, ventrally Tilleul Buff. Hairs on shoulders, back and flanks up to 6 mm, base of hairs Deep Neutral Gray, distal 2 mm Drab lightly tipped with Clay Color towards posterior. Hairs on forehead shorter than 4 mm, basal one-third Light Mouse Gray below narrow band of Mummy Brown, distal broad band of Drab tipped with Mummy Brown, hairs on rostrum and side of face similar but without Light Mouse Gray base. Ears lightly furred with 1.3 mm long Cinnamon hairs on both the inner and outer surfaces. Hairs on chin and side of mouth Pale Gull Gray. Hairs on ventral surface of body and throat up to 6 mm long, base of hairs Light Neutral Gray, distal three-quarters Pale Gull Gray. Hair on manus and pes up to 1.6 mm long, Tilleul-Buff; forearm and hind leg with Light Neutral Gray tipped with Tilleul-Buff.

Tail moderately well furred, hairs up to 5 mm long, on dorsal surface Clay Color; on ventral surface Vinaceous-Buff; at tip up to 4.5 mm long, extending slightly beyond tip but not forming tuft. On each side of face approximately 20 mysticial vibrissae, posteriorly these are up to 28 mm long, Clove Brown at base to Pale Gull Gray distally, on edge of lips shorter, up to 12 mm, Pale Gull Gray; two supraorbital vibrissae up to 16 mm long and 6 to 8 genal vibrissae up to 25 mm long with same colour as posterior mysticials, 2 or more submental vibrissae up to 6 mm long. Beneath chin 4 interramal vibrissae up to 12 mm long, Pale Gull Gray. On forearms up to 5 ulnar carpal vibrissae, Pale Gull Gray, up to 12 mm long; 2 to 3 vibrissae between the anconeal and medial antebrachial regions with the single anconeal vibrissa in the anconeal area longer and up to 10 mm.

Pes and tail

Pes terminal pads small, smooth; three interdigital pads moderately large, elongate, separate from each other; hallucal pads elongate, approximately half size of interdigital pads; metatarsal and posthallucal pads subequal in size to interdigital pads. All pads, except terminal ones, heavily striate. Tail much shorter than snout to vent length; base noticeably thickened in skin of CM 2894, not possible to detect incrassation.

Figure 5: Locality of *Pseudantechinus mimulus* in Northern Territory — indicated by arrows.

Distribution

Known only from type locality, Alexandria and North I., Sir Edward Pellew Group (Figure 5). Navigation charts covering this group of islands (by Hydrographic Service, R.A.N. Ed. Aug. 1971) indicate that at low tide both Centre I. and South West I. are connected by dry banks to the mainland. North I. is separated from Centre I. by a shallow channel *c.* 2.4 fathoms (= 4.4 m) deep. Current sea levels were reached around the broad shelves of the Australian coastline about 6500 yr BP, although there is evidence that seas may have fallen by 1 to 2 m in the Gulf of Carpentaria since *c.* 6500 yr BP (Hopley and Thom 1983). North I. would likely have been joined to other islands in this group at least by 6000 yr BP. However, given the nature of sedimentation shifts, particularly at the mouths of rivers, it is possible that disposition of sand banks and erosion channels between these islands may be of very recent origin and that the population of *P. mimulus* on North I. may have been much more recently connected to other islands in this group and the mainland than 6500 yr BP.

Remarks

The description of the holotype of *P. mimulus* suggests some differences from the specimens from North I. For example, in the holotype the length of head and body are subequal to the tail whereas in the North I. specimens the tail is significantly shorter (76-86% length of head and body). This difference could be attributed to the use of different measuring points by Thomas (1906) and by the collectors of the recent specimens; the latter measurements were from the snout to the vent length, whereas Thomas (1906) measured from snout to the root of the tail (Thomas 1888:vii). However Mr L.A. Smith reports that the tail of CM 3921 is noticeably shorter than that of holotype. It is of interest that in all four available *P. mimulus* specimens the total (head to tail) is similar at *c.* 150-160. L.A.S. also reports that the alisphenoid tympanic bullae of the holotype is both slightly longer and more inflated than CM 3921, and that the periotic tympanic wing is both slightly shorter and less inflated in the holotype. These differences are, however, slight and are not apparent from comparison of the three North I. specimens with photographs of the holotype.

Most measurements presented in Table 1 are similar for all four *P. mimulus* specimens; measurements not presented in Table 1 for North I. specimens indicate that they are also similar to values presented for the holotype in Tate (1947). For example (North I. values in brackets followed by holotype) palatal length (13.1-13.6) 13; anterior palatal foramen (2.0-2.6) 2.0; braincase width (11.2-12.0) 11.0; M^2-M^4 length (5.4-5.6) 5.2; crown lengths of: I^2 (0.44-0.50) 0.50; I^3 (0.41-0.47) 0.45; I^4 (0.50-0.52) 0.60; P^1 (0.77-0.88) 0.80; P^2 (0.88-0.99) 0.90; P^3 (0.62-0.81) 0.80; I$_1$ (0.49-0.54) 0.60; I$_2$ (0.37-0.44) 0.45; I$_3$ (0.38-0.42) 0.45; P$_1$ (1.07-1.18) 1.00; P$_2$ (1.17-1.17) 1.25.

The relative size of premolars in the holotype was stated by Thomas (1906) as follows "the last premolariform tooth, the 'secator' (= P^3) ... while similarly absent in the lower jaw, is in the upper well developed, two rooted, barely smaller than the tooth in front of it, and slightly larger than P^1". While this is also the case in the North I. specimens if these teeth are viewed laterally, the occlusal view of them indicates that P^3 is noticeably smaller than P^2.

In conclusion, while the North I. specimens generally agree with the descriptions available for *P. mimulus* by Thomas (1906), Tate (1947), Mr L. Smith (pers. comm.), Ms P. Jenkins (pers. comm.) and photographs of the holotype (Figure 2), the North I. specimens, compared to the holotype, are generally slightly larger, have a longer molar row and probably a shorter tail. Whether or not these differences are such as to require distinction of this island form will not be resolved until more specimens of the mainland form are available for study.

Acknowledgements

I am grateful to Mr Laurie Smith and Ms Paula Jenkins for their comparison of selected characters of CM 3921 from the Sir Edward Pellew Group with the holotype of *P. mimulus* in the British Museum. Photographs of the holotype are by courtesy of the Natural History Museum, London.

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A systematic revision of Australian Emballonuridae (Mammalia: Chiroptera).

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Abstract

Numerical and classical taxonomic approaches based on the morphology of the skull, teeth and external characters, including the morphology of the baculum and glans penis, have been applied to clarify the specific and generic status of the Australian Emballonuridae.

We now recognise the following eight Australian emballonurid species: *Saccolaimus flaviventris, S. mixtus, S. saccolaimus; Taphozous australis, T. georgianus, T. hilli, T. kapalgensis* and *T. troughtoni.*

The genera *Saccolaimus* and *Taphozous* in Australia are separated on cranial, dental and external morphology. A parallel study by us (unpublished data) on generic relationships within the family Emballonuridae, based on phylogenetic analysis of qualitative cranial data, supports the recognition of *Saccolaimus* and *Taphozous* as distinct genera.

Introduction

Emballonurids are widely distributed in the tropical and subtropical regions of the world from the Pacific islands through the Indo-Australian region to Africa and the New and Old Worlds (Hill and Smith 1984). The family is a diverse group comprising about 13 genera and about 50 species (Hill and Smith 1984, Corbet and Hill 1986).

Although there have been several systematic and evolutionary studies of emballonurids (Miller 1907, Thomas 1922, Sanborn 1937, Simpson 1945, Koopman and Cockrum 1967, Barghoorn 1977, Honacki *et al.* 1982, Hill and Smith 1984, Koopman 1984a, Robbins and Sarich 1988) the last major revision of the Australian Emballonuridae was by Troughton (1925). Subsequent to this, some new forms have been described (Sody 1931, Tate 1952, McKean and Friend 1979, Kitchener 1980). Although two genera and seven species are currently recognised in Australia, some named forms have been the cause of considerable taxonomic confusion over the last 50 years, at both generic and specific levels.

Both *Taphozous* E. Geoffroy, 1818 and *Saccolaimus* Temminck, 1838 are generally currently recognised in Australia (Mahoney and Walton 1988), although some modern authorities do not recognise these genera as distinct (Hill and Smith 1984). In Australia, *Taphozous australis* Gould, 1854 and *Saccolaimus flaviventris* (Peters, 1867) were the first species to be ascribed to their respective genera. Since then, 13 more forms have been described from Australia. However, seven species are recognised by most modern

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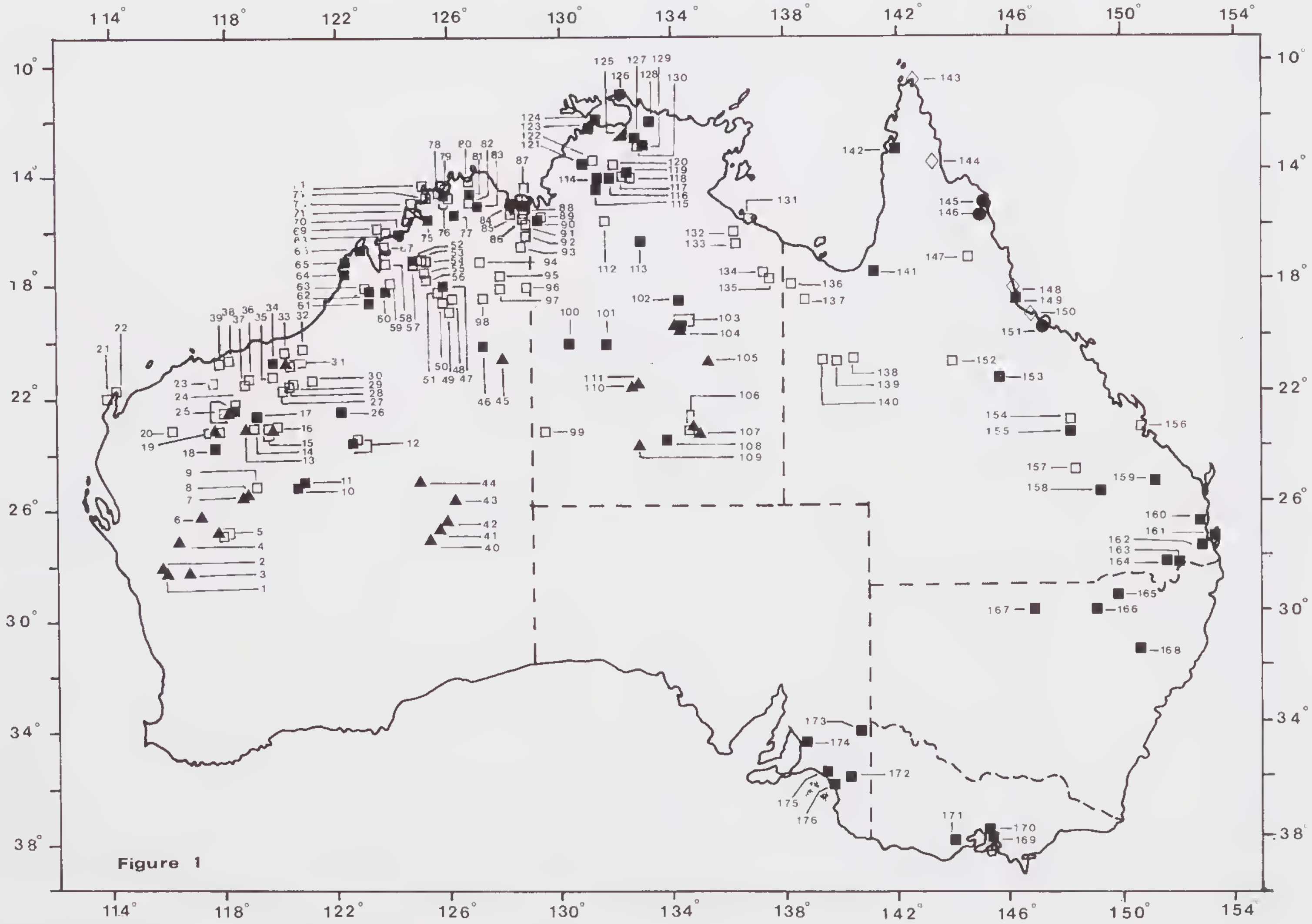

Figure 1 Collecting localities of Australian specimens examined. Species symbols are as follows: *Saccolaimus flaviventris* (■). *S. saccolaimus* (●), *Taphozous australis* (◇), *T. georgianus* (□), *T. hilli* (▲), *T. kapalgensis* (◢).

authorities in Australia (e.g. Strahan 1983, Mahoney and Walton 1988). The seven species and their synonyms, in brackets, are as follows: *Taphozous australis* Gould, 1854 (*T. fumosus* De Vis, 1905), *T. georgianus* Thomas, 1915 (*T. australis* Collet, 1887; *T. australis georgianus* Thomas, 1915; and *T. troughtoni* Tate, 1952), *T. kapalgensis* McKean and Friend, 1979, *T. hilli* Kitchener, 1980, *Saccolaimus saccolaimus* Temminck, 1838 (*S. crassus* Blyth, 1844; *S. pulcher* Elliot, 1844; *S. affinis* Dobson, 1875; *S. nudicluniatus* De Vis, 1905; and *S. flavimaculatus* Sody, 1931), *S. flaviventris* (Peters, 1867) (*S. hargravei* Ramsay, 1876; *S. affinis* var. *insignis* Leche, 1884 and *T. australis* Gould, 1854); and *S. mixtus* Troughton, 1925. An historic account of the current generic and specific taxonomic confusion is extensively treated in Chimimba (1987) and the nomenclatural history by Mahoney and Walton (1988).

This paper is an appraisal of the taxonomy of Australian emballonurids at both the generic and specific levels. We have utilised a wider range of morphological taxonomic techniques (numerical and classical) than has previously been applied to these taxa, and include most described Australian forms. Asian taxa that are morphologically similar to some Australian species are also included in this study.

Materials and Methods

Specimens Examined

This study was based on specimens fixed in 10% formaldehyde and preserved in 70% ethanol, including study skins and skulls. Collection localities of Australian specimens examined are indicated in Figure 1. Specimens examined are listed in Appendix I. The collecting localities provide a good representation of the geographic distributions of the named Australian forms. Asian forms included in our study are: *Saccolaimus saccolaimus* from India, Java, Solomon Islands and Borneo; *S. nudicluniatus* from the Solomon Islands and *T. longimanus* from Bali and India. Only specimens judged to be adult were used. Individuals were considered adult if they lacked any swelling of the metacarpal and phalangeal epiphyses, and/or had the sutures of the basicranial region closed.

Institutional Sources of Specimens

Specimens examined were from the following institutions: (to denote the institutional origin of specimens, their catalogue numbers are prefixed by the following abbreviations (see Appendix I)).

AM :	Australian Museum, Sydney.
AMNH :	American Museum of Natural History, New York.
B :	Zoology Department, University of Queensland, Brisbane.
C :	Museum of Victoria, Melbourne.
CAM :	Central Australian Wildlife Collections, Darwin.
CM :	Australian National Wildlife Collections, Canberra.
FMNH :	Field Museum of Natural History, Chicago.
JM :	Queensland Museum, Brisbane.
NTM :	Northern Territory Museum, Darwin.
SAM :	South Australian Museum, Adelaide.
WAM :	Western Australian Museum, Perth.

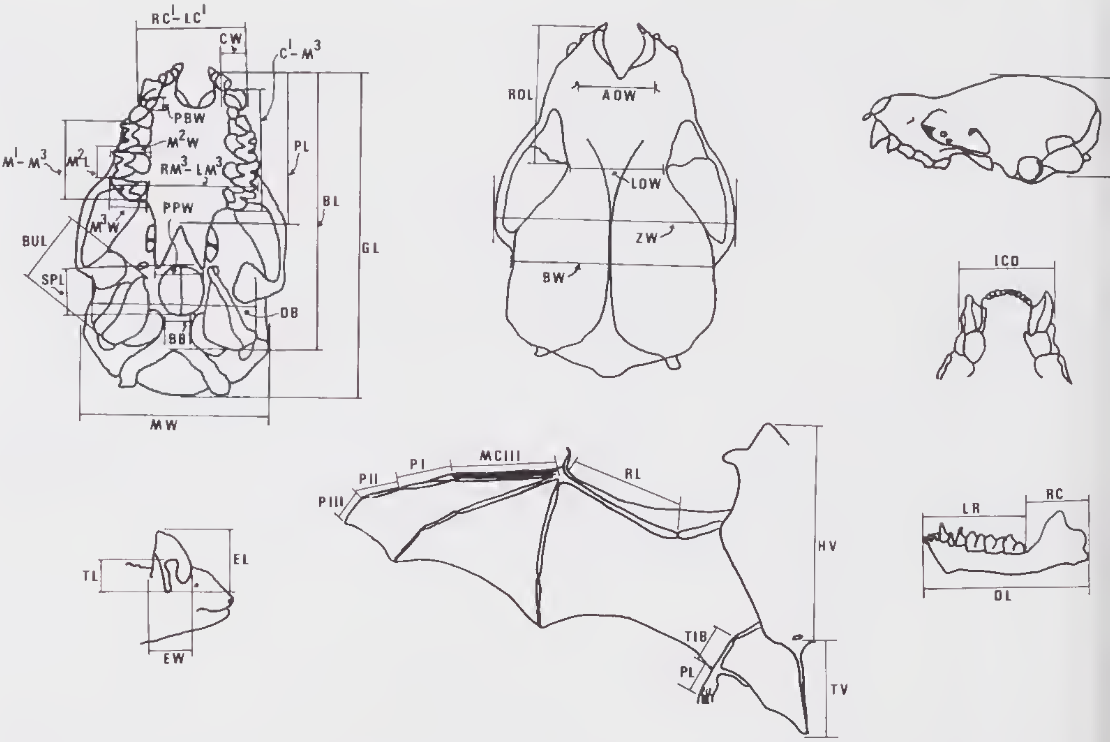

Figure 2 Abbreviations and the recording points of cranial, mandibular and external body measurements referred to in text. GL: greatest skull length; AOW: anteorbital width, between infraorbital foramina; LOW: least interorbital width; ZW: zygomatic width; ROL: rostrum length, from LOW to anterior edge of premaxilla; MW: mastoid width, between mastoid processes; BW: braincase width, at centre of zygomatic-squamosal contact; CH: cranial height, lower arm of calipers placed level with pre and basisphenoid, upper arm in contact with apex of skull; PL: palatal length; PPW: postpalatal width; BL: basicranial length, between anterior edge of foramen magnum and anterior edge of premaxilla; BUL: bulla length, excluding eustachian part; BB: width of basisphenoid, between cochlea; OB: distance outside bullae, caliper points in contact with anterodorsal edge of tympanic ring; CW: canine width, maximum diameter at base; RC^1-LC^1: inter upper canine distance, at base of cusp; C^1-M^3: upper maxillary tooth row crown length, anterior edge of C^1 to posterior edge of M^3; M^1-M^3: upper molar crown length, anterior edge of M^1 parastyle to posterior edge of M^3; M^{2}L: upper second molar crown length, anterior edge of parastyle to posterior edge of metastyle; M^{2}W: upper second molar crown width, lingual base of protocone to buccal face of paracone, at right angle to occlusal surface; M^{3}W: upper third molar crown width, as for M^{2}W; RM^3-LM^3: inter-upper third molar distance, across buccal face of paracone of RM^3 and LM^3; LR: lower tooth row, posterior edge of M^3 to anterior edge of dentary; RC: angular ramus to dentary condyle, caliper blade along anterior face of ramus and measuring to posterior edge of articular condyle; DL: dentary length, from condyle to anterior tip of dentary; SPL: sphenoid pit length; PBW; P^1 basal width; ICD: inter-lower canine distance, at base of cusp; HV: body length, from tip of rhinarium to anus; TV: tail length, from tip to anus; EL: ear length, apex to basal notch; EW: ear width across basal lobes; TL: tragus length, apex to basal notch; RL: radius length; MCIII: metacarpal III length; PI: digit III phalanx I length; PII: digit III phalanx II length; TIB: tibia length; and PL: pes length.

Morphology and Terminology

Terminology of tooth structure follows Slaughter (1970); skull and dentary terminology follows Kitchener and Caputi (1985) while that used for external morphology follows Hill and Smith (1984).

Characters

Twenty-eight quantitative skull and dentary characters (hereafter referred to as skull characters) and 11 external characters were recorded with Mitutuyo dial calipers and taken to the nearest 0.1 mm. The positions and abbreviations of these skull and external measurements are shown in Figure 2.

Measurements of Holotypes and Unique Specimens

Our measurements of holotypes and unique specimens are listed in Appendix II, measurements throughout are in mm.

Glans Penis, Baculum and Pelage

Alizarin S method for gross staining of calcium was used for the preparation of the bacula for examination (McGee-Russel 1958) and for assessing their positions within the glans penis. Descriptions of pelage and skin colour followed Ridgway's (1912) colour standards and nomenclature and were described from 'cabinet' skins.

Statistical Analyses

All statistical analyses were performed at the Western Australian Regional Computing Centre (W.A.R.C.C.) on a Cyber 845.

Sexual Dimorphism

Prior to any analysis the nature and extent of sexual dimorphism was first examined using a one-way analysis of variance (Zar 1974) generated by SPSS subprogramme ONEWAY (Nie *et al.* 1975). Only *Taphozous georgianus, T. hilli* and *Saccolaimus flaviventris* had adequate specimens to examine sexual dimorphism.

Delineation of Species by Shape in Relation to Size

To minimise the effects of size, size regression on a selected size variable was used. Through the SPSS subprogramme SCATTERGRAM (Nie *et al.* 1975), the original characters were logarithmically transformed in order to make their interrelationships linear. Intraspecific allometric regression equations based on the greatest skull length (GL) as an overall measure of size were then used to transform each coordinate to the value it would be expected to assume if that coordinate were of a size equivalent to the mean of all taxa (Thorpe 1976).

An *a priori* Recognition of Taxa

Principal Components Analysis (PCA) (Blackith and Reyment 1971, Wiley 1981, Pielou 1984) using quantitative size-free characters was used to assess the distinctiveness of all specimens examined. This analysis was conducted using the SPSS subprogramme FACTOR (Nie *et al.* 1975). Since the primary interest was to obtain scores and loadings of characters, R-mode factoring was adopted. Rotation of factors in general, simplifies the factor structure; consequently, Varimax rotation, which provides factors that are most easily interpretable in terms of the original variables (Nie *et al.* 1975) was further adopted. In addition, the number of factors extracted in factor analysis is highly dependent on the minimum eigenvalue (Nie *et al.* 1975) and is also a function of the correlation among variables (Sokal and Rohlf 1981). Only factors with an eigenvalue ≥ 1 were examined as this corresponds to a single variable in the original data.

In addition to PCA, a classical taxonomic approach was used to examine the morphological distinctiveness of taxa.

An *a posteriori* Recognition of Taxa

The groups obtained from PCA and the classical taxonomic approach were subjected to a stepwise Canonical Variates Analysis (CVA) performed through the SPSS subprogramme DISCRIMINANT (Nie *et al.* 1975; Hull and Nie 1981). This maximises differences between groups, assists recognition of characters important in separating groups, and the classification of individuals to groups. Because the computation of a covariance matrix in CVA is sample-dependent, groups represented by less than three individuals were not included in the "analysis phase", they were however included during the "classification phase".

Groupings of Morphological Data for Statistical Analyses

Some of the specimens had incomplete data sets because only skulls or externals were available. While PCA adjusts for missing variables in the computation of factor scores, CVA deletes a case from the analysis if it has a missing value (Nie *et al.* 1975). For these reasons, both PCA and CVA were performed using three groupings of data: (1) skull characters only; (2) skull, wing and tibia length (TIB); and (3) skull and external characters combined (obtainable only from alcohol preserved specimens).

The latter analysis resulted in the loss of many cases. We excluded postpalatal width (PPW), rostrum length (ROL), and upper second molar crown length (M^2L from the CVA because these measurement were missing from many specimens.

Cluster Analysis

To investigate how species cluster phenetically, cluster analysis was performed through SPSS X subroutine CLUSTER. The transformed mean character values were used to obtain a squared Euclidian distance between species (Mahalanobis 1936; Rao 1948). The squared Euclidian distance was used to calculate a similarity matrix. The similarity matrix was then subjected to a hierarchical cluster analysis using the Unweighted Pair Group Mathematical Averaging method (UPGMA) (Sneath and Sokal 1973; Wiley 1981). Some species (as indicated in Figure 1) were represented by many populations; species rather than local populations were therefore treated as OTU's.

Systematics

The means, ranges and standard deviations (in mm) of characters of the Australian emballonurids are presented in Table 1a for skull, dentary and teeth and Table 1b for external characters. In species in which the glans penis and bacula were examined, the baculum was always located at the very tip of the head mound of the glans penis as indicated in Figure 3a.

Table 1 (a) Skull, dentary, teeth and (b) external measurements, in mm, for adult *Taphozous georgianus, T. troughtoni, T. hilli, T. kapalgensis, T. australis, Saccolaimus saccolaimus, S. flaviventris* and *S. mixtus* from Australian localities. N = Sample size, x = mean, SD = standard deviation, Mn = minimum, Mx = maximum (for code to characters see Figure 2).

Skull, Dentary and Teeth Characters

		GL	AOW	LOW	ZW	ROL	MW	BW	CH	PL	PPW	BL	BUL	BB	OB
	N	259	258	260	253	262	251	255	253	257	210	252	253	253	240
	x	21.4	6.3	6.3	13.2	9.2	10.8	10.5	7.4	8.8	3.6	18.8	4.9	2.1	10.0
T. georgianus	SD	0.48	0.22	0.29	0.34	0.27	0.26	0.28	0.29	0.26	0.27	0.40	0.17	0.15	0.29
	Mn	20.0	5.8	5.6	12.1	8.6	10.1	9.8	5.7	8.1	2.8	17.7	4.3	1.7	9.2
	Mx	23.1	7.0	7.3	14.4	11.5	11.7	11.6	8.4	9.5	4.4	19.9	5.3	2.6	11.0
	N	4	4	4	4	4	4	4	4	4	4	4	4	4	4
	x	24.1	6.9	6.9	14.8	10.3	12.1	11.8	8.5	9.3	4.5	21.1	5.6	2.4	11.4
T. troughtoni	SD	0.13	0.14	0.40	0.10	0.10	0.13	0.10	0.13	0.25	0.26	0.19	0.10	0.21	0.13
	Mn	24.0	6.8	6.4	14.7	10.2	11.9	11.7	8.4	9.8	4.2	20.8	5.4	2.2	11.2
	Mx	24.3	7.1	7.3	14.9	10.4	12.2	11.9	8.7	10.3	4.7	21.2	5.6	2.6	11.5
	N	75	74	74	74	75	75	75	75	75	59	73	75	75	75
	x	20.0	6.0	6.2	12.8	8.0	10.4	10.5	7.4	7.3	3.6	16.8	5.1	2.0	9.9
T. hilli	SD	0.35	0.19	0.28	0.22	0.22	0.19	0.22	0.18	0.20	0.23	0.32	0.13	0.18	0.18
	Mn	19.1	5.6	4.7	12.3	7.1	9.9	9.9	7.0	6.8	3.2	16.0	4.9	1.5	9.5
	Mx	21.1	6.8	6.7	13.4	8.4	11.0	11.0	7.8	7.8	4.4	17.6	5.5	2.8	10.3
	N	9	9	9	9	9	9	9	9	9	5	9	9	9	8
	x	21.6	6.2	6.3	13.1	9.0	11.1	10.9	7.8	8.7	3.7	18.6	5.1	2.2	10.6
T. australis	SD	0.20	0.13	0.17	0.12	0.11	0.17	0.14	0.22	0.17	0.24	0.21	0.12	0.14	0.09
	Mn	21.4	6.0	6.1	12.9	8.8	10.8	10.6	7.4	8.5	3.5	18.5	4.9	2.0	10.5
	Mx	22.0	6.4	6.7	13.3	9.2	11.4	11.1	8.1	9.1	4.1	18.9	5.3	2.4	10.7
	N	3	3	3	3	3	3	3	3	3	2	3	3	3	3
	x	20.3	5.8	6.4	12.9	8.6	11.1	10.8	7.7	7.9	4.3	18.1	5.0	2.4	9.5
T. kapalgensis	SD	0.35	0.07	0.19	0.26	0.15	0.13	0.15	0.13	0.27	0.28	0.25	0.21	0.10	0.41
	Mn	20.0	5.8	6.2	12.6	8.4	11.0	10.6	7.6	7.6	4.1	17.9	4.8	2.3	9.1
	Mx	20.7	5.9	6.6	13.1	8.7	11.2	10.9	7.8	8.1	4.5	18.4	5.2	2.5	9.9
	N	106	107	104	104	109	106	106	107	107	69	103	106	105	101
	x	25.2	8.4	9.1	16.6	10.7	14.1	12.8	8.7	10.9	4.1	22.1	5.3	2.9	12.2
S. flaviventris	SD	0.73	0.44	0.50	0.60	0.37	0.53	0.43	0.40	0.51	0.41	0.68	0.27	0.29	0.42
	Mn	23.8	7.1	8.1	14.8	9.7	12.7	11.8	7.8	9.6	3.2	20.0	4.7	2.2	10.9
	Mx	27.0	9.7	10.3	17.9	11.6	15.7	14.3	9.7	12.3	5.6	23.6	6.0	3.8	13.3
	N	3	3	3	3	3	3	3	3	3	3	3	3	3	3
	x	24.4	7.3	8.3	16.5	10.0	14.2	13.1	9.6	9.9	4.0	20.6	5.1	3.5	12.7
S. saccolaimus	SD	1.3	0.39	0.62	0.96	0.34	0.50	0.55	0.60	0.47	0.40	0.81	0.16	0.35	0.46
	Mn	22.4	6.6	7.4	14.6	9.3	13.4	12.0	8.7	9.2	3.7	19.0	4.9	2.9	11.9
	Mx	25.9	7.8	9.0	17.3	10.6	15.1	13.8	10.1	10.6	4.6	21.8	5.8	4.0	13.4
	N	2	2	2	—	2	2	2	2	2	—	2	2	2	2
	x	21.8	6.6	7.8	—	8.8	12.1	11.6	8.1	8.7	—	18.8	4.8	3.3	11.3
S. mixtus	SD	0.14	0.28	0.23	—	0.22	0.01	0.06	0.18	0.21	—	0.13	0.11	0.13	0.42
	Mn	21.7	6.6	7.6	—	8.6	12.1	11.6	8.0	8.5	—	18.7	4.8	3.2	11.0
	Mx	21.9	6.6	7.9	—	8.9	12.1	11.6	8.3	8.8	—	18.9	4.9	3.4	11.6

Table 1a cont.

Skull, Dentary and Teeth Characters cont.															
		CW	RC^1-LC^1	C^1-M^3	M^1-M^3	M^{2}L	M^{2}W	M^{3}W	RM^3-LM^3	LR	RC	DL	SPL	PBW	ICD
T. georgianus	N	262	258	262	262	261	261	262	253	261	259	260	255	258	259
	X	2.0	4.1	9.7	5.2	2.1	2.5	2.2	9.4	11.7	5.0	18.1	4.2	0.60	3.0
	SD	0.10	0.15	0.26	0.18	0.11	0.12	0.13	0.26	0.33	0.34	0.42	0.20	0.07	0.13
	Mn	1.5	3.4	8.8	4.2	1.7	2.0	1.8	8.6	10.4	4.5	16.7	3.5	0.40	2.6
	Mx	2.3	4.5	10.5	5.7	2.5	2.9	2.6	10.3	14.5	6.0	19.3	4.7	0.80	3.3
T. troughtoni	N	4	4	4	4	4	4	4	4	4	4	4	4	4	4
	x	2.3	4.6	10.9	5.9	2.3	2.7	2.4	10.4	13.1	5.6	20.6	4.5	0.65	3.3
	SD	0.06	0.13	0.10	0.06	0.08	0.06	0.05	0.24	0.05	0.13	0.17	0.25	0.06	0.10
	Mn	2.2	4.5	10.8	5.8	2.2	2.6	2.3	10.2	13.0	5.5	20.3	4.2	0.60	3.2
	Mx	2.3	4.8	11.0	5.9	2.4	2.7	2.4	10.7	13.1	5.8	20.7	4.8	0.70	3.4
T. hilli	N	75	73	75	75	75	75	75	75	75	75	75	74	74	74
	x	1.7	3.5	8.6	4.7	1.9	2.3	2.0	9.1	10.6	4.4	15.9	4.1	0.46	2.8
	SD	0.06	0.61	0.53	0.11	0.09	0.09	0.12	0.22	0.17	0.19	0.44	0.17	0.07	0.13
	Mn	1.5	3.1	7.6	4.5	1.5	2.0	1.7	8.4	10.2	4.1	15.2	3.7	0.30	2.5
	Mx	1.8	4.8	9.8	5.0	2.1	2.4	2.3	9.7	11.0	5.0	18.8	4.4	0.70	3.1
T. australis	N	9	9	9	9	9	9	9	9	9	9	9	9	9	8
	x	2.1	4.0	9.6	5.1	2.0	2.4	2.1	9.3	11.5	5.0	17.6	3.4	0.58	3.2
	SD	0.08	0.08	0.13	0.07	0.13	0.11	0.07	0.11	0.09	0.19	0.21	0.15	0.07	0.06
	MN	2.0	3.9	9.4	5.0	1.8	2.2	2.0	9.2	11.4	4.8	17.4	3.2	0.50	3.1
	Mx	2.2	4.1	9.8	5.2	2.2	2.6	2.2	9.5	11.6	5.4	17.9	3.6	0.70	3.3
T. kapalgensis	N	3	3	3	3	3	3	3	3	3	3	3	3	3	3
	x	2.0	4.2	9.3	5.0	2.0	2.4	2.1	9.0	11.2	5.2	17.3	3.8	0.63	3.0
	SD	0.06	0.22	0.12	0.07	0.07	0.10	0.06	0.20	0.16	0.06	0.26	0.10	0.06	0.21
	Mn	2.0	4.0	9.2	5.0	1.9	2.3	2.1	8.8	11.0	5.1	17.1	3.7	0.60	2.8
	Mx	2.1	4.4	9.4	5.1	2.0	2.5	2.2	9.2	11.3	5.2	17.6	3.9	0.70	3.2
S. flaviventris	N	109	107	109	109	109	109	109	105	108	108	107	106	107	104
	x	2.2	6.4	11.5	6.3	2.6	3.0	2.4	11.5	14.1	6.1	21.5	2.9	1.5	4.1
	SD	0.11	0.27	0.39	0.25	0.16	0.20	0.17	0.43	0.42	0.30	0.57	0.28	0.12	0.21
	Mn	1.9	5.9	10.0	5.5	2.2	2.5	2.0	10.5	13.0	5.6	20.1	2.2	1.0	3.6
	Mx	2.4	7.1	12.4	6.8	2.9	3.5	2.8	12.7	15.0	6.8	22.7	3.5	1.8	4.7
S. saccolaimus	N	3	3	3	3	3	3	3	3	3	3	3	3	3	3
	x	2.2	5.7	11.2	6.0	2.5	3.1	2.3	11.2	13.4	6.0	20.6	3.6	1.4	4.0
	SD	0.12	0.34	0.30	0.21	0.08	0.23	0.11	0.31	0.65	0.27	0.61	0.44	0.12	0.18
	Mn	2.1	5.0	10.7	5.7	2.3	2.7	2.2	10.7	11.8	5.6	19.5	3.0	1.2	3.7
	Mx	2.5	6.2	11.7	6.4	3.5	2.5	2.5	11.7	14.1	6.3	21.4	4.1	1.5	4.3
S. mixtus	N	2	2	2	2	2	2	2	2	2	1	2	2	2	2
	x	1.8	4.6	9.9	5.5	2.2	2.4	2.1	10.1	11.9	5.7	18.6	4.0	0.95	3.1
	SD	0.07	0.22	0.18	0.04	0.09	0.04	0	0.15	0.36	0	0.18	0.04	0.07	0.23
	Mn	1.7	4.5	9.8	5.4	2.1	2.4	2.1	10.0	11.7	5.7	18.4	4.0	0.90	2.9
	Mx	1.8	4.8	10.0	5.5	2.2	2.4	2.1	10.2	12.2	5.7	18.7	4.0	1.0	3.2

Table 1b

		External Characters										
		HV	TV	EL	EW	TL	RL	MCIII	PI	PII	TIB	PES
T. georgianus	N	303	296	302	302	303	295	302	302	297	299	303
	x	72.8	30.0	20.5	14.7	6.9	68.1	61.4	20.6	24.5	27.2	12.4
	SD	3.5	2.9	1.4	1.4	0.69	2.1	2.1	0.96	1.1	1.1	0.72
	Mn	61.6	22.9	16.5	11.8	4.9	61.1	52.7	17.7	19.8	24.2	9.8
	Mx	80.0	39.4	24.1	25.6	8.9	73.4	65.9	23.7	29.1	30.8	14.7
T. troughtoni	N	4	4	4	4	4	4	4	4	4	4	4
	x	83.4	33.7	25.4	17.9	8.4	74.6	69.2	23.5	26.8	31.2	14.8
	SD	3.3	2.5	2.1	1.8	0.76	1.3	0.82	1.1	1.2	0.64	0.80
	Mn	79.4	31.5	22.4	16.2	7.7	72.7	68.1	22.2	25.4	30.6	13.8
	Mx	86.3	36.9	27.1	19.9	9.4	75.6	70.2	24.6	28.4	31.8	15.5
T. hilli	N	102	101	102	102	102	102	102	102	102	102	102
	x	72.6	30.3	21.1	15.4	6.7	67.7	59.9	19.6	23.4	26.8	13.0
	SD	3.1	2.3	1.3	0.94	0.70	1.6	1.5	0.69	0.95	0.88	0.66
	Mn	64.7	23.9	18.5	13.6	5.0	60.4	56.0	17.0	20.7	25.0	10.7
	Mx	81.1	37.7	23.7	18.2	8.6	71.7	64.2	21.6	26.8	31.3	14.3
T. australis	N	13	13	13	13	13	13	13	13	13	13	13
	x	70.0	28.5	22.3	16.2	7.4	65.4	59.2	19.8	22.6	25.7	12.1
	SD	3.7	1.7	1.1	0.96	0.74	1.1	1.1	0.57	0.78	0.75	0.55
	Mn	61.0	25.1	20.2	14.7	5.9	63.5	57.2	18.7	20.8	24.5	11.1
	Mx	74.8	30.6	24.0	17.5	9.0	67.6	60.9	20.9	23.7	27.1	13.0
T. kapalgensis	N	2	2	2	2	3	3	3	3	3	3	2
	x	71.5	22.8	17.0	13.4	6.1	59.3	59.2	21.3	22.1	23.3	12.2
	SD	3.7	0	0.75	0.26	0.67	0.38	1.3	0.28	0.71	0.39	0.26
	Mn	68.8	22.8	16.5	13.2	5.6	58.9	57.8	21.1	21.4	23.0	12.1
	Mx	74.1	22.8	17.6	13.6	6.6	59.7	60.2	21.6	22.8	23.7	12.4
S. flaviventris	N	101	100	104	105	104	106	106	106	105	106	106
	x	81.8	27.0	19.6	14.3	8.1	75.0	77.6	33.4	31.7	30.3	14.1
	SD	3.5	2.8	1.3	1.1	0.84	2.8	2.7	1.5	1.9	1.3	1.3
	Mn	72.3	21.3	16.5	11.1	5.8	65.7	72.6	28.9	27.7	26.7	11.1
	Mx	91.9	33.3	23.0	17.1	9.9	82.1	84.2	36.5	35.9	32.9	16.5
S. saccolaimus	N	3	3	3	3	3	3	3	3	3	3	3
	x	85.7	32.5	18.7	15.6	6.5	74.1	71.6	28.0	28.0	28.6	17.1
	SD	7.7	1.7	1.8	0.55	1.1	3.1	3.3	1.9	1.5	1.6	2.5
	Mn	76.9	30.9	16.6	15.1	5.6	69.2	65.7	25.6	25.6	27.0	14.3
	Mx	90.7	34.2	19.9	16.2	7.7	78.6	75.9	30.2	29.8	30.5	19.1
S. mixtus	N	2	1	1	1	1	2	2	2	2	2	2
	x	74.3	22.6	18.3	14.5	7.6	63.6	62.2	23.5	23.7	24.2	13.1
	SD	2.6	0	0	0	0	0.75	0.88	1.3	0	0.69	1.3
	Mn	72.5	22.6	18.3	14.5	7.6	63.1	61.6	22.6	23.7	23.7	12.2
	Mx	76.2	22.6	18.3	14.5	7.6	64.2	62.8	24.4	23.6	24.7	14.1

Saccolaimus Temminck, 1838

Saccolaimus Temminck, C.J. (1838). Over de geslachten *Taphozous, Emballonura, Urocryptus* en *Diclidurus.* Tijdschr. Natuur. Ges. Physiol. 5: 1-34 pl. 1.

Type species

Taphozous saccolaimus Temminck, 1838 by absolute tautonymy.

Taphonycteris Dobson, G.E. (1876). A monograph of the genus *Taphozous* Geoff. Proc. Zool. Soc. Lond. 1875: 546-556 (548,555) (originally proposed as subgenus of *Taphozous* Geoffroy, 1813).

Referred Australian species

Saccolaimus saccolaimus (Temminck, 1838)
Saccolaimus flaviventris (Peters, 1867)
Saccolaimus mixtus Troughton, 1925

Diagnosis (mean values)

The following diagnosis refers only to Australian emballonurids.

Saccolaimus differs from *Taphozous* in being considerably longer in all measurements; skull heavily rather than lightly ossified; sagittal crest pronounced rather than absent or weak; band separating the anterior lacerate foramen and sphenorbital sinus wide rather than narrow; premaxilla almost abuts rather than overlaps nasals; postorbital ridge strong, joining the sagittal crest near or well posterior to postorbital ridges rather than weak and joining at postorbital ridge; bullae complete rather than incomplete, with less rather than greater than 50 percent of the cochlea exposed; frontal region of skull relatively broad rather than narrow; lower outline of dentary strongly convex rather than concave beneath premolars; anterior premolar relatively large rather than small, almost one-third rather than one-fifth of height and crown area of posterior premolar; sphenoid pit generally shorter rather than longer relative to greatest skull length; base of sphenoid pit v-shaped rather than flat; posteroventral face of basisphenoid in contact with both bulla and cochlea rather than with cochlea only; paraoccipital process same length or slightly longer, rather than shorter than occipital condyles; braincase broader with parietal generally posterolaterally flattened such that braincase wider rather than narrower relative to greatest skull length; first upper molar parastylar area reduced rather than well developed; inner margin of ear not papillate. Length of baculum and glans penis of *S. flaviventris* and *S. saccolaimus* (the two species of *Saccolaimus* available for examination), were longer than in *Taphozous* spp.: baculum (1.0-1.1 v. 0.3-0.4); glans penis (4.2-6.5 v. 2.1-3.3).

Distribution

Saccolaimus occurs in the Indo-Malayan region and Australia and one species *(S. peli)* occurs in West, Central, East and parts of southern Africa (Liberia to Zaire to W. Kenya, Gabon and N.E. Angola) (Honacki *et al.* 1982).

Saccolaimus flaviventris (Peters, 1867)

Figures 3b, 4a, 5; Table 1.

Taphozous flaviventris Peters, W. (1987). On *Taphozous flaviventris,* Gould, a new species of bat from Australia. Proc. Zool. Soc. London 1866: 430.

Taphozous australis flaviventris Dobson, G.E. (1876). A monograph of the genus *Taphozous,* Geoff. Proc. Zool. Soc. Lond. 1875: 546-548.

Taphozous hargravei Ramsay, E.P. (1876). Description of a supposed new species of bat, from Stanwell, near Bulli, N.S.W. Proc. Linn. Soc. N.S.W. 1: 81-82.

Taphozous affinis insignis Leche, W. (1884). On some species of Chiroptera from Australia. Proc. Zool. Soc. Lond. 1884: 49-54.

Holotype

AM 137 (from register compiled by Secretary, Palmer, about 1877) female skin (wet) and skull, from Northern Territory.

Relevant taxonomic decisions

Troughton, E. le G. (1925). A revision of the genera *Taphozous* and *Saccolaimus* (Chiroptera) in Australia and New Guinea, including a new species, and a note on two Malayan forms. *Rec. Aust. Mus.* 14: 313-341 pls 47-48.

Diagnosis (mean values)

Differs from *S. mixtus* in that skull, dentary, teeth and external body measurements larger: mastoid width (14.1 v. 12.1), distance outside bullae (12.2 v. 11.3), canine width (2.2 v. 1.8), inter-upper canine distance (6.4 v. 4.6), upper maxillary tooth row crown length (11.5 v. 9.9), digit III/phalanx I length (33.4 v. 23.5); sphenoid pit deep rather than shallow, posterior margined by an overlapping edge rather than open, median septum as high as the floor of mesopterygoid fossa rather than to a level slightly below that of fossa; males with a secondary gular sac present rather than absent; radial-metacarpal pouch present rather than absent; frontal depression less deeply excavated.

Although of similar skull and body proportions, *S. flaviventris* differs from *S. saccolaimus* in having a relatively smaller sphenoid pit (2.9 v. 3.6), longer digit III/phalanx I length (33.4 v. 28.0) and inter-upper canine distance (6.4 v. 5.7); frontal region of skull relatively broad rather than narrow; posterior floor of mesopterygoid fossa deeply grooved rather than smooth; sphenoid pit deep rather than shallow, median septum as high as floor of mesopterygoid fossa rather than well below level of fossa; zygomata thin and of uniform size rather than large and constricted posteriorly. Glans penis longer (5.6 v. 4.2) and of uniform width rather than club shaped, ventral proximal end smooth rather than with an elevated skin. Baculum narrow distally rather than bifurcated, proximally club-shaped rather than spatulate.

Description (means and ranges)

Skull and Dentary (Figure 5)

Skull large: greatest skull length 25.2 (23.8-27.0); zygomatic width 16.6 (14.8-17.9), mastoid width 14.1 (12.7-15.7), distance outside bullae 12.2 (10.9-13.3), canine width 2.2 (1.9-2.4), inter-upper canine distance 6.4 (5.9-7.1), upper maxillary tooth row crown length 11.5 (10.0-12.4); sagittal crest well developed, reaches occiput; lamboidal crest well developed; zygomata of uniform size; sphenoid pit deep with a median septum rising as high as floor of mesopterygoid fossa; sphenoid pit margined posteriorly by an overlapping edge; mesopterygoid fossa deeply grooved; lower outline of mandible markedly convex beneath premolars to almost straight posteriorly; upper anterior premolar large, equal to or almost half size of posterior premolar, cusps long and sharp.

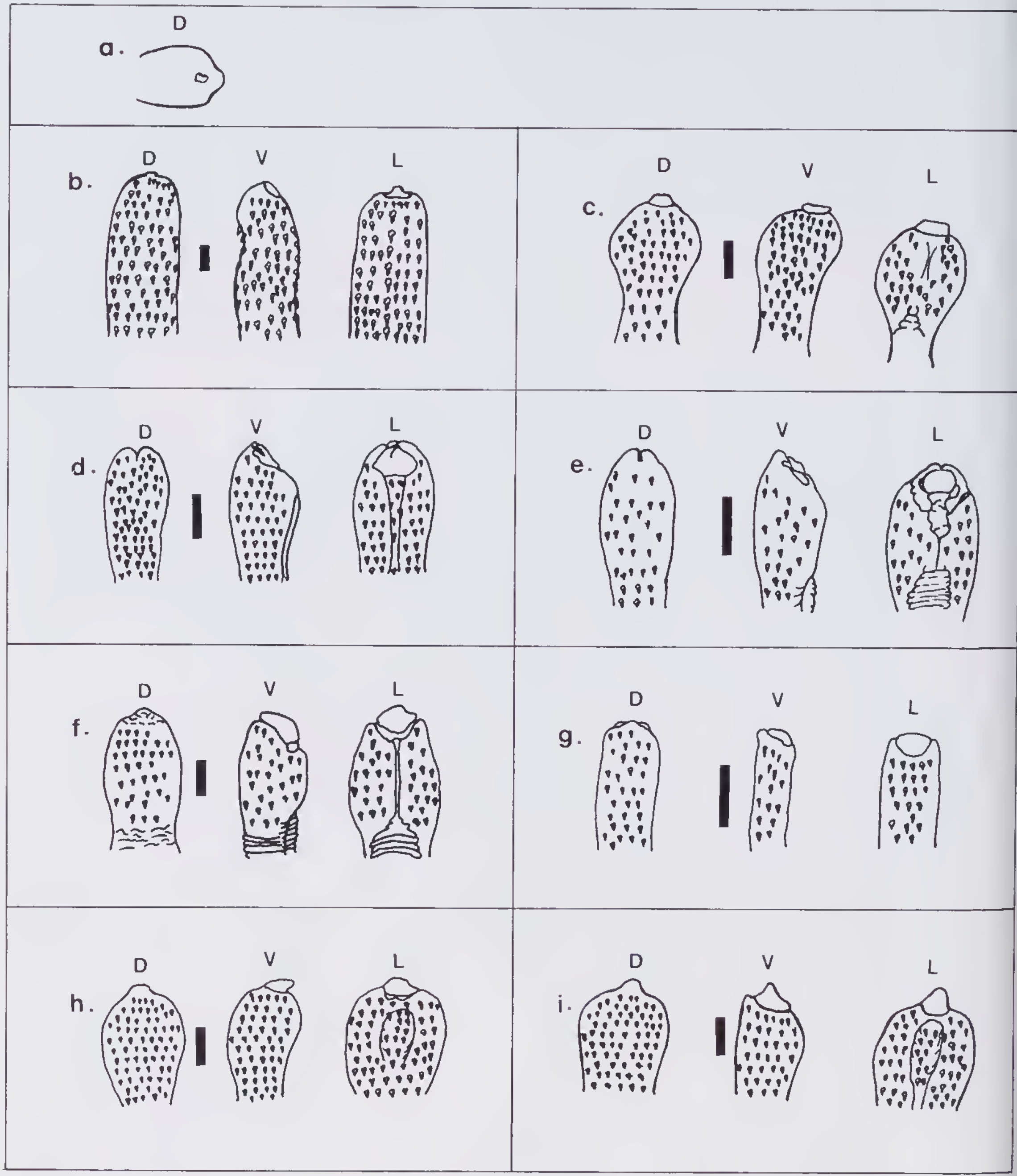

Figure 3 The positioning of the baculum within the glans penis (a) and the ventral (V), dorsal (D) and lateral (L) views of the glans penis of *Saccolaimus flaviventris* (b), *S. saccolaimus* (c), *Taphozous australis* (d), *T. georgianus* (e), *T. troughtoni* (f), *T. hilli* (g), *T. kapalgensis* (h) and *T. longimanus* (i). Scale lines are 1.0 mm.

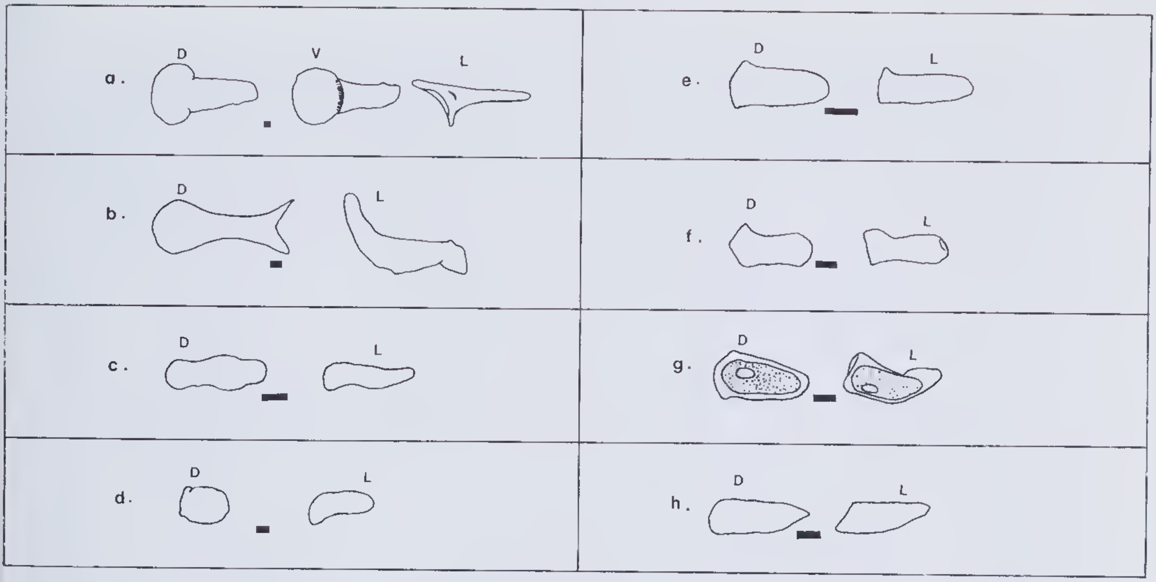

Figure 4 Dorsal (D), lateral (L) and some ventral (V) views of bacula of *Saccolaimus flaviventris* (a), *S. saccolaimus* (b), *Taphozous australis* (c), *T. georgianus* (d), *T. troughtoni* (e), *T. hilli* (f), *T. kapalgensis* (g) and *T. longimanus* (h). Scale lines are 1.0 mm.

External Morphology

Size generally large: radius length 75.0 (65.7-82.1); radial-metacarpal pouch absent in both sexes; large gular sac, with a secondary sac posterior to main sac in males but almost absent in females; outer edge of ear halfway between corner of mouth and posterior base of tragus; inner edge of tragus evenly concave, rounded but somewhat even above with a deep notch just below the top of outer edge.

Pelage and Skin Colour

Dorsal pelage predominantly Black; head well furred to between eyes with Cheatura Black, snout sparsely haired to its tip with this colour; outside ear almost naked except for sparse Brownish Olive hairs at base; similar coloured hairs sparsely but evenly cover inside of ear; shoulder thickly furred with Cream Buff; fur of back extends a short distance onto wing membrane to a line drawn between upper third of humerus and femur, the long fur barely extends onto interfemoral but ends in a lightly haired straight line; ventrally wing membranes lightly haired. The ventral body Cream Buff, with fur extending to sides just behind ear; fur on ventral surface of neck region Colonial Buff; ventral surface of propatagium and plagiopatagium thinly covered with Cream Buff along edge of humerus and radius to radial-metacarpal joint and along edge of body and uropatagium, especially around anal region. Skin of plagiopatagium and propatagium Deep Colonial Buff proximally and Brownish Olive dorsally; skin of dactylopatagium Brownish Olive; skin of ear Black, skin of rhinarium, tragus, inside of ear close to entrance and side of face Brownish Olive.

Figure 5 Skull and dentary of *Saccolaimus flaviventris* (CAM M602). Ventral view of skull is presented a
stereopairs. Scale lines are 5.0 mm.

Glans Penis

Length 5.6 (5.1-6.5) (N = 6); dorsally of uniform width 2.1 (2.0-2.2); laterally reduced in size on distal one-third; thick short spines present, with thickness decreasing distally; thicker spines located on ventral side with thickest on mid-ventral line; urethral opening subcircular with a relatively short head mound from ventral distal edge (Figure 3b).

Baculum

Relatively long 1.3 (1.0-1.5) (N = 6); narrower distally, proximally club-shaped, inflated laterally (Figure 4).

Distribution

Hall and Richards (1979) and Richards (1983a) state that *S. flaviventris* is widespread over Australia except Tasmania, occurring both in the tropics and well to the south of the tropic of Capricorn (Parker 1973). Specimens examined confirm that in Victoria, *S. flaviventris* extends to the cool temperate climate (38^{0}S) despite the emballonurids' preference for tropical and subtropical regions (Koopman 1984b; Hill and Smith 1984; Taylor 1984) (Figures 1 and 6e).

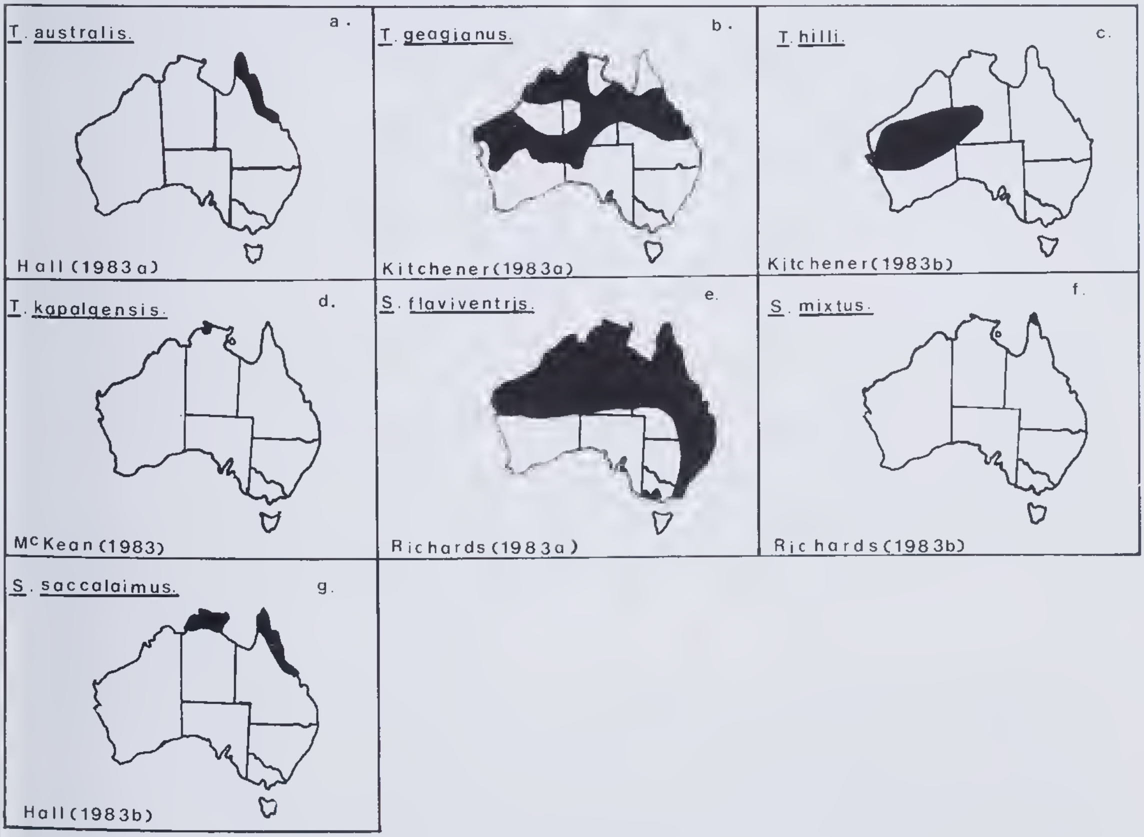

Figure 6 Geographic distribution of *Saccolaimus* and *Taphozous* species in Australia.

Natural History

Saccolaimus flaviventris is relatively rare in collections although it is reported from a wide range of habitats (Richards 1983a). It roosts in tree hollows. It tends to be solitary when roosting but does form small groups of two to six individuals in late winter and spring (Hall and Richards 1979).

It is insectivorous and predatory (Vestjens and Hall 1977), usually foraging above the canopy, but foraging height varies with cover. Its apparent rarity is probably due to its flying so high and fast that it is seldom collected (Richards 1983a).

Aitken (1975) and Richards (1983a) speculate that *S. flaviventris* may be migratory in southern Australia because there are reports of exhausted individuals of these species in open situations. A stepwise multiple regression analysis showed no significant correlations between subcutaneous and mesentric fat categories of individuals between seasons or from individuals from more southern localities (unpublished data).

Pregnancies are always restricted to the right uterine horn. A single young is born between December and mid-March. Subadults are only collected in January and February. There is no indication of an old corpus luteum in either the left or right ovary of the only pregnant female examined that was collected in February, suggesting that it did not breed a second time in one season. However, this requires confirmation. In males, there is no significant difference throughout the year in reproductive parameters, nor is there a significant correlation between male reproductive parameters and depth of the throat pouch (Chimimba and Kitchener 1987).

Specimens Examined

Listed in Appendix 1.

Saccolaimus saccolaimus (Temminck, 1838)

Figures 3c, 4b, 7; Table 1.

Taphozous saccolaimus Temminck, C.J. (1838). Over de geslachten *Taphozous, Emballonura, Urocryptus* en *Diclidurus*. Tijdschr. Natuur. Ges. Physiol. 5: 1-34 pl. 1.

Taphozous crassus Blyth, E. (1844). *Taphozous crassus*. J. Asiat. Soc. Bengal 13: 491.

Taphozous pulcher Elliott, D.G. (1844). *Taphozous pulcher*. J. Asiat. Soc. Bengal 13: 492.

Taphozous affinis Dobson, G.E. (1875). Description of a new species of *Taphozous* from Labuan. Ann. Mag. nat. Hist. 16(4): 232.

Taphozous nudicluniatus De Vis, C.W. (1905). Bats. Ann. Qld. Mus. 6: 36-40.

Taphozous granti Thomas, O. (1911). Two new Eastern Bats. Ann. Mag. nat. Hist. 8(8): 378-379.

Saccolaimus flavimaculatus Sody, H.J.V. (1931). Six new mammals from Sumatra, Java, Bali and Borneo. Natuurw. Tijdschr. Ned. Ind. 91: 349-360.

Relevant taxonomic decisions

Dobson, G.E. (1876). Monograph of the Asiatic Chiroptera and a catalogue of the species of bats in the collection of the Indian Museum, Calcutta. *Trustees of the Indian Museum*. 228 pp; Tate, G.H.H. (1941). Notes on Oriental *Taphozous* and allies. *Am.*

Mus. Novit. 1141: 1-5; Troughton, E. le G. (1925). A revision of the genera *Taphozous* and *Saccolaimus* (Chiroptera) in Australia and New Guinea, including a new species, a note on two Malayan forms. *Rec. Aust. Mus.* 14: 313-341 pls 47-48; and Goodwin, R.E. (1979). The bats of Timor: systematics and ecology. *Bull. Am. Mus. nat. Hist. 163: 73-122.*

Lectotype

Rijksmuseum (NH), Leiden, RMNH 33630, male skin, skull not extracted, from Djawa (= Java), Indonesia, designated by Tate, G.H.H. (1941). Results of the Archbold Expeditions No. 37. Notes on Oriental *Taphozous* and allies. Am. Mus. Novit. 1141: 1-5.

Lectotype is *Taphozous saccolaimus* specimen 'a' of Jentink, F.A. (1888). Museum d'Histoire Naturelle des Pays-Bas. Tome XII. Catalogue systematique des mammiferes (rongeurs, insectivores, cheiroptères, édentés et marsupiax). Leiden: E.J. Brill, 280 pp.

Diagnosis (mean values)

Saccolaimus saccolaimus differs from *S. mixtus* by its larger overall size: mastoid width (14.2 v. 12.1), distance outside bullae (13.3 v. 12.7), canine width (2.2 v. 1.8), inter-upper canine distance (5.7 v. 4.6), upper maxillary tooth row crown length (11.2 v. 9.9), digit III/phalanx 1 length (28.0 v. 23.5); sphenoid pit shorter (3.6 v. 4.0); radial-metacarpal pouch absent rather than present; tragus more circular and bulbous above, hind margin convex rather than concave; frontal depression of skull shallower rather than deeply excavated; posterior floor of mesopterygoid fossa smooth rather than deeply grooved; sagittal crest prominently reaching occiput rather than just reaching occiput; sphenoid pit deep rather than shallow, with a rather low median septum.

Saccolaimus saccolaimus differs from *S. flaviventris* as outlined in the earlier diagnoses of *S. flaviventris.*

Description (mean and range)

Skull and Dentary (Figure 7)

Skull larger: greatest skull length 24.4 (22.4-25.9); zygomatic width 16.5 (14.6-17.3), mastoid width 14.2 (13.4-15.1), distance outside bullae 12.7 (11.9-13.4), canine width 2.2 (1.9-2.4), inter-upper canine distance 6.4 (5.9-7.1), upper maxillary tooth row crown length 11.5 (10.0-12.4); frontal depression not so deeply excavated; posterior floor of mesoptergoid fossa smooth; sphenoid pits deep and divided by comparatively low median septum that is not as high as floor of mesopterygoid fossa; lower outline of mandible convex beneath premolars.

External Morphology

Large size: radius length 74.1 (69.2-78.6); radial-metacarpal pouch absent in both sexes; outer base of ear originating much closer to tragus than corner of mouth; gular pouch present in males, and well defined by an almost naked area encircled posteriorly by rudimentary pouch edges in females; tragus bulbous above and circular in upper outline.

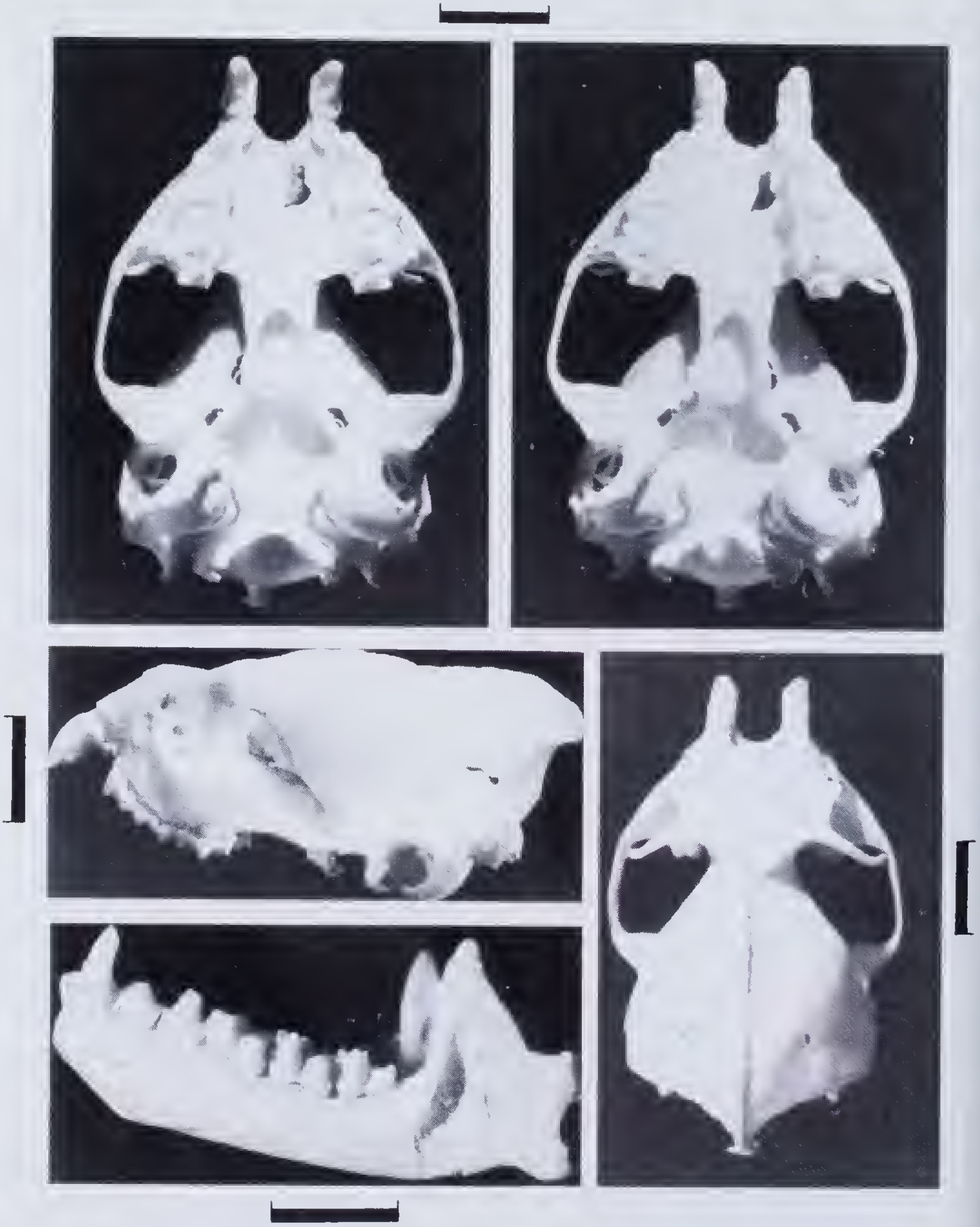

Figure 7 Skull and dentary of *Saccolaimus saccolaimus* (WAM M23324). Ventral view of skull is presented as stereopairs. Scale lines are 5.0 mm.

Pelage and Skin Colour

Dorsal pelage predominantly Clove Brown, scattered with white spots, mottled with irregular patches of white hairs at base. Similar pelage as above sparsely covers face in front of eyes, and as a vertical band of hair behind eyes and external basal third of ear conch; rest of ear naked; tragus and inside of ear evenly but sparsely haired; ventral body surface Bister, scattered with white hairs and fur extends onto wing in area between humerus and femur; posteriorly, ventral surface fur does not extend past femora but ends near tail base; shoulder and proximal third of humerus covered with light longish hairs to a line between upper half of humerus and femur; interfemoral membrane sparsely furred with Clove Brown hairs on dorsal surface, ventrally, fur shorter and thin; chin sparsely haired to level with outer ear base; antebrachial membrane sparsely furred; a post-radial band of Light Buff hairs present, forming a thickish patch in radial-metacarpal angle. Skin of uropatagium, plagiopatagium, propatagium and chin Olive Brown; skin of face, lips, tragus, ear and dactylopatagium Clove Brown.

Glans Penis

Length 4.2 (N = 1): club shaped, both dorsally and laterally, spines present; prominent midventral swelling, terminates into an elevated convoluted skin proximally; tip at urethral opening with approximately rectangular mound, visible from all sides (Figure 3c).

Baculum

Relatively long: 1.1 (N = 1), distally spatulate and proximally club shaped; laterally, rather sinusoidal-shaped (Figure 4b).

Distribution

From India to Sri Lanka through S.E. Asia to Sumatra, Borneo, Java and Timor; Papua New Guinea and Solomon Islands (Honacki *et al.* 1982; Koopman 1984b). In Australia, the species is restricted to northern and northeastern coastal areas from Townsville to Cooktown but is also found in the Alligator River region and Arnhem Land in the Northern Territory (Hall 1983b) (Figure 6g). McKean *et al.* (1980) speculate that *S. saccolaimus* might be expected to occur in tropical Western Australia.

Natural History

Saccolaimus saccolaimus is uncommon in collections. It is mainly insectivorous and predatory, roosts in hollow trees, closed forests, caves and a variety of man-made structures (Hall 1983b). In Australia, Compton and Johnson (1983) observed a colony of *S. saccolaimus* roosting in hollows in Poplar Gum near Townsville, Queensland, although they did not comment on the numbers or group structure. Although gregarious, the species does not form tight clusters (Hall 1983b).

Medway (1977) observed that the Asian *S. saccolaimus* in India have a single young. Females with unweaned juveniles and others in advanced pregnancy were observed in September. There is no study of reproduction of the Australian *S. saccolaimus*, apart from the limited observations by Hall (1983b) who observed that females bear one young and lactate during the tropical wet season. Additionally, Compton and Johnson (1983) noted that *S. saccolaimus* females collected in mid-December in Queensland had advanced pregnancies or attached young.

Specimens Examined

Listed in Appendix I.

Saccolaimus mixtus Troughton, 1925

Figure 8; Table I

Saccolaimus mixtus Troughton, E. le G. (1925). A revision of the genera *Taphozous* and *Saccolaimus* (Chiroptera) in Australia and New Guinea, including a new species, and a note on two Malayan forms. Rec. Aust. Mus. 14: 313-341 pls 47-48.

Holotype

AM A3257 male, skin (wet), skull not extracted, from Port Moresby, Papua New Guinea.

Diagnosis (mean values)

Saccolaimus mixtus differs from *S. flaviventris* and *S. saccolaimus* in being smaller in addition to other characteristics as outlined in the diagnoses of *S. flaviventris* and *S. saccolaimus*.

Description (means and ranges)

Skull and Dentary (Figure 8).

Skull medium sized: greatest skull length 21.8 (21.7-21.9); mastoid width 12.1, distance outside bullae 11.3 (11.0-11.6), canine width 1.8 (1.7-1.8), inter-upper canine distance 4.6 (4.5-4.8), upper maxillary tooth row crown length 9.9 (9.8-10.0), sphenoid pit length 4.0; frontal depression of skull deep; interorbital region broad, with edges markedly concave; sagittal crest just reaches occiput; a deep groove present on posterior floor of mesopterygoid fossa; sphenoid pit rather shallow, with median septum barely reaching floor of mesopterygoid fossa; dentary lower outline beneath premolars broadly convex, or straight, convexity reaches its maximum beneath posterior premolar.

External Morphology

Medium size: radius length 63.6 (63.1-64.2); radial-metacarpal pouch present; gular sac present in males (females not examined); tragus slightly thickened, rounded, with sac lower inner margin concave, sloping gradually upwards to form obliquely rounded top.

Pelage and Skin Colour

Dorsal pelage Prout's Brown, darkest on head and shoulders, neck region speckled with Buff Brown; ventral surface unicoloured with light shade of greyish Buff Brown; dark brown thick tuft of hair from an area posterior to eye which continues in a sparser band to inside of ear; upper outer two-thirds of ear naked; face anterior to eye thinly furred; dorsally, fur does not extend far onto wing membrane, only to between upper quarter of femur and upper half of humerus; fur does not extend to interfemoral membrane beyond a line level with the anal opening, the rest of the membrane, however, sparsely furred; ventrally, light hairs cover wing membrane to a line along radius, terminating in a thick patch at radial-metacarpal joint; wing membrane and ear conch dark brown and lighter coloured between the digits: ear conch dark brown.

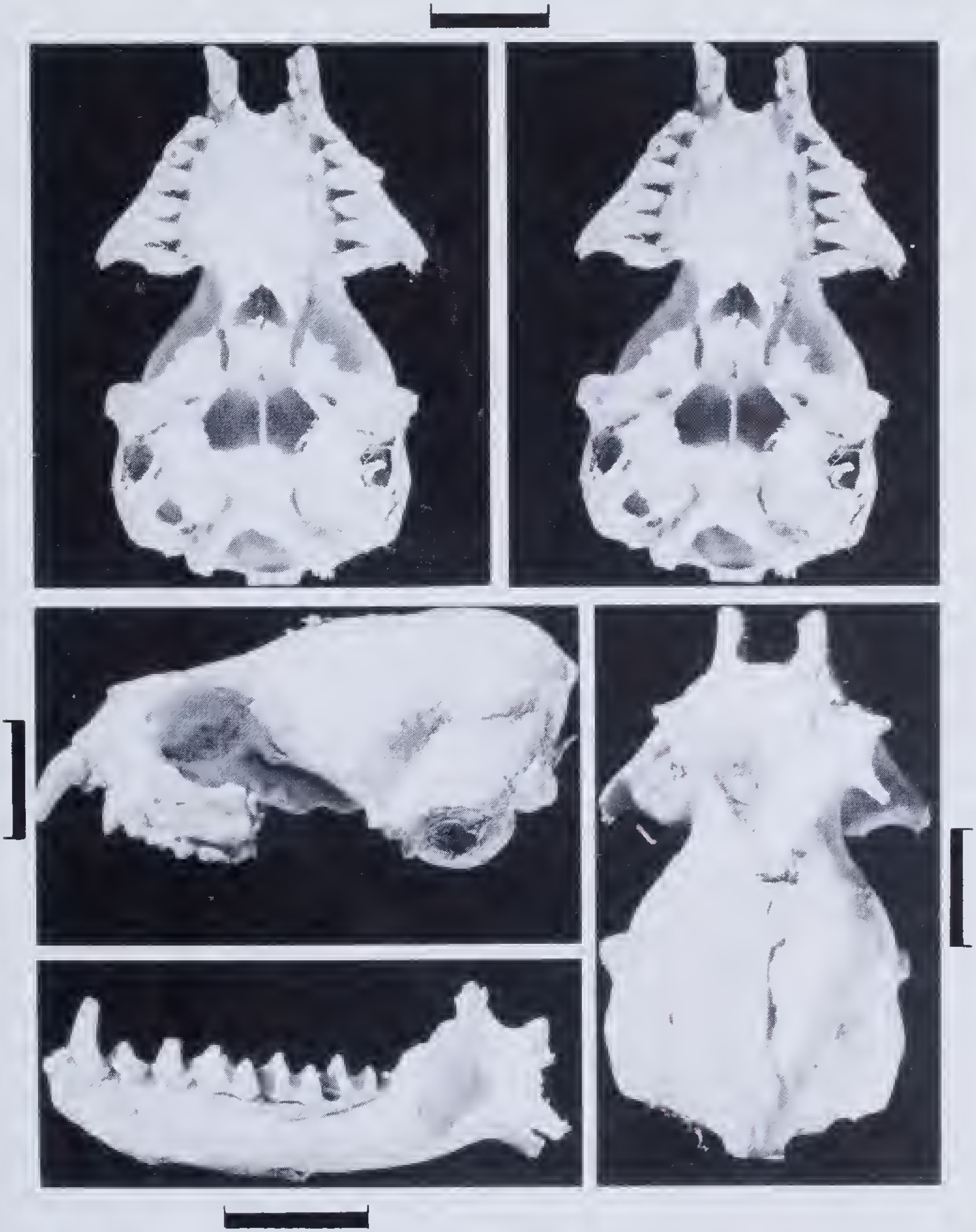

Figure 8 Skull and dentary of *Saccolaimus mixtus* (AM M3258, paratype). Ventral view of skull is presented as stereopairs. Scale lines are 5.0 mm.

Glans Penis

Not available for examination.

Baculum

Not available for examination.

Distribution

Saccolaimus mixtus is chiefly a south east Papua New Guinea species (Honacki *et al.* 1982; Koopman 1984b). In Queensland, three specimens have been collected from Brown's Creek, Pascoe River, in the northern part of Cape York Peninsula and another seven from Weipa (Figure 6f).

Natural History

Saccolaimus mixtus is rare in collections. In western Papua New Guinea it roosts in limestone caves (Richards 1983b). It is insectivorous and predatory, it forages above the canopy in tall open forests. No information is available on its reproduction.

Specimens Examined

Listed in Appendix 1.

Taphozous Geoffroy, 1813

Taphozous Geoffroy (Saint-Hilaire), É. (1813). Description des mammifères qui se trouvent en Égypte, pp 99-144. In: *Description de l'Egypte, ou recueil des observations et des recherches qui ont été faites en Égypte pendant l'expédition de l'armee Francaise* (Ed. E.F. Jomard). Histoire Naturelle. Paris: L'Imprimerie Impériale Tom. 2 Deuxéme livr. (Vol. IX) (113-114, 126-128).

Type Species

Taphozous perforatus Geoffroy, 1813 by subsequent designation, see Miller, G.S. (1907). The families and genera of bats. Bull. U.S. Natl. Mus. 57: i-xvii, 1-282, pls 1-14.

Referred Australian species

Taphozous australis Gould, 1854
Taphozous georgianus Thomas, 1915
Taphozous troughtoni Tate, 1952
Taphozous kapalgensis McKean and Friend, 1979
Taphozous hilli Kitchener, 1980

Diagnosis (mean values)

The following diagnosis refers only to Australian emballonurids.

Differs from *Saccolaimus* in being considerably smaller in all measurements. Skull moderately rather than heavily ossified; sagittal crest either absent or weak rather than well developed, barely reaches occiput, often terminates with a rounded crest that prominently reaches occiput; anterior lacerate foramen and sphenorbital sinus separated by a thin rather than a wide band; premaxilla almost overlap rather than abut nasals; postorbital ridges weak rather than strong, joining sagittal crest at rather than near or well posterior to postorbital ridges; bulla incomplete rather than complete with greater rather than less than 50 percent of cochlear region exposed; frontal region relatively narrow rather than wide; lower outline of mandible markedly concave rather than convex beneath premolars; anterior premolar relatively small, almost one-fifth rather than one-third height and crown area of posterior premolar; sphenoid pit generally larger, with a flat base rather than small with a v-shaped base; posteroventral face of basisphenoid in contact with cochlea only, rather than with both cochlea and bulla; paraoccipital process shorter than rather than almost level or longer than occipital condyle; braincase relatively robust and narrower relative to greatest skull length; first upper molar parastylar area well developed rather than reduced; inner margin of ear papillate. Baculum and glans penis relatively smaller than in *Saccolaimus* (see diagnosis of *Saccolaimus* for comparative measurements).

Distribution

Distributed in the Ethiopian, Palaearctic, Indo-Malayan and Australian Regions (Koopman 1970, Tate 1941).

Taphozous australis Gould, 1854

Figures 3d, 4c, 9, Table 1

Taphozous australis Gould, J. (1854). The mammals of Australia. Pt. 6, London (1 unnumbered page of text. 14th pl of Pt. 6 (= Vol. 3 pl. 32)

Taphozous fumosus De Vis, C.W. (1905). Bats. Ann. Qld. Mus. 6: 36-40.

Relevant taxonomic decision

Troughton, E. le G. (1925). A revision of the genus *Taphozous* and *Saccolaimus* (Chiroptera) in Australia and New Guinea, including a new species, and a note on two Malayan forms. Rec. Aust. Mus. 14: 313-341 pls 47-48.

Syntypes

BMNH 55.11.7.10, skin and skull and BMNH 55.11.7.11, skin and skull, from maritime caves in sandstone cliffs, Albany Island, Queensland.

Diagnosis (mean values)

Differs from *T. georgianus* in having shorter sphenoid pit (3.8 v. 4.2) and digit III/phalanx 1 length (19.8 v. 20.6); larger mastoid width (11.1 v. 10.8); wider distance outside bullae (10.6 v. 10.0); gular sac present in males and represented by a rudimentary edge in females rather than absent; intertemporal constriction wide rather than narrow; width of braincase at zygomatic arch (BW) wide rather than narrow, e.g. BW: greatest skull length ratio: 0.5 v. 0.49; cranium more inflated; sphenoid pit anteriorly broadly rounded rather than pear shaped, anterior edge terminating approximately 1 mm from the large vacuities outside nasal cavities rather than reaching forward to hind level of these vacuities; sagittal crest weak, not reaching occiput. Glans penis larger (3.1 v. 2.1), with more spines per unit area, head with two mounds one large and the other secondary, rather than a single complex mound; mid ventral ridge uniform, not terminating in an elevated skin. Baculum larger (0.4 v. 0.3), laterally expanded at mid length and sinusoidal in lateral profile rather than small and stump like.

Differs from *T. hilli* in having slightly larger skull, dentary, teeth and external characters: zygomatic width (13.1 v. 12.8), mastoid width (11.1 v. 10.4), distance outside bullae (10.6 v. 9.9), canine width (2.1 v. 1.7), inter-upper canine distance (4.0 v. 3.5), upper maxillary tooth row crown length (9.6 v. 8.6); sphenoid pit smaller (3.4 v. 4.1); frontal depression of skull more deeply excavated; anterior rim of mesopterygoid fossa v-shaped rather than rounded; basisphenoid pit rounded rather than angular; canines large rather than slender; inter-temporal constriction broader; sphenoid pit terminates anteriorly almost 1 mm from large vacuities outside nasal cavity rather than level with these vacuities. Glans penis long (3.1 v. 2.1), constricted proximally rather than a more uniform rod shape; head with two mounds rather than with a single one. Baculum narrower (0.1 v. 0.3), and sinusoidal in lateral profile, not expanded proximally.

Differs from *T. kapalgensis* in averaging slightly larger: zygomatic width (13.1 v. 12.9), distance outside bullae (10.6 v. 9.5), upper maxillary tooth row crown length (9.6 v. 9.3); sphenoid pit shorter (3.4 v. 3.8); intertemporal constriction broader; sphenoid pit broadly rounded anteriorly, edge terminating about 1 mm from vacuities rather than reaching forward to hind level of these vacuities; frontal depression more deeply excavated; zygomatic arch without anterior spike; lambdoidal and sagittal crests weak rather than well developed. Glans penis slightly shorter (3.1 v. 3.3), head with two mounds rather than a single sharply pointed mound. Baculum lateral and dorsal width slightly smaller (0.2 v. 0.3, 0.1 v. 0.2 respectively), dorsally expanded in lateral profile at distal one-third rather than approximate bullet shaped, not differentially ossified.

Differs from *T. troughtoni* in having smaller skull, dentary, teeth and external characters: zygomatic width (12.9 v. 14.8), mastoid width (11.1 v. 12.1), distance outside bullae (9.5 v 11.4), canine width (2.1 v. 2.3), inter-upper canine distance (4.0 v. 4.6), upper maxillary tooth row crown length (9.6 v. 10.9), sphenoid pit length (3.4 v. 4.5), digit III phalanx I length (19.8 v. 23.5); males with gular pouch, females with rudimentary edge of pouch rather than absent; postorbital process much shorter; mesopterygoid fossa anterior rim less v-shaped rather than sharply v-shaped; sagittal and lambdoidal crests not sharply edged, weaker. Glans penis head with two mounds rather than one; proximal ventral skin at tip not elevated midventrally. Baculum longer (0.4 v. 0.3), dorsal profile swollen mid length rather than bullet shaped, lateral profile sinusoidal rather than bullet shaped.

Description (means and ranges)

Skull and Dentary (Figure 9)

Generally medium sized in most characters: greatest skull length 21.6 (21.4-22.0); zygomatic width 13.1 (12.9-13.3), mastoid width 11.1 (10.8-11.4), distance outside bullae 10.6 (10.5-10.7), canine width 2.1 (2.0-2.2), inter-upper canine distance 4.0 (3.9-4.1), upper maxillary tooth row crown length 9.6 (9.4-9.8), sphenoid pit length 3.4 (3.2-3.6), inter-temporal constriction broad; sphenoid pit short; frontal depression deeply excavated; interorbital region flattened; sphenoid pit deep, median septum rising as high as floor of mesopterygoid fossa; cranium moderately inflated; sphenoid pit rounded anteriorly, anterior edge terminating approximately 1 mm from large vacuities outside nasal cavities; sagittal crest weak, not reaching occiput.

Figure 9 Skull and dentary of *Taphozous australis* (AM M4419). Ventral view of skull is presented as stereopairs. Scale lines are 5.0 mm.

External Morphology

Medium sized: radius length 65.4 (63.5-67.6); males with gular sac, represented by a rudimentary edge only in females; radial-metacarpal pouch present.

Pelage and Skin Colour

Dorsal pelage predominantly Bister with Pale Olive Buff guard hairs; ventral hairs Snuff Brown; sides of proximal half of abdomen heavily furred with Tawny Olive fur; forehead (except area of frontal depression) and chin sparsely haired with Buffy Brown; ear with inner margin speckled with Buffy Brown hair externally, fur extending to lower quarter of external base, remainder either naked or very faintly haired with Buffy Brown hair; sparse Avellaneous fur extends to wing membranes above and below to a line drawn between the proximal one-third of humerus and femur; interfemoral membrane furred dorsally with Tawny Olive to a line where tail perforates membrane, and ventrally not beyond anus and femora; plagiopatagium sparsely furred with Tawny Olive fur posteriorly, antebrachial membrane naked on both surfaces except area close to shoulders; skin of plagiopatagium, rhinarium, lips, face, tragus and ears Saccardo's Umber; basal half of chin almost bare; dactylopatagium Sepia.

Glans Penis

Length 3.1 (3.0-3.1) (N = 3); surface with high density of spines; spines of uniform size; head of glans penis with two mounds, one large, the other secondary (Figure 3d).

Baculum

Length 0.4 (0.3-0.5) (N = 3); dorsal profile swollen mid length; lateral profile sinusoidal (Figure 4c).

Distribution

Except for one old record from southeastern Papua New Guinea which Koopman (1984b) and Honacki *et al.* (1982) speculate is probably accidental or erroneous, the species is restricted to Australia and the Torres Strait Islands, N.E. coastal Queensland and Cape York Peninsula (Figure 6a).

Natural History

Taphozous australis is uncommon in collections. Roosting sites include caves, rock ledges and boulders. Individuals usually roost separately, but clusters of two to five bats may form in winter. The species is usually solitary or forms small social aggregations. It is insectivorous and predatory and leaves roosting sites just after dark to hunt for insects. Feeding is at the daytime roosting sites or at nearby feeding stations (Hall 1983a).

Knowledge on reproduction in *T. australis* is scanty although Hall (1983a) observed that groups of breeding females have been found in September and speculates that most births probably occur in October or November. In males, the testes are abdominal in September but scrotal in April.

There is a build up of body fat in autumn. However, it is not known whether this species undergoes hibernation. Hall (1983a) observed that individuals captured in mid August were inactive for about 10 minutes after being disturbed.

Specimens Examined

Listed in Appendix I.

Taphozous georgianus Thomas, 1915

Figures 3e, 4d, 10; Table 1

Taphozous australis georgianus Thomas, O. (1915). Scientific results from the mammal survey No. XI K. — Notes on *Taphozous* and *Saccolaimus*. J. Bombay nat. Hist. Soc. 24: 57-63.

Holotype

BMNH 44.2.27.59 female skin (wet) and skull from King George Sound, Western Australia.

Relevant taxonomic decisions

Troughton, E. le G. (1925). A revision of the genus *Taphozous* and *Saccolaimus* (Chiroptera) in Australia and New Guinea, including a new species, and a note on two Malayan forms. *Rec. Aust. Mus.* 14: 313-341 pls 47-48; and McKean, J.L. and Price, W.J. (1967). Notes on some Chiroptera from Queensland, Australia. *Mammalia* 31: 101-119.

Diagnosis (Mean values)

Differs from *T. australis* as described in the diagnosis of *T. australis.*

Differs from *T. hilli* in that skull, dentary, teeth and external characters average slightly larger: zygomatic width (13.2 v. 12.8), mastoid width (10.8 v. 10.4), canine width (2.0 v. 1.7), inter-upper canine distance (4.1 v. 3.5), upper maxillary tooth row crown length (9.7 v. 8.6), digit III/phalanx I length (20.6 v. 19.6); gular sac absent in both sexes rather than present in males and represented by a rudimentary area in females; frontal depression deeply excavated rather than shallow; mesopterygoid groove anterior rim v-shaped rather than rounded; basiphenoid pit rounded rather than angular; canines larger and wider rather than slender and short. Glans penis longer (2.8 v. 2.1), head complex and larger rather than a simple mound, proximal end with ventral elevated convoluted edge rather than simple. Baculum smaller (0.3 v. 0.4), a tiny almost oval stump in dorsal profile rather than an irregular shape.

Differs from *T. troughtoni* by averaging smaller in most skull, dentary and external characters: zygomatic width (13.2 v. 14.8), mastoid width (10.8 v. 12.1), distance outside bullae (10.0 v. 11.4), canine width (2.0 v. 2.3), inter-upper canine distance (4.1 v. 4.6), upper maxillary tooth row crown length (9.7 v. 10.9), sphenoid pit length (4.2 v. 4.5), digit III/phalanx I length (20.6 v. 23.5); postorbital process short rather than extremely long; mesopterygoid fossa anterior rim not sharply v-shaped; sagittal and lambdoidal crests weaker rather than sharply edged; glans penis shorter (2.3 v. 3.0), head with mound complex rather than simple, midventral line wider rather than narrower. Baculum tiny, almost oval in dorsal profile rather than bullet shaped.

Differs from *T. kapalgensis* in having smaller mastoid width (10.8 v. 11.1), but larger: zygomatic width (13.2 v. 12.9); distance outside bullae (10.0 v. 9.5); upper maxillary tooth row crown length (9.7 v. 9.3), sphenoid pit length (4.2 v. 3.8), digit III/phalanx I length (20.6 v. 21.3); relatively wider interorbital and palatal regions; gular pouch absent in both males and females rather than present in males and represented by a rudimentary edge in females; frontal depression of skull deeply excavated rather than shallow; sphenoid pit edge more circular; upper canines short, more robust and slightly projecting outwards rather than not projecting outwards; inflection of concavity at anterior end of dentary sharp rather than slight; zygomatic spike absent rather than present. Glans penis shorter (2.8 v. 3.3), less inflated laterally; proximal end with elevated convoluted edge rather than without convolution; head with complex rather than simple, elevated and sharply pointed mound. Baculum smaller (0.3 v. 0.4), tiny almost oval stump in dorsal profile, uniformly ossified rather than bullet shaped in dorsal profile and differentially ossified.

Description (means and ranges)

Skull and Dentary (Figure 10)

Generally medium sized: greatest skull length 21.4 (20.0-23.1); zygomatic width 13.2 (12.1-14.4); mastoid width 10.8 (10.1-11.7); distance outside bullae 10.0 (9.2-11.0); canine width 2.0 (1.5-2.3); inter-upper canine distance 4.1 (3.4-4.5), upper maxillary tooth row crown length 9.7 (8.8-10.5), sphenoid pit length 4.2 (3.5-4.7); intertemporal constriction narrow; sphenoid pit pear-shaped, anterior ends narrowed, terminating level with posterior edge of large vacuities outside nasal cavities; sagittal crest weak but reaching occiput.

External Morphology

Medium sized: radius length 68.1 (61.1-73.4); gular sac absent in both sexes; tragus outer margin concave on upper half; radial-metacarpal pouch present.

Pelage and Skin Colour

Dorsum clearly bicoloured: anterior half (with a bare chin) Olive Brown speckled with Buff Brown guard hairs, posterior half Mummy Brown; ventral surface Brownish Olive speckled with Deep Neutral Gray — this pelage also covers anal region; uropatagium ventral surface sparsely haired with Drab along humerus, radius and to radial-metacarpal pouch; skin of plagiopatagium, ears, rhinarium, uropatagium, dactylopatagium and lips Sepia; skin of forehead bare, Sepia.

Glans Penis

Length 2.8 (2.7-2.9) (N = 6); head mound complex with numerous skin folds; midventral line elevated and terminating proximally into a convoluted elevated skin; spines present except at dorsal tip (Figure 3e).

Baculum

A small almost oval stump in dorsal profile 0.3 (0.2-0.35) (N = 6), with ventrolateral proximal protuberance (Figure 4d).

Distribution

Extensive distribution across northern Australia and extends some distance south of the Tropic of Capricorn in Western Australia. There are no published records of this species from near its alleged type locality in Western Australia (contrast Figures 1 and 6b).

Natural History

Taphozous georgianus is very common in tropical and subtropical regions of Australia. Roosting sites include caves, rock fissures and abandoned mines. Because it

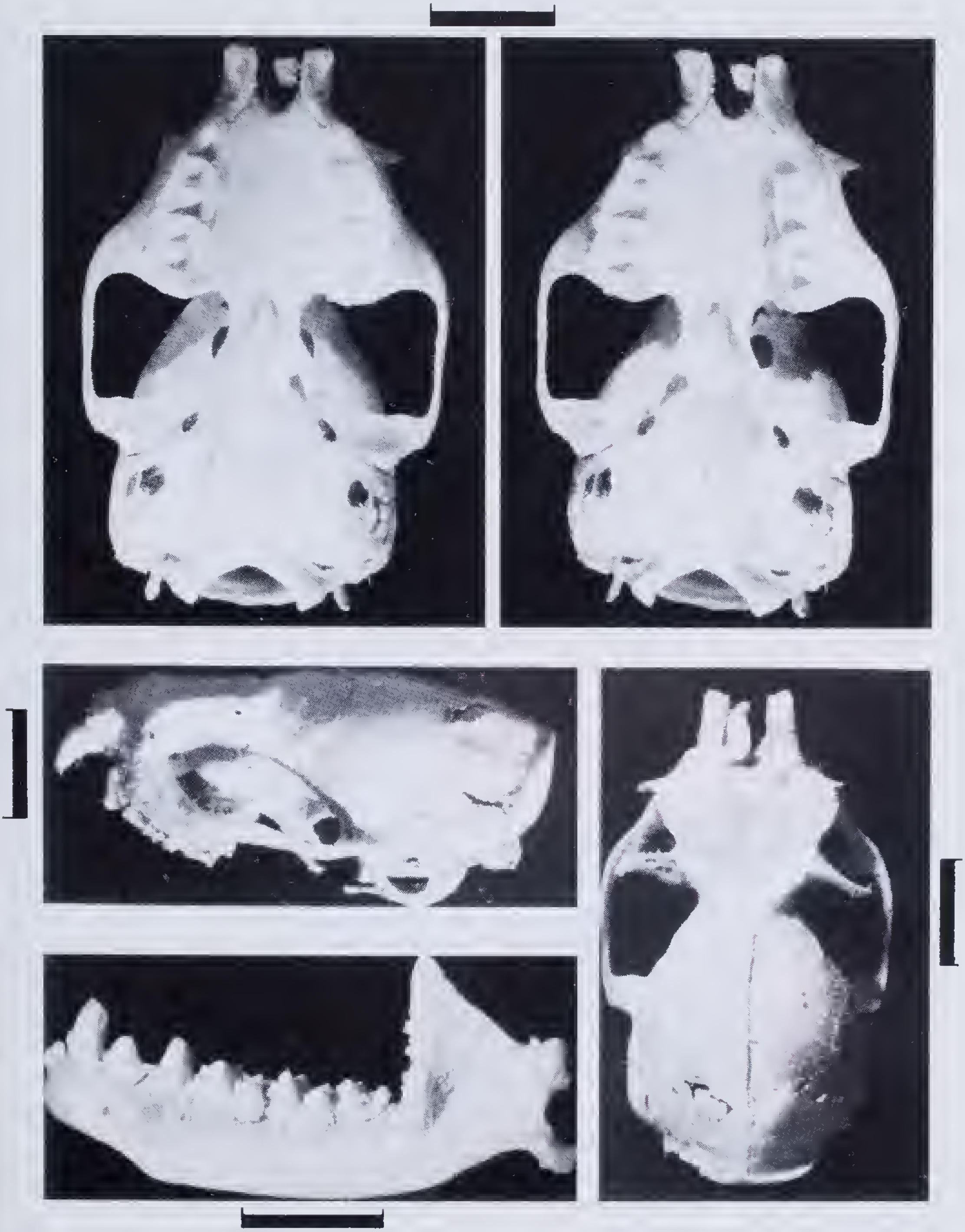

Figure 10 Skull and dentary of *Taphozous georgianus* (WAM M23032). Ventral view of skull is presented as stereopairs. Scale lines are 5.0 mm.

occupies man-made structures soon after they have been vacated its distribution may have expanded in recent times. Populations of this species appear to be locally mobile and they are known to vacate a cave for a considerable part of the year (Kitchener 1983a). Although up to 17 individuals have been collected from one cave the species is usually solitary or forms small aggregations (Kitchener 1983a). However, in two abandoned horizontal asbestos mines in the Hamersley Range and in a vertical mine at Cobra Station (both areas located in the Pilbara region of Western Australia) more than 50 individuals were observed by the senior author in a single mine. Also roosting in the same cave were individuals of *Eptesicus* (= *Pipistrellus*) *finlaysoni*, (see Hill and Harrison, 1987; Volleth and Tidemann 1989). The greatest numbers were found at the end or in the darker portions of the cave. The bats were mainly located roosting in the roof in a horizontal mine or in cracks in a vertical mine. Roosting individuals had a characteristic crab-like posture.

It is insectivorous with an apparent preference for Coleoptera. The bat is frequently seen foraging at intermediate heights above a wide variety of vegetation types and over pools and creeks (Kitchener 1983a).

Kitchener (1973) found that females give birth to young between October and February with only the right ovary functional and foetus only occur in the right uterine horn. In males spermatogenesis proceeds throughout the year but the position of the testes varies seasonally, being scrotal in summer and more abdominal in autumn, winter and spring. Although Kitchener (1973, 1976) concluded that *T. georgianus* is monoestrous, there is the possibility that it may give birth to young a second time during this long breeding season. This fact may not be detected in museum specimens if corpora lutea persists for only a short period following parturition (Chimimba and Kitchener 1987). More importantly, the study by Kitchener (1973) included specimens of *T. hilli* (described subsequently) and will need to be re-examined.

Specimens Examined

Listed in Appendix 1.

Taphozous troughtoni Tate, 1952

Figures 3f, 4e, 11; Table 1.

Taphozous troughtoni Tate, G.H.H. (1952). Results of the Archbold Expedition. No. 66. Mammals of Cape York Peninsula, with notes on the occurrence of rain forest in Queensland. Bull. Am. Mus. nat. Hist. 98: 563-616.

Holotype

AMNH 162708 female, skin and skull, from Rifle Creek, 10 miles East of Mt Isa, N.W. Queensland.

Diagnosis (mean values)

Differs from *T. australis* and *T. georgianus* as described in the diagnoses of the two species.

Differs from *T. hilli* in that skull, teeth, dentary and external characters average larger: zygomatic width (14.8 v. 12.8), mastoid width (12.1 v. 10.4), distance outside bullae (11.4 v. 9.9), canine width (2.3 v. 1.7), inter-upper canine distance (4.6 v. 3.5), upper maxillary tooth row crown length (10.9 v. 8.6), sphenoid pit length (4.5 v. 4.1), digit III/phalanx I length (23.5 v. 19.6); gular sac absent in both sexes rather than present in males and rudimentary in females; more steeply excavated frontal depression; mesopterygoid fossa posterior rim sharply v-shaped rather than rounded; postorbital processes relatively long rather than shorter; lambdoidal crest much more sharply edged, flattening at its apex to a more rounded crest. Glans penis larger (3.0 v. 2.1), head with mound elevated and pointed rather than simple; swollen midventrally with a proximal skin elevated and convoluted rather than a more uniform proximal outline. Baculum smaller (0.3 v. 0.4), bullet shaped rather than with more irregular outline.

Differs from *T. kapalgensis* generally by its larger size: zygomatic width (14.8 v. 12.9), mastoid width (12.1 v. 11.1), distance outside bullae (11.4 v. 9.5), canine width (2.3 v. 2.0), inter-upper canine distance (4.6 v. 4.2), upper maxillary tooth row crown length (10.9 v. 9.3), sphenoid pit length (4.5 v. 3.8), digit III/phalanx I length (23.5 v. 21.3); both sexes without a gular sac rather than present in males and rudimentary in females; postorbital processes extremely long rather than short; mesopterygoid fossa anterior rim more sharply v-shaped; sagittal and lambdoidal crest sharply edged rather than weak; zygomata without spike. Glans penis shorter (3.0 v. 3.3), spines slightly larger rather than minute and almost reduced to wart-like structures; head mound large with a small secondary mound rather than a single small, pointed mound; midventrally elevated, with a proximal elevated convoluted skin rather than elevated distally only. Baculum smaller (0.3 v. 0.4), uniformly rather than differentially ossified, bullet shaped rather than irregular outline with marked dorsoventral constriction.

Description (means and ranges)

Skull and Dentary (Figure 11)

Large *Taphozous:* greatest skull length 24.1 (24.0-24.3); zygomatic width 14.8 (14.7-14.9), mastoid width 12.1 (11.9-12.2), distance outside bullae 11.4 (11.2-11.5), canine width 2.3 (2.2-2.3), inter-upper canine distance 4.6 (4.5-4.8), upper maxillary tooth row crown length 10.9 (10.8-11.0), sphenoid pit length 4.5 (4.2-4.8); extremely long postorbital processes; sagittal and lambdoidal crests sharply edged; mesopterygoid fossa anterior rim sharply v-shaped.

External Morphology

Large: radius length 74.6 (72.7-75.6); gular sac absent in both males and females; radial-metacarpal pouch present.

Pelage and Skin Colour

Predominant pelage colour on dorsal surface Olive Brown, guard hairs, however, Pale Mouse Gray; ventral surface hairs Olive Brown from chin to shoulders, posteriorly, Saccardo's Umber with guard hairs Pale Mouse Gray; uropatagium, close to abdomen from shoulder to femur and including anal region heavily furred with Saccardo's Umber; lower surface of plagiopatagium along radius and humerus to radial-metacarpal pouch sparsely furred with Mouse Gray; skin of rhinarium, plagiopatagium, uropatagium, lips, face, tragus and dactylopatagium Fuscous; area of frontal depression not furred, Fuscous.

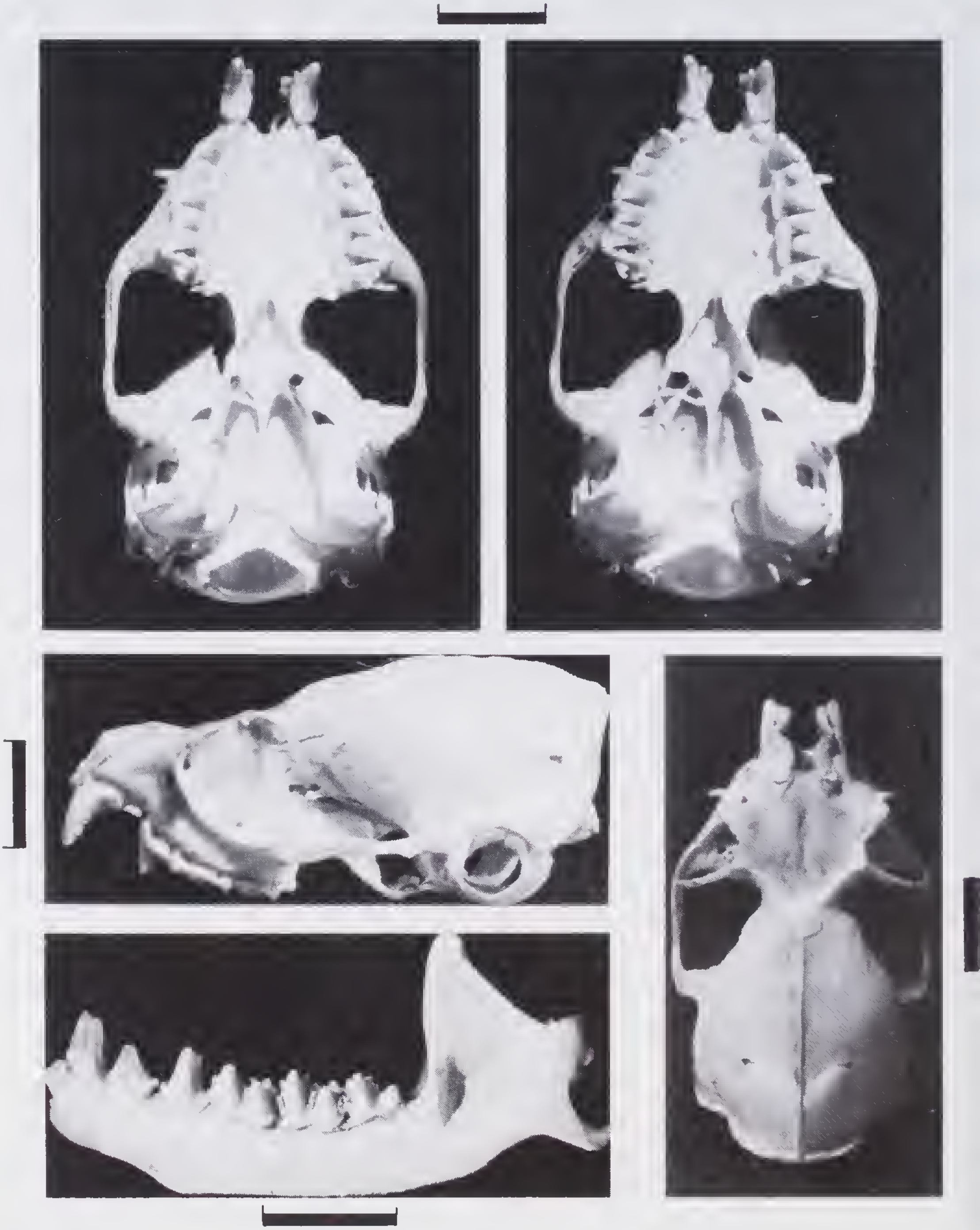

Figure 11 Skull and dentary of *Taphozous troughtoni* (CM M13213). Ventral view of skull is presented a stereopairs. Scale lines are 5.0 mm.

Glans Penis

Length 3.0 (N = 1), head with two mounds, one large, the other secondary, mid-ventrally elevated, terminating proximally with an elevated convoluted skin (Figure 3f).

Baculum

Length 0.3 (N = 1), simple, bullet shape (Figure 4e).

Distribution

Taphozous troughtoni has only been recorded from the Mt Isa area, N.W. Queensland.

Natural History

The species is very rare in collections and nothing is recorded of its natural history.

Taphozous hilli Kitchener, 1980

Figures 3g, 4f, 12, Table 1

Taphozous hilli Kitchener, D.J. (1980). *Taphozous hilli* sp. nov. (Chiroptera: Emballonuridae), a new Sheath-tailed bat from Western Australia and Northern Territory. Rec. West. Aust. Mus. 8: 161-169.

Holotype

WAM M 18260, adult female skin (wet) and skull extracted from Marandoo Mine site, 4.8 km 180° from Mt Bruce (22°30'03"S, 118°08'30"E), Hamersley Range National Park (No. A 30082), Western Australia.

Diagnosis (mean values)

Differs from *T. australis, T. georgianus* and *T. troughtoni* as described in the earlier diagnoses of these species.

Differs from *T. kapalgensis* in having slightly smaller skull, tooth, dentary and external characters: mastoid width (10.4 v. 11.1), canine width (1.7 v. 2.0), inter-upper canine distance (3.5 v. 4.2), upper maxillary tooth row crown length (8.6 v. 9.3), digit III/ phalanx I length (19.6 v. 21.3); distance outside bullae and sphenoid pit length longer (9.9 v. 9.5, 4.1 v. 3.8 respectively); palatal and interorbital regions wider; zygomatic arch more slender, constricted posteriorly rather than with spike. Glans penis smaller (2.1 v. 3.3), uniform rod shape rather than expanded distally with ventral keel, ventrally, head mound not elevated and pointed, spines larger not reduced to wart-like structures. Baculum dorsally more irregularly shaped, less inflected dorsoventrally, evenly ossified.

Description (means and ranges)

Skull and Dentary (Figure 12)

Skull small: greatest skull length 20.0 (19.1-21.1); zygomatic width 12.8 (12.3-13.4), mastoid width 10.4 (9.9-11.0), distance outside bullae 9.9 (9.5-10.3), canine width 1.7 (1.5-1.8), inter-upper canine distance 3.5 (3.1-4.5), upper maxillary tooth row crown length 8.6 (7.6-9.8), sphenoid pit length 4.1 (3.7-4.4); frontal depression less steeply excavated, shallower; mastoid region less inflated laterally resulting in a more robust cranium; sagittal crest low or absent; lambdoidal crest poorly developed at apex resulting in a more rounded crest; postorbital width broad; rostrum narrow anteriorly; mesopterygoid groove present, posteriorly constricted; mesopterygoid fossa anterior rim round; sphenoid pit angular, long; inner anterior rim of orbit flattened; zygomatic arch

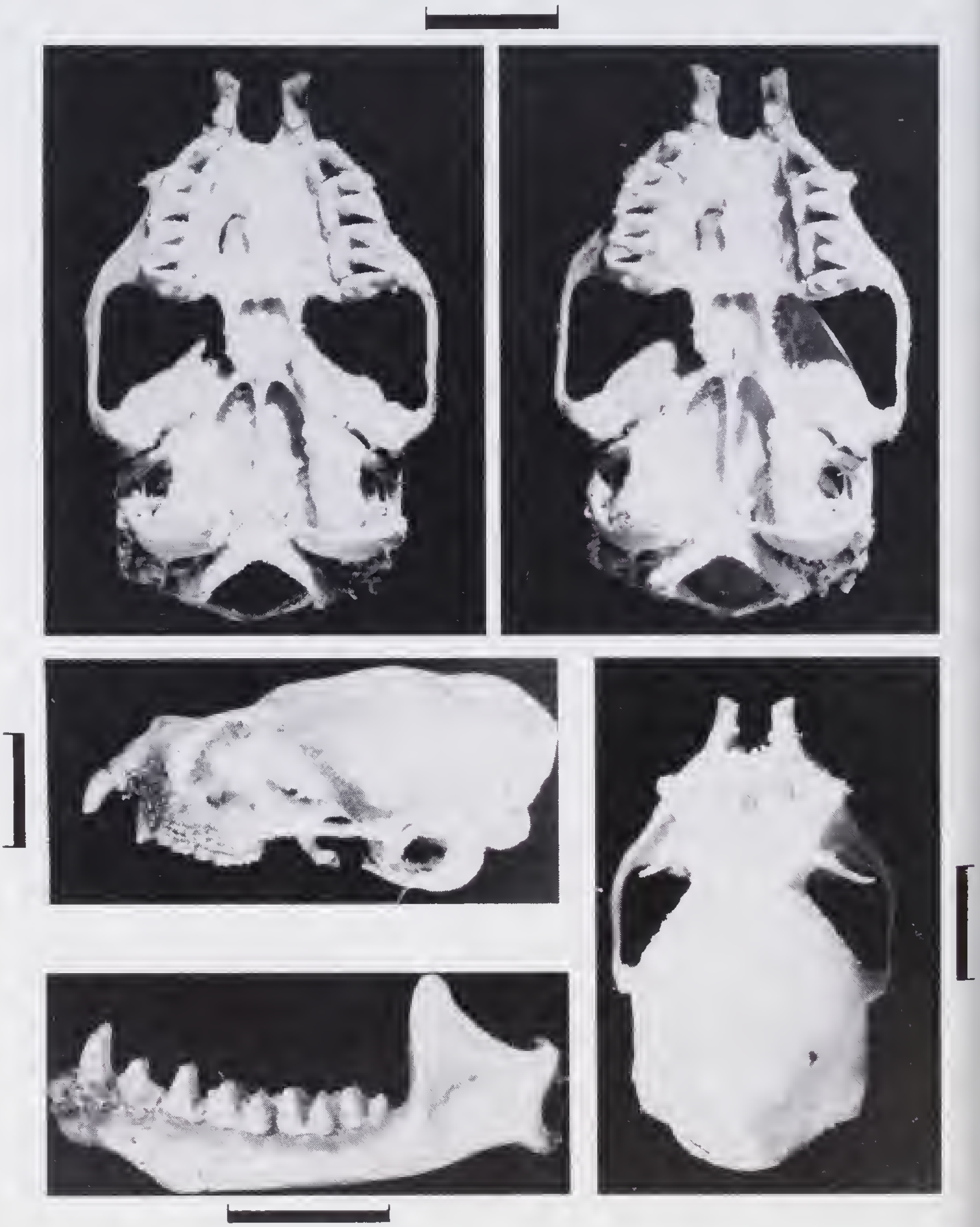

Figure 12 Skull and dentary of *Taphozous hilli* (WAM M18260, holotype). Ventral view of skull is presented as stereopairs. Scale lines are 5.0 mm.

slender, constricted posteriorly; canines short, slender, small anterobasal cusp about a third length of the tooth; anterior upper premolar weak; posterior premolar with small anterobasal cusp and reduced cingulum.

External Morphology

Small size: radius length 67.7 (60.4-71.7); gular pouch present in males and represented by a rudimentary edge in females; radial-metacarpal pouch present.

Pelage and Skin Colour

Dorsal pelage on head to sternal region Mummy Brown, rump Bister — these colours from tips of hairs, basal two-thirds of which Buckthorn Brown; Raw Umber hairs cover area where tail passes dorsally through sheath; ventral pelage from head to chest Sepia tipped with Olive Brown, posteriorly Snuff Brown tipped with Saccardo's Umber; uropatagium furred lightly in anal region only; propatagium sparsely covered with Clay colour hairs; plagiopatagium lightly furred with Deep Olive hairs along edges of upper arm and forearm; patch of dense Buffy Brown hairs at entrance of radial-metacarpal pouch; few Buffy Brown hairs cover ventral side of radial-metacarpal pouch; skin of plagiopatagium, lips, face, tragus and ears Olive Brown; skin of dactylopatagium Olive Brown, skin of rhinarium Bister; the first third of chin bare but posterior two-thirds sparsely covered with Olive Brown hairs; fur on forehead not as dense as rest of dorsum, dominant pelage Isabella from guard hairs.

Glans Penis

Length 2.1 (2.0-2.2) (N = 6), rod shaped, surface with minute spines pointing proximally; head of glans penis with small mound visible laterally and ventrally but barely visible dorsally (Figure 3g).

Baculum

Small 0.4 (0.3-0.5) (N = 6), shape irregular, laterally flat at the proximal end, ventral and dorsal surfaces slightly concave (Figure 4f).

Distribution

Widely distributed in the semi-arid Pilbara, Murchison regions and Gibson Deserts of Western Australia as far east as Tennant Creek in the Northern Territory (Figure 6c).

Natural History

This insectivorous bat is probably common. Extensive mining operations in Western Australia have probably led to the extension of its range and may continue to do so since this species appears to utilise adits and mines soon after they have been abandoned by man. *Taphozous hilli* and *T. georgianus* have been observed roosting together. As the two species are of almost similar size, it would be interesting to know how they partition available resources. Differences in the masticatory apparatus (see morphometric analyses results) suggest that they may eat different prey. Although it remains to be demonstrated that the neck-gland plays a role in social behaviour (Kitchener 1983b), the depth of the pouch surrounding the neck gland in males of *T. hilli* is correlated with seasonal enlargement of the seminiferous tubules and accessory male glands (Kitchener 1976). A single young is born between early summer and mid-autumn. After parturition, the female reproductive organs become relatively quiescent until early winter. Males appear to be in active reproductive conditions throughout the year.

Specimens Examined

Listed in Appendix I.

Taphozous kapalgensis McKean and Friend, 1979

Figures 3h, 4g, 13; Table 1

Taphozous kapalgensis McKean, J.L. and Friend, G.R. (1979). *Taphozous kapalgensis,* a new species of Sheath-tailed bat from Northern Territory, Australia. Vict. Nat. 96: 239-241.

Holotype

CM 4800, male, skin and skull, from 'Kapalga', at the edge of a western flood plain of the South Aligator River near Rookery Point (12°32'S, 132°23'E), Northern Territory.

Diagnosis (mean values)

Taphozous kapalgensis differs from *T. australis, T. georgianus, T. troughtoni* and *T. hilli* as described in the earlier diagnoses of these species.

Description (means and ranges)

Skull and Dentary (Figure 13)

Medium size: greatest skull length 20.3 (20.0-20.7); zygomatic width 12.9 (12.6-13.1), mastoid width 11.1 (11.0-11.2), distance outside bullae 9.5 (9.1-9.9), canine width 2.0 (2.0-2.1), inter-upper canine distance 4.2 (4.0-4.4), upper maxillary tooth row crown length 9.3 (9.2-9.4), sphenoid pit length 3.8 (3.7-3.9); palatal and interorbital regions relatively narrow; sphenoid pit circular in outline; upper canines long, slender, not projecting outwards; inflection at anterior end of dentary only slight and not sharp or abrupt as in the other *Taphozous* species; zygomata constricted posteriorly, anterior spike present.

External Morphology

Medium size: radius length 59.3 (58.9-59.7); gular sac developed in males and represented by a rudamentary edge in females; radial-metacarpal pouch present.

Pelage and Skin Colour

Dorsal pelage predominantly Isabella Brown tipped on forehead with Buffy Brown; pelage fine, rather long on hind neck; chin hairs Isabella; rest of the ventral surface Buckthorn Brown, although guard hairs Light Ochraceous-Buff, lateral edges of posterior two-thirds of ventral region Light Ochraceous-Buff; along radius and towards radial-metacarpal pouch plagiopatagium sparsely haired with Light Ochraceous, close to pouch Light Ochraceous to Salmon; skin of plagiopatagium and uropatagium Dresden Brown, dactylopatagium Buckthorn Brown; uropatagium sparsely furred with Dresden Brown on anal region only; upper surface of uropatagium with sparse Isabella Brown fur along edges of body and over interfemoral membrane to point where tail protrudes; a band of Dresden Brown hairs extends over ventral surface of patagium between humerus and femur; ventral surface of patagium furred with Dresden Brown along outer edge of radius; tragus and ears Isabella; rhinarium Tawny-Olive.

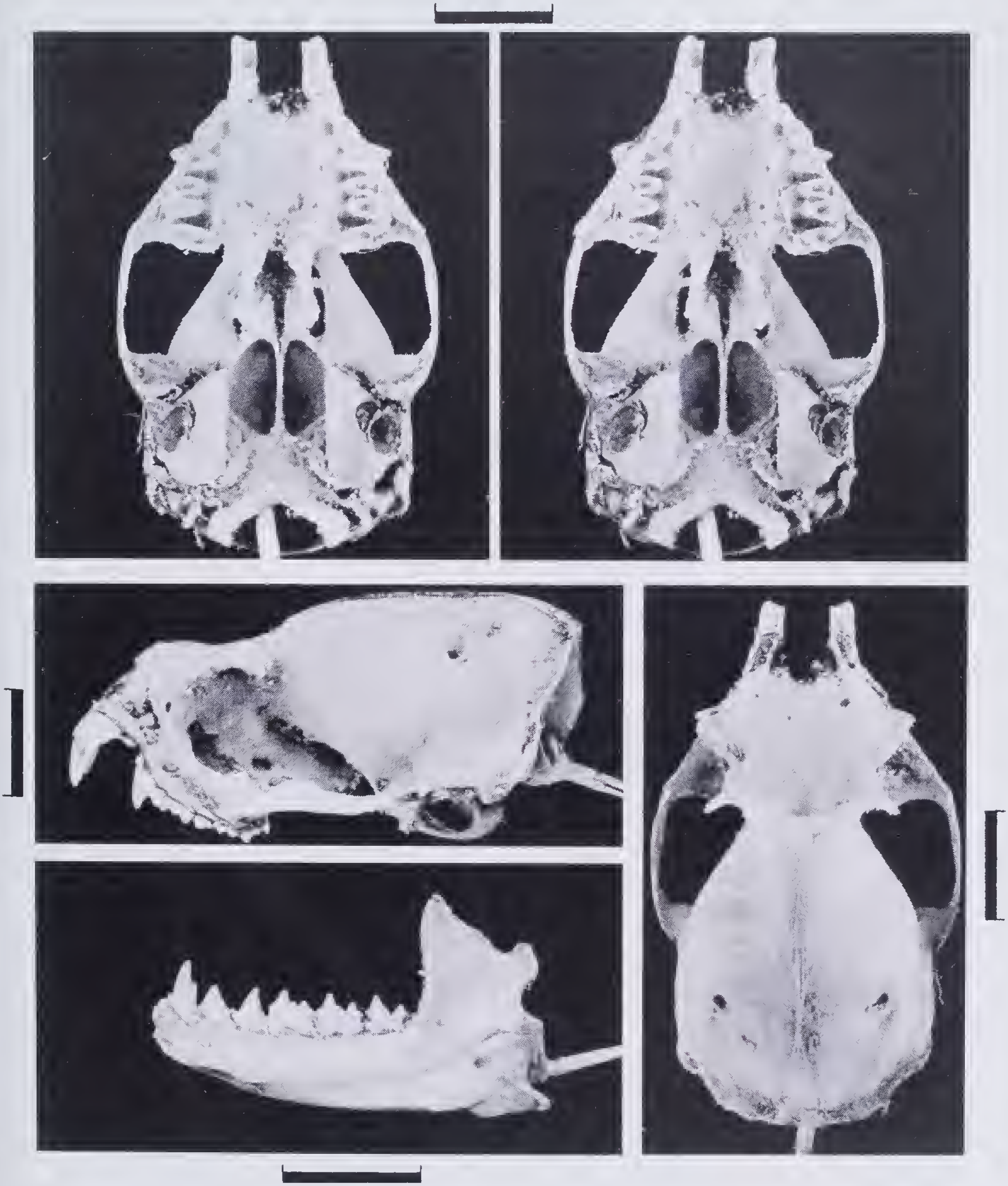

Figure 13 Skull and dentary of *Taphozous kapalgensis* (CM M4800, holotype). Ventral view of skull is presented as stereopairs. Scale lines are 5.0 mm.

Glans Penis

Length 3.3 (N = 1), head swollen, terminating in mound, with ventral keel, spines minute, almost reduced to wart-like structures (Figure 3h).

Baculum

Length 0.4 (N = 1), irregular outline, particularly in lateral profile, constricted at about distal third of length, differentially ossified (Figure 4g).

Distribution

Known only from northern Arnhem Land, Northern Territory (McKean 1983). McKean (1983) however, speculates that it may occur at the top end of the Northern Territory as there have been reports from the local residents of a similar bat in the Rose and Roper Rivers regions (Figure 6d).

Natural History

Rare. Its habitat includes open woodland and closed forest. It roosts in trees. It is insectivorous and has been observed to feed above tree canopy but comes lower when feeding over water (McKean 1983). Nothing else is known of its biology.

Taxonomic Remarks

Comparisons of the baculum and glans penis of *T. kapalgensis* with that of *T. longimanus* (Figures 3h, 3i and 4g and 4h respectively) show some basic differences. While the shape of the glans penis are generally similar the spines are low wart-like structures in *T. kapalgensis* whereas in *T. longimanus*, they are slightly larger. The head mounds are pointed in both species but are more sharply pointed in *T. longimanus*. The midventral keel in *T. kapalgensis* is confined to the distal end, it occupies the entire length of the glans penis in *T. longimanus*. The baculum is of similar length in both species but in *T. longimanus* it is more simple in outline, uniformly ossified and distally constricted; the baculum of *T. kapalgensis* is irregularly shaped and differentially ossified. These basic differences combined with the observed separation using both principal component analysis and canonical variate analyses (see subsequent section) on skull, dentary and external characters support the view that *T. kapalgensis* and *T. longimanus* are not conspecific.

Specimens Examined

Listed in Appendix I.

Morphometric Analyses: Results

Sexual dimorphism

A one-way analysis of variance within *T. georgianus*, *T. hilli* and *S. flaviventris* revealed no sexual dimorphism over all 39 characters examined. Overall, character F-ratios ranged from 0.01 to 1.36 in *T. georgianus*, 0.09 to 2.32 in *T. hilli* and 0.01 to 3.41 in *S. flaviventris*. This finding justified the pooling of males and females in the subsequent analyses.

Principal Components Analyses

Similar results were obtained when PCA's were performed using the following groupings of data: skull characters only; skull, wing and tibia length (TIB); and skull plus all external characters combined. The latter analyses, however, resulted in loss of many cases. Consequently, results presented are based on skull characters alone.

Only two factor axes from PCA's of all groupings of data had eigenvalues greater than 1. The two factor axes based on skull characters explained 87.7% of the variation. The first axis accounts for 81.9% of the variance with an eigenvalue of 20.5. The patterns of these two factor axes are shown in Figure 14. The currently recognised genera in Australia, *Taphozous* and *Saccolaimus* are not clearly separated in factor space. The results indicate that the two genera cannot be discriminated on a single axis, but they do not show any overlap. Discrete clusters are readily distinguishable for the currently recognised species in Australia: *T. hilli, T. kapalgensis* and *S. mixtus. Taphozous*

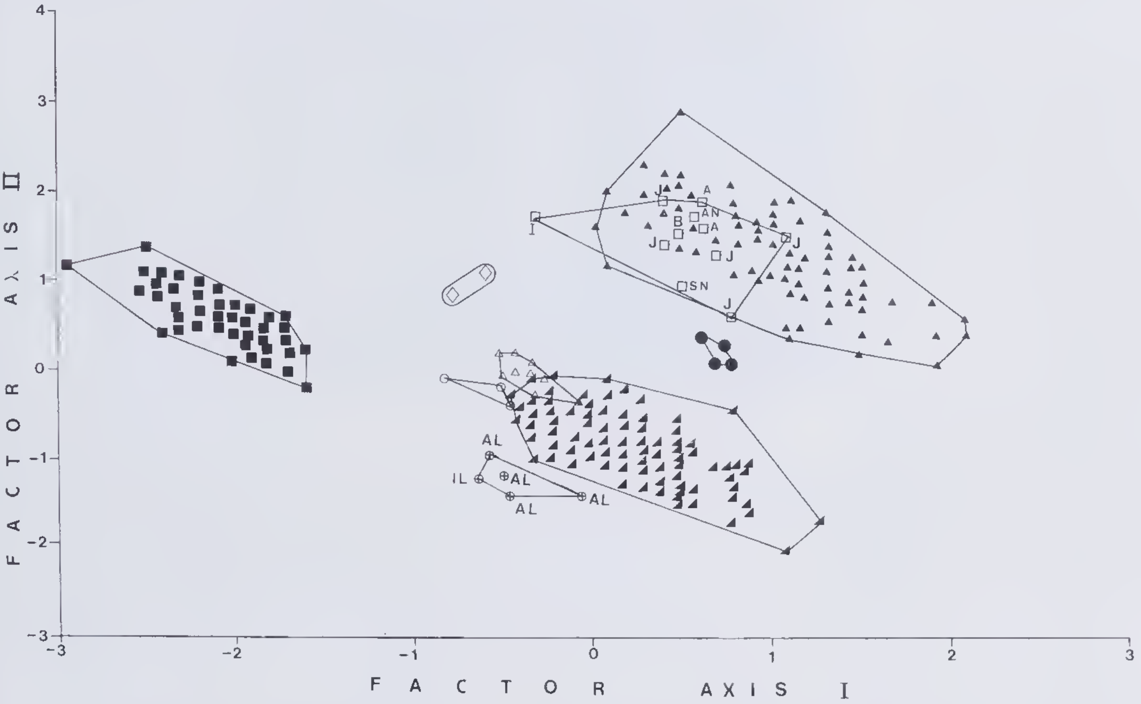

Figure 14 Scores of the first two factor axes of Australian and some Asian emballonurids examined. Data are size-free skull characters, excluding postpalatal width (PPW), with males and females combined. Species symbols are as follows: *Saccolaimus flaviventris* (▲), *S. mixtus* (◇), *S. saccolaimus* (□), *Taphozous australis* (△), *T. georgianus* (◢), *T. hilli* (■), *T. kapalgensis* (○), *T. longimanus* (●) and *T. troughtoni* (●). The locality codes for *S. saccolaimus* individuals are as follows: A = *S. saccolaimus* from Australia, AN = *S. 'nudicluniatus'* from Australia, SN = *S. 'nudicluniatus'* from the Solomon Islands, B = *S. saccolaimus* from Borneo, I = *S. saccolaimus* from India, J = *S. saccolaimus* from Java. The locality codes for *T. longimanus* individuals are as follows: AL = *T. longimanus* from Bali, IL = *T. longimanus* from India. Most points for *S. flaviventris, T. georgianus* and *T. hilli* represent multiple specimens.

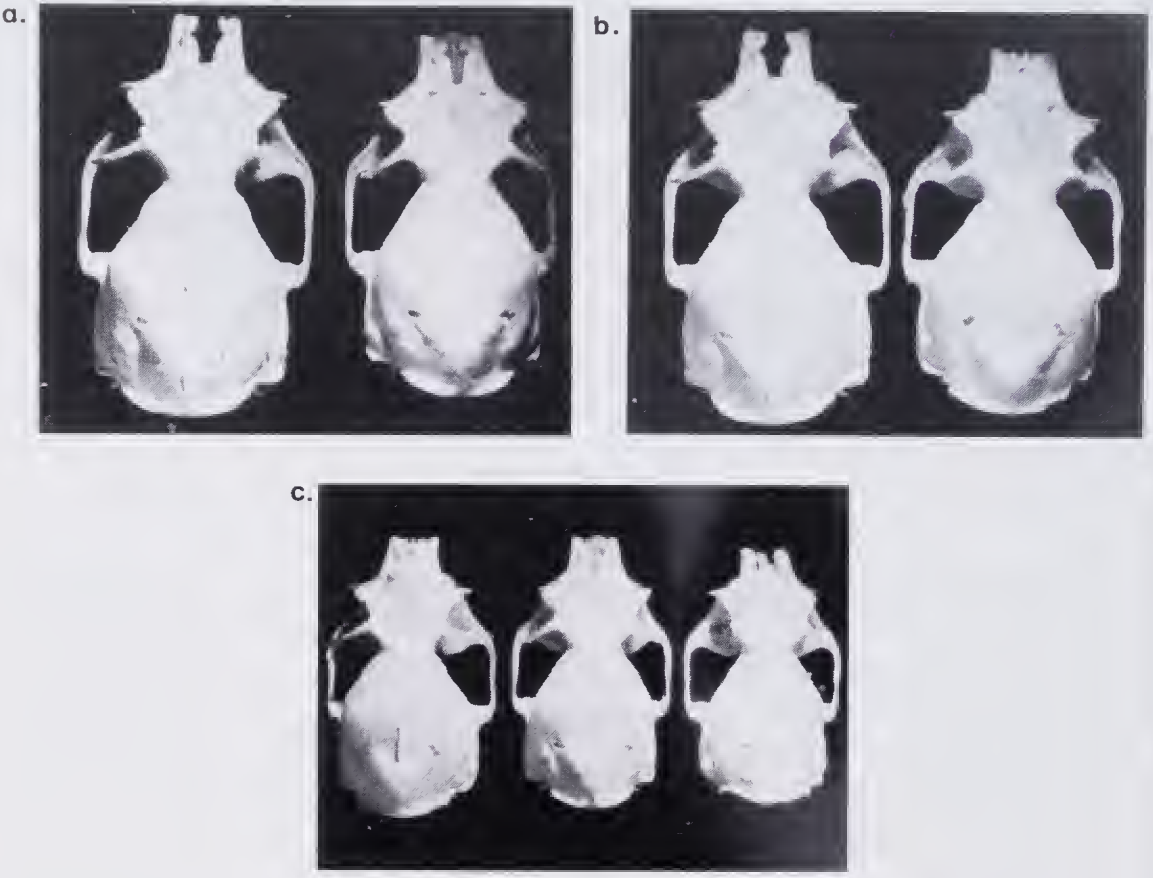

Figure 15 Dorsal view of specimens of *Taphozous georgianus* and *T. troughtoni* collected in sympatry and allopatry to illustrate the differences in dimensions of the two taxa.

(a) Sympatric specimens of *T. troughtoni* (CM M13213) (left) and *T. georgianus* (CM M13216 (right).

(b) Specimens of *T. troughtoni* (CM M13213) from Mount Isa, Queensland (left) and *T. georgianus* from Rockhampton, Queensland (JM M9976) (right).

(c) Specimens of *T. georgianus* from Rockhampton (JM M9976) Queensland, Locality 156 (left), Mount Isa (CM M13213), Queensland, locality 140 (centre) and Derby (WAM M23032) Western Australia, locality 58 in Figure 1 (right).

australis overlaps with *T. georgianus* by five individuals. Similarly, with the exception of the single specimen from India (I), all other individuals of *S. saccolaimus* lie within the *S. flaviventris* cluster. There are no association trends between individuals of *S. saccolaimus* from India (I), Java (J), Borneo (B) and Australia (A); neither are there any trends between individuals designated *S. nudicluniatus* from Australia (AN) or the Solomon Islands (SN) and individuals of *S. saccolaimus* regardless of their collecting locality. All individuals plot randomly in factor space with respect to geographic origin so that phenotypic separation is not evident between the Australian and the Asian *S.*

saccolaimus or between *S. saccolaimus* and *S. nudicluniatus*. Individuals of *T. longimanus* included in the analysis to ascertain the status of *T. kapalgensis* show the two species as distinct on the second factor axis. Within *T. longimanus* there are no trends between Indian (IL) and Balinese (AL) *T. longimanus* to suggest a high variability of the species over its range that might question the status of *T. kapalgensis*.

This analysis also separates the frequently synonymised *T. georgianus* and *T. troughtoni* on the second factor axis. Locality 140 in Queensland (Mount Isa) (Figure 1) is a good example where individuals of both *T. georgianus* and *T. troughtoni* examined occur in broad sympatry. Also available were specimens of *T. georgianus* from nearby allopatric localities 138 (Cloncurry) and 139 (Ballara). Comparative measurements presented in Appendix II and dimensions shown in Figure 15 show that individuals of *T.*

Table 2. Standardised factor scores of each character for the two factors generated from principal components analysis of *Taphozous georgianus*, *T. troughtoni*, *T. hilli*, *T. australis*, *T. kapalgensis*, *T. longimanus*, *Saccolaimus flaviventris*, *S. saccolaimus* and *S. mixtus* using skull characters, with males and females combined (for code to characters see figure 2).

		FACTOR AXES	
CHARACTER		1	2
1	Anteorbital width (AOW)	0.649	0.691
2	Least inter-orbital width (LOW)	0.559	0.778
3	Zygomatic width (ZW)	0.662	0.777
4	Rostrum length (ROL)	0.878	0.416
5	Mastoid width (MW)	0.617	0.772
6	Braincase width (BW)	0.536	0.819
7	Cranial height (CH)	0.487	0.757
8	Palatal length (PL)	0.862	0.449
9	Postpalatal width (PPW)	0.296	0.537
10	Basicranial length (BL)	0.843	0.492
11	Bulla length (BUL)	-0.046	0.760
12	Width of basisphenoid (BB)	0.504	0.707
13	Distance outside bullae (OB)	0.559	0.794
14	Canine width (CW)	0.901	0.116
15	Inter-upper canine distance (RC^1-LC^1)	0.643	0.712
16	Upper maxillary tooth row crown length (C^1-M^3)	0.832	0.453
17	Upper molar crown length (M^1-M^3)	0.801	0.540
18	Upper 2nd molar crown length (M^2L)	0.720	0.567
19	Upper 2nd molar crown width (M^2W)	0.724	0.546
20	Upper 3rd molar crown width (M^3W)	0.780	0.234
21	Inter-upper 3rd molar distance (RM^3-LM^3)	0.621	0.744
22	Lower tooth row length (LR)	0.822	0.539
23	Angular ramus to dentary condyle (RC)	0.754	0.541
24	Dentary length (DL)	0.844	0.499
25	Sphenoid pit length (SPL)	-0.440	-0.727
26	P^1 basal width (PBW)	0.689	0.660
27	Inter-lower canine distance (ICD)	0.662	0.699

Table 3. Standardised factor scores of each character for the two factors generated from principal components analysis of *Taphozous georgianus*, *T. troughtoni*, *T. hilli*, *T. australis*, *T. kapalgensis*, *T. longimanus*, *Saccolaimus flaviventris*, *S. saccolaimus* and *S. mixtus* using skull and external body characters, with males and females combined (for code to characters see figure 2).

CHARACTER		FACTOR AXES	
		1	2
1	Anteorbital width (AOW)	0.635	0.651
2	Least inter-orbital width (LOW)	0.560	0.727
3	Zygomatic width (ZW)	0.688	0.676
4	Rostrum length (ROL)	0.854	0.397
5	Mastoid width (MW)	0.613	0.732
6	Braincase width (BW)	0.557	0.777
7	Cranial height (CH)	0.505	0.734
8	Palatal length (PL)	0.824	0.440
9	Postpalatal width (PPW)	0.429	0.441
10	Basicranial length (BL)	0.826	0.470
11	Bulla length (BUL)	0.109	0.747
12	Width of basisphenoid (BB)	0.483	0.665
13	Distance outside bullae (OB)	0.581	0.765
14	Canine width (CW)	0.709	0.060
15	Inter-upper canine distance (RC^1-LC^1)	0.672	0.604
16	Upper maxillary tooth row crown length (C^1-M^3)	0.816	0.454
17	Upper molar crown length (M^1-M^3)	0.777	0.513
18	Upper 2nd molar crown length (M^{2}L)	0.698	0.535
19	Upper 2nd molar crown width (M^{2}W)	0.694	0.535
20	Upper 3rd molar crown width (M^{3}W)	0.768	0.190
21	Inter-upper 3rd molar distance (RM^3-LM^3)	0.636	0.691
22	Lower tooth row length (LR)	0.799	0.512
23	Angular ramus to dentary condyle (RC)	0.738	0.509
24	Dentary length (DL)	0.822	0.482
25	Sphenoid pit length (SPL)	-0.385	-0.685
26	P^1 basal width (PBW)	0.627	0.666
27	Inter-lower canine distance (ICD)	0.650	0.661
28	Body length (HV)	0.517	0.584
29	Tail length (TV)	-0.155	-0.145
30	Ear length (EL)	-0.011	-0.073
31	Ear width (EW)	-0.149	0.162
32	Tragus length (TL)	0.450	0.383
33	Radius length (RL)	0.629	0.608
34	Metacarpal III length (MCIII)	0.682	0.670
35	Digit III/phalanx I length (PI)	0.652	0.677
36	Digit III/phalanx II length (PII)	0.663	0.621
37	Tibia length (TIB)	0.642	0.550
38	Pes length (PES)	0.184	0.740

georgianus are smaller regardless of whether they are from sympatric or close allopatric localities (138, 139 and 140) or from more eastern allopatric localities (i.e. localities 147, 152, 154, 156 and 157).

Standardised factor scores for the two factor axes are shown in Table 2. The most important characters are standardised values of the rostrum length (ROL), palatal length (PL), basicranial length (BL), canine width (CW), upper maxillary tooth row crown length (C^1-M^3), upper molar crown length (M^1-M^3), upper second molar crown length (M^2L), upper second molar crown width (M^2W), upper third molar crown width (M^3W), lower tooth row length (LR), angular ramus to dentary condyle length (RC) and dentary length (DL). ROL, PL and BL relate to the lengthwise antero — and midventral shape of the basicranium; CW, C^1-M^3, M^1-M^3, M^2L, M^2W and M^3W relate to the shape of the masticatory apparatus; LR, RC, and DL relate to the lengthwise shape of the dentary. Important characters on the second factor axis are the standardised values of the least interorbital width (LOW), zygomatic width (ZW), mastoid width (MW), braincase width (BW), cranial height (CH), bulla length (BUL), width of the basisphenoid (BB), distance outside bullae (OB), inter-upper canine distance (RC^1-LC^1), inter-upper third molar distance (RM^3-LM^3), sphenoid pit length (SPL) and inter-lower canine distance (ICD). All characters with high loadings on the second factor axis generally relate to width of skull and shape of aspects of the basicranium. Specifically, MW, BW and CH define the anteroventral shape of the skull. BUL, BB, OB and SPL define the shape of the posteroventral part of the basicranium.

Analysis based on a combination of skull and all external characters basically reveals the importance of the same skull characters as in Table 2 on both factor axis 1 (81.7% variance, eigenvalue = 22.9) and factor axis 2 (4.8% variance, eigenvalue = 1.3). However, of the external characters, only the pes length (PL) seems to be important and only on the second factor axis (Table 3).

Canonical Variates Analyses

The groups specified for canonical variates analyses included *T. hilli, T. troughtoni, T. kapalgensis* and *T. longimanus*, which were distinct in the PCA's. Although there were obvious overlaps between *T. georgianus* and *T. australis* and between *S. saccolaimus* and *S. flaviventris*, these four taxa were also treated as separate groups in the canonical variates analyses. This was because a conventional taxonomic examination of individuals revealed them to be morphologically distinct despite similar skull and body proportions. Unlike *T. georgianus, T. australis* males have a gular pouch, while this area is represented by a naked area in females. Furthermore, the sphenoid pit extends further into the pterygoid area in *T. georgianus*. Similarly, unlike *S. flaviventris, S. saccolaimus* has a smooth posterior floor of the mesopterygoid fossa which lacks a deep groove. In addition, the sphenoid pit is shallower in *S. saccolaimus*, with the median septum not as high as the floor of the mesopterygoid fossa. Since *S. mixtus* was only represented by two specimens, it was not included in the "analysis phase"; it was however, included during the "classification phase" of the CVA.

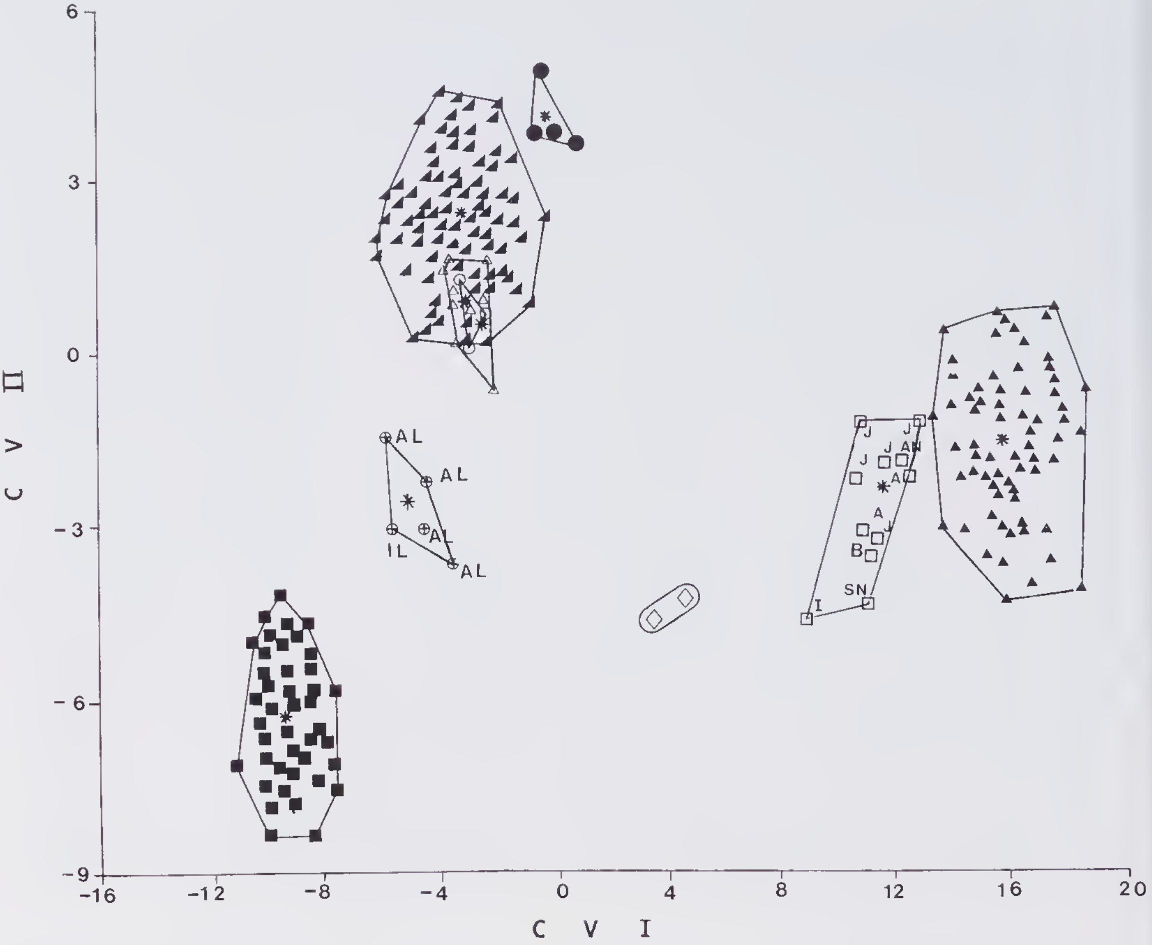

Figure 16 Scores of the first and second canonical variates axes for Australian emballonurids examined, together with *Saccolaimus saccolaimus* and *Taphozous longimanus* from Asia. Data are size-free skull characters, excluding postpalatal width (PPW), with males and females combined. Species symbols are: *S. flaviventris* (▲), *S. mixtus* (◇), *S. saccolaimus* (☐), *T. australis* (△), *T. georgianus* (◢), *T. hilli* (■), *T. kapalgensis* (○), *T. longimanus* (●) and *T. troughtoni* (●).

Codes for *S. saccolaimus* and *T. longimanus* individuals are as for figure 14. The distribution of specimens about the group centroid (*) are shown. Most points in *S. flaviventris*, *T. georgianus* and *T. hilli* represent multiple specimens.

Similarly to PCA, results obtained from the CVA based on the three groupings of data were similar. For simplicity, results presented are based on skull characters alone. The first five CV axes account for 99.8% of the total variation: CV1, 81.9%; CV2, 12.1%; CV3-5, 5.8%. A plot of individual scores with minimum convex polygons of the first two CV axes is shown in Figure 16. By using Mahalanobis' distance between clusters of individuals belonging to the two genera currently recognised in Australia, both axes show no absolutely clear separation between members of *Taphozous* and *Saccolaimus* although two divergent lines of variation are evident; there is, for example, no overlap between members of these genera on the first CV axis (*S. mixtus* and *T. troughtoni* are close). This first axis, generally represents overall size and is a reflection of the fact that the *Saccolaimus* studied are generally larger overall than *Taphozous. Taphozous hilli, S. mixtus, S. flaviventris* and *S. saccolaimus* form discrete clusters; these are maximally separated on the first CV axis. In addition, *T. troughtoni* forms a distinct cluster and is separated from the above on the second CV axis. The first CV axis maximises the separation between the frequently synonymised *T. troughtoni* and *T. georgianus. Taphozous kapalgensis* lies within the *T. australis* cluster, which in turn lies within the *T. georgianus* cluster, except for one individual. However, *T. australis* is separated from

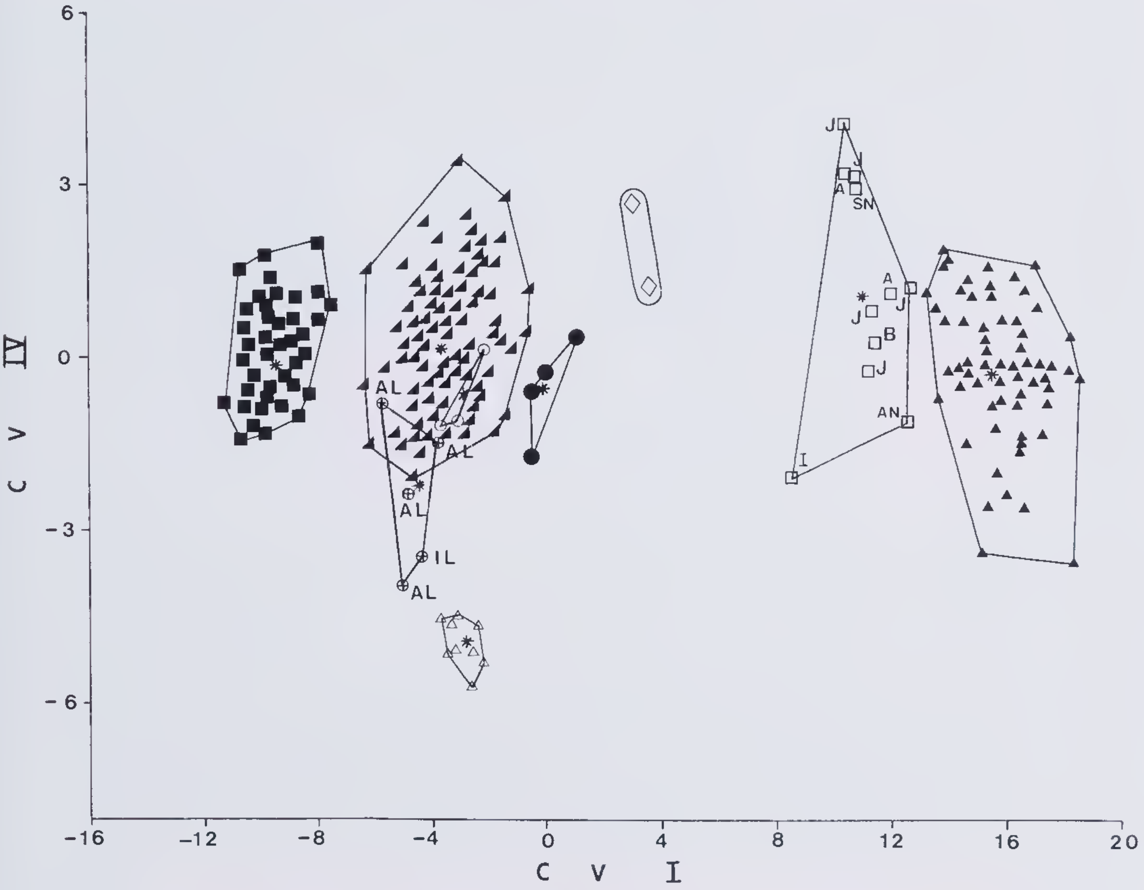

Figure 17 Scores of the first and fourth canonical variates axes for Australian emballonurids, together with Asian *Saccolaimus saccolaimus* and *Taphozous longimanus*. Data are skull characters, excluding postpalatal width (PPW), rostrum length (ROL) and upper second molar crown length (M^2L), with males and females combined. For symbols of species and codes for some individuals, see Figure 14. Most points in *S. flaviventris, T. georgianus* and *T. hilli* represent multiple specimens. The group centroids are indicated by (*).

both *T. kapalgensis* and *T. georgianus*, on the fourth axis (Figure 17), whereas *T. kapalgensis* is separated from both on the fifth CV axis (Figure 18). In CV space, the latter figures indicate the intermediate position of *S. mixtus* between members of the currently recognised genera.

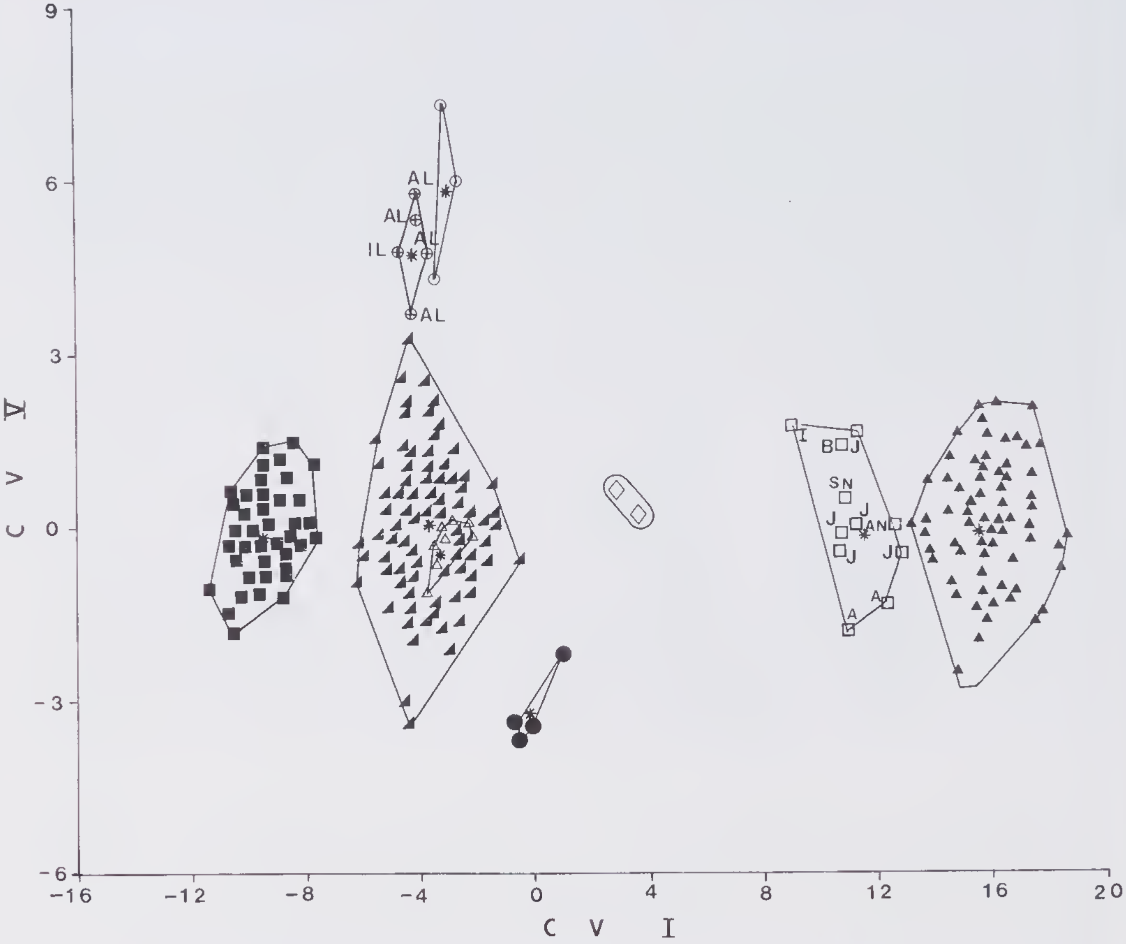

Figure 18 Scores of the first and fifth canonical variates axes for Australian emballonurids, together with Asian *Saccolaimus saccolaimus* and *Taphozous longimanus*. Data are skull characters, excluding postpalatal width (PPW), rostrum length (ROL) and upper second molar crown length (M^2L), with males and females combined. For symbols of species and codes for some individuals, see Figure 14. Most points in *S. flaviventris*, *T. georgianus* and *T. hilli* represent multiple specimens. The group centroids are indicated by (*).

All CV axes examined (Figures 16, 17 and 18) consistently separate *T. kapalgensis* from *T. longimanus* regardless of whether individuals of *T. longimanus* were collected from India (IL) or Bali (AL). Similarly, in *S. saccolaimus*, there are no geographic trends among individuals from India (I), Australia (A), Java (J) and Borneo (B). Neither are there any apparent geographic trends between individuals previously designated *S.*

nudicluniatus from Australia (AN), Solomon Islands (SN), and all other individuals of *S. saccolaimus* regardless of their origin. Overall, 90.3% of specimens were correctly classified to the seven species we recognise.

Table 4. Standardised canonical variates axis coefficients of characters, obtained from the stepwise canonical variates analysis of *Taphozous georgianus, T. troughtoni, T. hilli, T. australis, T. kapalgensis, T. longimanus, Saccolaimus flaviventris, S. saccolaimus* and *S. mixtus* using skull measurements, excluding postpalatal width (PPW), rostrum length (ROL), and upper second molar crown length (M^2L), with sexes combined (for code to characters see figure 2).

CHARACTER		Variate I	Variate II	Variate III	Variate IV	Variate V
1	Anteorbital width (AOW)	0.137	-0.187	-0.298	-0.027	-0.258
2	Least inter-orbital width (LOW)	0.125	-0.327	-0.235	0.013	0.142
3	Zygomatic width (ZW)	0.112	-0.170	-0.145	0.565	-0.019
4	Mastoid width (MW)	0.415	0.204	0.260	0.302	0.526
5	Braincase width (BW)	-0.028	-0.324	0.174	-0.189	0.200
6	Cranial height (CH)	-0.143	0.001	0.457	-0.218	-0.111
7	Palatal length (PL)	0.112	0.333	-0.022	-0.330	-0.342
8	Basicranial length (BL)	-0.060	0.448	-0.304	-0.098	0.039
9	Bulla length (BUL)	-0.369	-0.318	-0.276	-0.383	0.036
10	Width of basisphenoid (BB)	0.128	0.077	0.316	0.005	0.221
11	Distance outside bullae (OB)	-0.166	-0.147	0.371	-0.368	-0.973
12	Canine width (CW)	-0.205	0.660	0.373	-0.476	0.199
13	Inter-upper canine distance (RC^1-LC^1)	0.626	0.283	-0.091	0.135	0.490
14	Upper maxillary tooth row crown length (C^1-M^3)	0.653	0.355	0.051	0.075	0.445
15	Upper molar crown length (M^1-M^3)	0.104	-0.315	0.033	0.113	-0.140
16	Upper 2nd molar crown width (M^2W)	0.023	0.051	0.808	0.483	0.024
17	Upper 3rd molar crown width (M^3W)	-0.056	0.120	0.022	-0.109	0.104
18	Inter-upper 3rd molar distance (RM^3-LM^3)	-0.129	-0.166	-0.128	-0.001	-0.302
19	Lower tooth row length (LR)	-0.035	-0.243	-0.034	0.301	-0.279
20	Angular ramus to dentary condyle (RC)	0.203	0.107	0.116	0.043	0.216
21	Dentary length (DL)	0.002	0.462	-0.192	0.024	-0.281
22	Sphenoid pit length (SPL)	-0.471	0.151	0.306	0.687	-0.120
23	P^1 basal width (PBW)	0.395	-0.247	0.004	0.178	0.182
24	Inter-lower canine distance (ICD)	0.081	0.001	0.123	0.288	0.003

Characters with high loadings in the first CV axis (Table 4) relate to the standardised values of the inter-upper canine distance (RC^1-LC^1) and the upper maxillary tooth row crown length (C^1-M^3). Both these characters relate to the shape of the anteroventral basicranium. The canine width (CW) is the most important character on the second CV axis (12.1% variance). Important on the fourth CV axis, which is instrumental in maximising the separation between *T. georgianus* and *T. australis* (Figure 17) are the zygomatic width (ZW) and the sphenoid pit length (SPL). The mastoid width (MW) and the distance outside bullae (OB) are important on the fifth CV axis (0.4% variance), which is important in distinguishing *T. kapalgensis* and *T. georgianus* (Figure 18). The mastoid width (MW) and the distance outside bullae (OB) relate to the posteroventral shape of the basicranium. An examination of the important CV axes of the analysis that was performed using a combination of skull and all external characters (Table 5) shows a

Table 5. Standardised canonical variates axis coefficients of characters, obtained from the stepwise canonical variates analysis of *Taphozous georgianus, T. troughtoni, T. hilli, T. australis, T. kapalgensis, T. longimanus, Saccolaimus flaviventris, S. saccolaimus* and S. mixtus using skull and all external measurements combined, excluding postpalatal width (PPW), rostrum length (ROL), and upper second molar crown length (M^2L), with sexes combined (for code to characters see figure 2).

	CHARACTER	Variate I	Variate II	Variate III	Variate IV	Variate V
1	Anteorbital width (AOW)	0.098	0.006	-0.201	0.102	0.361
2	Least inter-orbital width (LOW)	0.169	-0.318	-0.189	-0.017	-0.066
3	Zygomatic width (ZW)	0.044	-0.022	-0.311	0.396	-0.147
4	Mastoid width (MW)	0.363	-0.045	-0.118	0.004	-0.285
5	Braincase width (BW)	0.054	-0.330	0.301	-0.088	0.212
6	Cranial height (CH)	-0.041	0.052	-0.406	-0.249	-0.130
7	Palatal length (PL)	0.133	0.321	0.187	-0.119	0.239
8	Basicranial length (BL)	-0.178	0.628	-0.294	-0.141	-0.205
9	Bulla length (BUL)	0.286	-0.416	-0.154	-0.314	0.088
10	Width of basisphenoid (BB)	0.002	0.073	0.382	-0.014	-0.172
11	Distance outside bullae (OB)	-0.190	-0.129	0.435	-0.236	0.707
12	Canine width (CW)	0.324	0.608	0.190	-0.480	-0.119
13	Inter-upper canine distance (RC^1-LC^1)	0.342	0.193	0.009	0.149	-0.145
14	Upper maxillary tooth row crown length (C^1-M^3)	0.471	0.254	0.325	-0.032	-0.301
15	Upper molar crown length (M^1-M^3)	0.206	-0.227	0.095	0.195	0.043
16	Upper 2nd molar crown width (M^2W)	-0.079	0.088	0.145	0.386	-0.264
17	Upper 3rd molar crown width (M^3W)	-0.071	0.106	-0.102	-0.224	0.041
18	Inter upper 3rd molar distance (RM^3-LM^3)	-0.113	-0.206	0.024	0.049	0.161
19	Lower tooth row length (LR)	-0.021	-0.257	-0.027	0.135	0.164
20	Angular ramus to dentary condyle (RC)	0.198	0.081	0.008	-0.013	-0.132
21	Dentary length (DL)	0.010	0.518	0.099	0.053	0.153
22	Sphenoid pit length (SPL)	-0.484	0.013	0.067	0.518	-0.267
23	P^1 basal width (PBW)	0.450	-0.263	-0.104	0.028	-0.010
24	Inter lower canine distance (ICD)	0.173	0.019	-0.022	0.314	-0.070
25	Body length (HV)	0.043	-0.103	0.172	0.263	-0.090
26	Tail length (TV)	-0.060	0.088	0.038	0.066	0.005
27	Ear length (EL)	-0.147	0.055	0.087	-0.150	0.391
28	Ear width (EW)	-0.040	0.031	-0.089	-0.107	0.142
29	Tragus length (TL)	0.123	0.064	-0.170	-0.092	0.238
30	Radius length (RL)	-0.280	-0.003	0.065	0.121	0.166
31	Metacarpal III length (MCIII)	0.081	-0.312	-0.027	-0.092	-0.058
32	Digit III, phalanx I length (PI)	0.693	-0.155	-0.286	-0.077	-0.225
33	Digit III, phalanx II length (PII)	-0.145	0.206	-0.187	0.166	0.169
34	Tibia length (TIB)	-0.159	0.131	0.022	0.400	0.380
35	Pes length (PES)	-0.005	-0.129	0.374	0.203	0.274

similarity in skull character loadings. However, of the external characters, only the digit III/phalanx I length (PI) is important, on the first CV axis.

Cluster Analysis

There was a marked congruence when the three combinations of data were analysed separately. Analysis based on skull characters alone is presented. This is because alcohol preserved specimens were not available for *S. mixtus* and most specimens of *S. saccolaimus* to allow computation of mean values. The results of the UPGMA clustering of the eight species of *Taphozous* and *Saccolaimus* delineated are shown in Figure 19. The currently recognised genera are not separate in this phenogram because *S. mixtus* clusters with *T. troughtoni. Taphozous georgianus, T. australis* and *T. kapalgensis* form a distinct group with very little morphological differentiation between them. These three species are more similar to *T. troughtoni* and *S. mixtus* than the distinctive *T. hilli. Saccolaimus saccolaimus* and *S. flaviventris* are phenetically similar to each other and are very distinct from the other species.

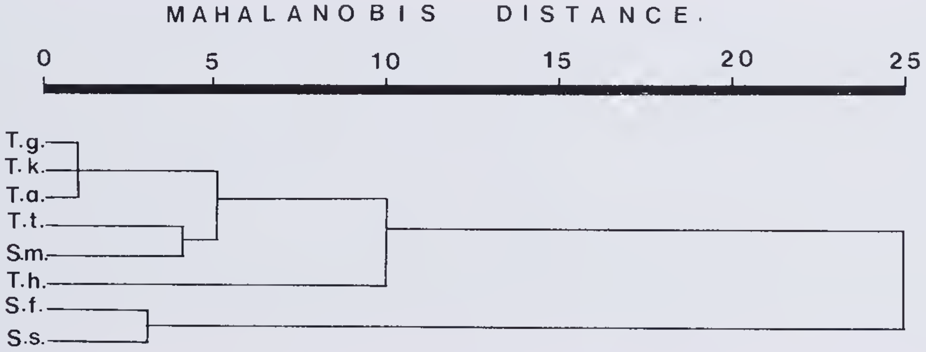

Figure 19 Phenetic relationships of Australian emballonurid species derived by UPGMA cluster analysis. Data are size-free skull characters with males and females combined. Species codes are as follows: *Saccolaimus flaviventris* (S.f), *S. mixtus* (S.m), *S. saccolaimus* (S.s.), *Taphozous australis* (T.a), *T. georgianus* (T.g), *T. hilli* (T.h), *T. kapalgensis* (T.k), and *T. troughtoni* (T.t).

Discussion

There is no strong phenetic separation between *Saccolaimus* and *Taphozous*, although the two genera can be discriminated on the first CV axis. However, the classical taxonomic approach and phylogenetic studies of generic relationships within the Emballonuridae using morphology (Chimimba 1987), and protein electrophoresis and immunology (Robbins and Sarich 1988) separate these genera. The following Australian species are considered valid: *S. flaviventris; S. mixtus; S. saccolaimus; Taphozous australis, T. georgianus, T. hilli, T. kapalgensis* and *T. troughtoni.*

Earlier workers considered that the large *T. troughtoni* was part of a size cline in *T. georgianus* which increases in size from west to east (McKean and Price 1967, Koopman 1984b). However, several points in the present study argue against this synonymy. Firstly, the individuals of *T. troughtoni* examined were collected from Ballara and

Mount Isa in Queensland (Localities 139 and 140 respectively in Figure 1), the latter being the type locality of *T. troughtoni* (Tate 1952). There is also a specimen of *T. georgianus* from Mount Isa (CM 13216) and another from Cloncurry (JM 6550, Locality 138 in Figure 1), an area very close to Mount Isa, suggesting that the two taxa are not geographically separated. Our data show that individuals of *T. georgianus* are smaller than those of *T. troughtoni* in both sympatry and allopatry. In addition, specimens of *T. georgianus* collected further to the east of Mount Isa, Ballara and Cloncurry are also smaller than specimens of *T. troughtoni.* This suggests that while *T. georgianus* may show an eastward increase in size, *T. troughtoni* does not form part of this size cline. Secondly, despite these size differences, the analyses were performed after corrections for size were made, and yet the morphological differences between the two taxa are still apparent. Thirdly, although phenetic relationships based on cluster analyses show that *T. troughtoni* has affinities with *T. georgianus, T. australis* and *T. kapalgensis,* the phenogram confirms a fairly high degree of morphological dissimilarity between *T. troughtoni* and *T. georgianus* (together with *T. kapalgensis* and *T. australis*).

Jones and Genoways (1970) have noted the presence of many sibling species in microchiropteran bats. This fact is stressed by Baverstock (1989) who stated that "many zoologists seem unaware of the high incidence of "cryptic" species". Studies on Australian bats using molecular techniques (Adams *et al.* 1987a, b, 1988), and morphological approaches using multivariate statistics (Carpenter *et al.* 1978; McKean *et al.* 1978; Campbell and Kitchener 1980; Tidemann *et al.* 1981; Kitchener and Caputi 1985; Kitchener *et al.* 1986, 1987) support this view. A most important aspect of the studies cited above is the high degree of concordance between results based on the morphological data and those of parallel studies based on electrophoretic data, although in several instances electrophoretic data indicated the presence of species that could be identified only with great difficulty, or not at all, using morphology. Consequently it is suggested that there is need to further examine the Australian emballonurids using electrophoretic data.

Examination of bacula and glans penis in this study are mostly based on small samples. While these support the Australian species recognised by us, examination of a more extensive sample is required. This is necessary to distinguish different growth stages or stages in ossification of the glans penis and bacula respectively such as observed in Australo-Papuan *Pipistrellus* and *Falsistrellus* by Kitchener *et al.* (1986).

Generally, there was some difficulty separating *T. australis, T. georgianus* and *T. kapalgensis* using PCA. Following the suggestion by Gould and Woodruff (1978) and Gould (1984) of the biological importance of minor axes of PCA (which may also be true for CVA), the minor axes indicate that the three species are morphologically distinct. This distinctiveness is also supported by the traditional taxonomic approach. Cluster analysis also shows that *T. australis, T. georgianus* and *T. kapalgensis* are phenetically very close.

Our results leave little doubt that *T. kapalgensis* and *T. hilli* are not conspecific as suggested by Koopman (1984b). Further, *T. kapalgensis* is distinct from the most similar oriental species, *T. longimanus* (which does not appear to be highly variable over its range as suggested by Dobson, 1878).

We show that *S. nudicluniatus* is conspecific with *S. saccolaimus,* which is in agreement with Goodwin (1979). Although we examined few specimens of *S. saccolaimus* there appeared little variation over its range from India to the Solomon Islands, which is consistent with the observations of McKean *et al.* (1980).

Taphozous troughtoni and *S. mixtus* have closest phenetic affinities with the species cluster, *T. australis, T. georgianus* and *T. kapalgensis.* In the original description of *T. troughtoni,* Tate (1952) recognised the similarity of *T. troughtoni* with *T. georgianus* and *T. australis* but not with *S. mixtus* indicating that the development of the bulla greatly influenced Tate. Within species currently referred to *Taphozous* in Australia, *T. hilli* is the most distinct morphologically. *Saccolaimus flaviventris* and *S. saccolaimus* are phenetically similar to each other, and are the most distinct morphologically of all Australian emballonurids.

Characters determined by CVA to be particularly important in separating Australian emballonurids relate to the inter-upper canine distance, upper maxillary tooth row crown length, canine width, zygomatic width, sphenoid pit length, mastoid width, distance outside bullae, digit III/phalanx I length and pes length. Some of these characters have been used previously to diagnose these species. The most important of these relate to the sphenoid pit length, the bulla length, canine width and pes length. Kitchener (1980) found that the canine was one of the most important diagnostic characters between *T. hilli* and *T. georgianus.* Importantly, these two species were separated on an axis in which the canine width was the only character with a high loading. The *a priori* determination of pes length as an important character accords with Monticelli (1889) who observed that feet were an important distinguishing character between members of *Taphozous* and *Saccolaimus.* In general, Hollister (1913), Thomas (1922) and Troughton (1925) placed much emphasis on the structure of the bulla and the sphenoid pits to distinguish between members of *Taphozous* and *Saccolaimus.* Troughton (1925) attached much importance to the structure of the sphenoid pits to distinguish *T. georgianus* and *T. australis.* In this study, the minor axis instrumental in maximising the separation between *T. georgianus* and *T. australis* involves the sphenoid pit length as one of the important characters. The structure of the sphenoid pit and the bullae have also been used extensively to separate Old World members of *Taphozous* and *Saccolaimus* (Barghoorn 1977); New World members of the subfamily Emballonurinae (Sanborn 1937) and within members of the genus *Emballonura* in the Indo-Australasian region (Tate and Archbold 1939).

Other characters determined as important in distinguishing taxa in this study mostly relate to teeth, the dentary and the width of the skull. These characters can be viewed from a functional standpoint. It is possible that effects of resource partitioning by different species contribute to the importance of the teeth and the dentary. Freeman (1981) relates characteristics of the dentary to possible functional differences in molossid bats. She suggested that thickening of the dentary and increase in the area of insertion of the temporalis muscle at the coronoid process may be related to diet. Similarly, the wideness of the skull may be a result of feeding on different size and texture of food by different species, which in turn may cause changes in the magnitude of forces acting on the skull and the mandible produced by the forces of mastication. Hildebrand (1974) and Buckland-Wright (1978) report that bone thickens where more stress occurs and that mammalian skull bones constantly undergo change by absorption and remodelling of bone tissue that may be functionally influenced.

There are no significant differences between males and females within the emballonurids in which the sample size was adequate for examination: *Taphozous georgianus, T. hilli* and *S. flaviventris.* All these species are predominantly cave dwelling. Without suggesting a biological explanation, Carpenter *et al.* (1978) reported that in Australian *Eptesicus* (×*Pipistrellus,* see Hill and Harrison 1987; Volleth and Tidemann 1989), sexual dimorphism is less pronounced in cave dwelling species than it is in the forest dwelling ones. In most phyllostomatids (Baker *et al.* 1972; Power and Tamsitt 1973; McLellan 1984) and some vespertilionids (Findley and Traut 1970; Myers 1978), males are larger than females. Exceptions are the phyllostomatid *Ametrida centurio* (Peterson 1965) and some vespertilionids (Myers 1978, Campbell and Kitchener 1980) where females are larger than males. The larger females have been associated with a need to compensate for the extra flight load during pregnancy (Ralls 1976).

Key to Genera and Species of Australian Emballonuridae

The Key is to be used in conjunction with pertinent diagnoses, descriptions and measurements in Table 1.

1a Bulla complete, with less than 50 percent of cochlea exposed; skull heavily ossified; saggital crest pronounced and reaching occiput; upper anterior premolar proportionately larger, almost one-third of both height and crown area of posterior premolar; a wide band separating anterior lacerate foramen and sphenorbital sinus; lower outline of dentary convex beneath premolar; posteroventral face of basisphenoid region in contact with both bulla and cochlea; paraoccipital process level or slightly longer than occipital condyles; inner margin of ear not papillate . . . . Australian *Saccolaimus* 2

1b Bulla incomplete, with greater than 50 percent of cochlea exposed; skull not heavily ossified; saggital crest absent or much weaker, barely reaching occiput or often terminating into a more rounded crest; upper anterior premolar relatively small, almost one-fifth of both height and crown area of posterior premolar; anterior lacerate foramen and sphenorbital sinus separated by a thin band; lower outline of dentary markedly concave beneath premolars; posteroventral face of basisphenoid in contact with cochlea only;

paraoccipital process shorter than occipital condyles; parastylar area well developed; inner margin of ear papillate .... Australian *Taphozous* 4

2a Radial-metacarpal pouch present, size smaller: greatest skull length averages 21.8 (21.7-21.9), radius length averages 63.6 (63.1-64.2); forehead more excavated.................... *Saccolaimus mixtus*

2b Radial-metacarpal pouch absent, size larger: greatest skull length ranges between 22.4-27.0, radius length ranges between 65.7-82.1; forehead less excavated. 3

3a Mesopterygoid fossa deeply grooved; sphenoid pit posteriorly margined by an overlapping edge; sagittal crest reaches occiput but not so prominently .... *Saccolaimus flaviventris*

3b Mesopterygoid fossa smooth; sphenoid pit posteriorly more open; sagittal crest prominently reaching occiput...... *Saccolaimus saccolaimus*

4a Gular sac present in males and represented by a rudimentary edge in females 5

4b Gular sac absent in both sexes 7

5a Anterior rim of mesopteryoid fossa rounded; canines shorter and slender with small anterobasal cusp about one-third length of tooth; posterior premolar with a small anterobasal cusp; angular basisphenoid pit; less steeply excavated frontal depression.. *Taphozous hilli*

5b Anterior rim of mesopterygoid fossa v-shaped; canines relatively longer and less slender and lacking a small anterobasal cusp; posterior premolar lacking small anterobasal cusp; rather pear-shaped basisphenoid pit; frontal depression deeply excavated 6

6a Sphenoid pit do not reach level of large vacuities outside nasal cavities but ending about 1 mm from them; zygomata without spike .... *Taphozous australis*

6b Sphenoid pits reaching to level of nasal cavities; zygomata with spike .... *Taphozous kapalgensis*

7a Anterior rim of mesopterygoid fossa less v-shaped; postorbital processes relatively shorter; sagittal and lambdoidal crests relatively weak; size generally smaller, greatest skull length averaging 21.4 (20.0-23.1).......... *Taphozous georgianus*

7b Anterior rim of mesopterygoid fossa sharply v-shaped; postorbital process extremely long; sagittal and lambdoidal crests sharply edged; size larger, greatest skull length averaging 24.1 (24.0-24.3) .... *Taphozous troughtoni*

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Appendix I Australian emballonurid specimens examined. Collecting locality numbers are those indicated in Figure 1.

Taphozous australis

Locality 143

Possession Island 10°44′, 142°24′, 13 males, 1 female, AM (M4412-17, M4419-22, M4424-25). Locality 144 Coen, 13° 57′, 143°12′, 1 male, JM (M9495). *Locality* 150 Townsville, 10°16′, 146°49′, 1 male, CM (M2176).

Taphozous georgianus

Locality 5

Wilgie Mia, 26°56′, 117°42′, 1 male, CM (M2122). *Locality 9* Three Rivers Homestead, 25°08′, 119°09′, 1 female, WAM (M15235). *Locality 12* Durba Spring, 23°45′20″, 122°31′00, 4 males, 6 females, WAM (M14384-87, M14390-95). *Locality 14* Opthalmia Range, 23°16′50″, 119°11′20″, 1 male, 1 female, WAM (M19503-04). *Locality 15* Opthalmia Range, 23°18′00″, 119°35′20″. 2 females, WAM (M18039-40). *Locality 16* Mt Newman, 23°19′, 119°45′, 1 male, WAM (M6718.003). *Locality 19* Paraburdoo Minesite, 23°13′30″, 117°37′00, 1 male, 1 female, WAM (M14935-36). *Locality 20* Ullawarra Station, 23°24′, 116°10′, 4 males, 6 females, WAM (M4324-30, M4332-34). *Locality 21* Yardie Creek Homestead, 22°02′45″, 114°01′30″, 1 male, 3 females, WAM (M18146-49). *Locality 22* Yardie Homestead, 21°52′, 114°03′, 1 male, WAM (M7476). *Locality 23* Tambrey Homestead, 21°35′00″, 117°33′40″, 1 male, 3 females, WAM (M4319, M4321.001-.002, M4342). *Locality 24* Yampire Gorge (includes Wittenoom Gorge), 22°25′, 119°27′, 4 males, 4 females, WAM (M4318.002-.003. M18288, M18290-92, M19616-17). *Locality 25* Hamersley Range National Park (includes Mt Bruce), 22°36′00″, 118°08′30″, 1 male, 4 females, WAM (M14594-95, M18256-57, M18655). *Locality 27* Hopetoun Mine, 21°55′00″. 120°12′30″, 3 males, WAM (M11050, M11052, M11054). *Locality 28* Nullagine, 21°53′, 120°07′, 1 male, 6 females, WAM (M10536, M11040-45). *Locality 29* Mosquito Creek, 21°44′00″, 120°28′30″, 2 males, 2 females, WAM (M11034-35, M11037-38). *Locality 30* Oakover River, 21°31′, 121°10′, 1 female, WAM (M24328). *Locality 31* Bamboo, 20°55′45″, 120°13′15″, 7 males, 5 females, WAM (M3251-52, M3254-58, M3262, M3276-77), CM (M2151). *Locality 32* Callawa Homestead, 20°22′05″, 120°49′20″, 3 females, WAM (M10560, M16762-63). *Locality 33* Shay Gap, 20°31′, 120°08′, 3 males, 7 females. WAM (M16764-M16772, M16778). *Locality 35* Marble Bar, 21°20′, 119°42′, 1 male, WAM (M3261). *Locality 36* Pulleunah Hill, 21°32′30″, 118°59′00″, 2 females, WAM (M9606-M9607). *Locality 37* Woodstock, 21°37′, 118°57′, 1 male, 1 female, WAM (M7465-66). *Locality 38* Peawah Camp Well, 20°44′, 118°01′, 1 male, WAM M7470. *Locality* 39 Whim Creek, 20°50′, 117°50′, 2 males, 1 female, WAM (M7458-60). *Locality 48* Bugle Gap, Lawford Range, 18°39′45″, 126°03′05″, 3 males, 1 female, WAM (M5709, M5712-13, M5718). *Locality 49* Wattle Spring Creek, 19°14′, 126°03′. 1 female, WAM M24367. *Locality 50* Outcamp Hill, 18°33′30″, 125°55′00″, 5 males, 3 females, WAM (M5706-08, M5710-11, M5713, M5715). *Locality 51* Sadlier Range, 18°18′, 125°35′, 1 male, 1 female, WAM (M5720-21). *Locality 53* Napier Range, including Winjina Gorge, 17°25′35″, 124°25′05″, 8 males, 7 females, WAM (M7472, M18325-29, M18331-32), CM (M1512, 1515-20). *Locality 54* Inglis Gap, includes Lennard River Gorge, 17°07′, 125°11′, 1 male, 2 females, WAM (M7468-69, M18541). *Locality 55* Tunnel Creek, 17°37′, 125°09′, 2 males, 2 females. WAM (M7462-64, M24044). *Locality 56* Leopold Downs Homestead, 17°54′45″, 125°17′12″, 3 females. WAM (M24033-35). *Locality 57* Napier Downs Homestead, 17°14′, 124°38′. 1 male, WAM (M8135). *Locality 58* Derby, 17°18′, 123°38′, 1 male, 2 females, WAM (M7050, M24031-32). *Locality 59* Mt Anderson, 18°01′, 123°56′, 5 males, 2 females, WAM (M5534-37, M18457, M18464-65). *Locality 63* Edgar Range, 18°25′, 123°05′, 4 females, WAM (M15046-47, M14132, M17461). *Locality 68* Koolan Island, 16°08′00″, 123°46′30″, 1 female, WAM M4897. *Locality 69* Cockatoo Island, 16°05′20″, 123°36′00″, 1 female, WAM (M4898). *Locality 71* Augustus Island, 15°22′30″, 124°35′20″, 1 male, 1 female. WAM (M9280-81). *Locality 72* Bat Island, 15°06′10″, 124°54′30″, 3 males, 1 female, WAM (M10460-63). *Locality 73* Boongarie Island, 15°06′00″, 125°12′40″, 5 males, WAM (M10454, M10456-59). *Locality 74* Bigge Island, 14°30′40″, 125°07′47″, 2 males, 1 female, WAM (M15414-16). *Locality 76* Mitchell Plateau, 14°49′30″, 125°50′40″, 1 male, WAM M15702. *Locality 78* Mitchell Plateau, 14°53′40″, 125°45′20, 1 female, WAM M15686. *Locality 79* Mitchell Plateau, 14°36′30″, 125°52′00″, 3 males, 2 females, WAM (M15689-90, M15692, M15697, M15699). *Locality 80* Kalumburu

Mission, 14°17′30″, 126°38′40″, 2 males, 2 females, WAM (M4080-82, M7457). *Locality 82* Drysdale River National Park, 15°01′, 126°49′, 1 female, WAM M14096. *Locality 85* Parry Creek, 15°30′, 128°13′, 1 female, WAM M7471. *Locality 86* Kununnura, 15°46′30″, 128°44′00″, 1 female, WAM B231. *Locality 87* Ningbing Bore, 15°14′00″, 128°40′30″, 1 female, WAM M7467. *Locality 88* Cave Springs, includes Mount Cecil, 15°32′, 128°50′, 4 males, 4 females, WAM (M7053/002, M7053/004, M7053/006-007, M7059/001-003, M19665). *Locality 89* Keep River National Park, 15°45′, 128°04′, 1 male, 1 female, CM (M524-525). *Locality 91* Argyle Downs (includes Aboriginal Cave) 16°04′15″, 128°46′35″, 1 male, 4 females, WAM (M9608, M9614, M11459, M11465). *Locality 92* Ord River Area, 16°23′, 128°43′, 3 males, 5 females, WAM (M9605, M9612, M11498-99, M11500-02, M11613). *Locality 93* Lissadell Homestead (New), 16°39′57″, 128°31′03″, 2 males, 5 females, WAM (M16899, M16992-97). *Locality 94* Bull Hole Bore, 17°19′55″, 127°05′15″, 6 females, WAM (M18458-63). *Locality 95* Old Halls Creek, 17°55′00″, 127°49′30″, 1 female, WAM M7474. *Locality 96* Mount Bradley, 18°22′00″, 128°47′30″, 2 males, WAM (M6995/001-002). *Locality 97* Halls Creek, 18°21′, 127°49′, 3 males, 5 females, WAM (M18315-22). *Locality 98* Halls Creek, 18°34′, 127°15′, 1 female, WAM M24366. *Locality 99* Kintore Cave, Near Katherine, 23°18′, 129°24′, 5 males, 4 females, C (5003-04, 5051-55, 5057-58). *Locality 106* 8 km east of Arltunga, 23°28′, 134°43′, 2 males, 3 females, CM (M4428-4430, M4435, M4437). *Locality 112* Delamere Station, 15°44′, 131°32′, 3 females, SAM (M6655, M7053-54). *Locality 117* Katherine, 14°29′, 132°12′, 3 males, 2 females, WAM (M6256-58, M6263-64). *Locality 118* Katherine Gorge National Park, 14°19′, 132°28′, 1 male, 2 females, CM (M636, M649-50). *Locality 120* Pine Creek, 13°49′, 131°50′, 2 males, 1 female AM M9491, CM (M3984, M10027). *Locality 122* Green Ant Creek, 13°36′, 131°12′, 1 male, CM M4141. *Locality 131* Portsite Centre Island, Sir Edward Pellew Group, 15°33′, 136°47′, 2 males, 1 female, CM (M2554-55, M13193). *Locality 132* Caranbirini Waterhole, 16°16′, 136°05′, 2 females, CM (M11821, M11924). *Locality 133* Amelia Spring, 16°36′, 136°11′, 1 female, CM M11785. *Locality 134* Nicholson River, 17°46′, 137°05′, 1 female, NTM M5982. *Locality 135* China Well, 17°50′, 137°25′, 2 males, CM (M6922-23). *Locality 136* Accident Creek, 18°04′, 138°12′, 2 males, 2 females, SAM (M6806-07, M6809-10). *Locality 137* Riversleigh, 18°45′, 138°35′, 5 males, 1 female, WAM B (298-303). *Locality 138* Cloncurry, 20°42′, 140°30′, 1 male, JM M6550, *Locality 140* Native Bee Mine, Mount Isa, 20°44′, 139°29′, 1 female, CM M13216. *Locality 147* Chillagoe, 17°09′, 144°31′, 4 males, 3 females, CM (M2058, M2346, M13190-91, M13194, M13197-98). *Locality 152* Mount Etna, 20°58′, 148°01′, 2 females, AM (M8117-18). *Locality 154* Capella, 25°05′, 148°01′, 1 male, 2 females, JM (M13855-57). *Locality 156* Rockhampton, 23°22′, 150°32′, 2 males, 3 females, AM (M6024-25), CM M13212, JM (M9975-76). *Locality 157* Rewan Station, South West Rolleston, 24°58′, 148°22′, 1 female, JM M15816.

Taphozous hilli

Locality 1

Tallering Homestead, 28°15′, 115°51′, 6 males, 6 females, WAM (M10673-78, M10680-85). *Locality 2* Tallering Peak, 28°06′, 115°38′, 6 males, 6 females, WAM (M11030, M12712, M12714-19, M12459-60). *Locality 3* Yalgoo, 28°18′45″, 116°38′00″, 6 males, 6 females, WAM (M10115-20, M10125-30). *Locality 4* Murgoo Homestead, 27°28′40″, 116°22′10″, 3 males, 3 females, WAM (M9653, M10239-40, M10244-45). *Locality 5* Wilgie Mia, 26°56′, 117°42′, 6 males, 5 females, WAM (M3803-08, M4639, M5964, M8187, M10148-49). *Locality 6* Gnumartina Bat Cave, 26°22′30″, 117°08′10″, 1 female, WAM M4303. *Locality 7* Peak Hill Gold Mine, 25°36′00″, 118°43′30″, 3 females, WAM (M12211-13). *Locality 8* Peak Hill, 25°36′, 118°49′, 1 male, 2 females, WAM (M10716-18). *Locality 13* Mount Meharry, 23°12′00″, 118°49′30″, 1 male, 6 females, WAM (M16751, M16815, M16817, M16818/001, M16819-20, M18252). *Locality 15* Opthalmia Range, 23°10′, 118°50′, 1 female, WAM M18041. *Locality 19* Paraburdoo Minesite, 23°13′30″, 117°37′00″, 1 male, WAM M14937. *Locality 25* Hamersley Range National Park (including Mt Bruce), 22°39′03″, 118°08′30″, 2 males, 3 females, WAM (M18260 (holotype), M18261, M18264-65). *Locality 31* Bamboo, 20°55′00″, 120°13′15″, 2 females, WAM (M3273, M7056). *Locality 40* Muggan Rock Holes, 27°01′, 125°20′, 1 male, 2 females, WAM (M5241/001-002), CAM M408. *Locality 41* Manunda Rock Hole, 26°50′50″, 125°39′30″, 1 male, WAM M4626. *Locality 42* Gahnda Rock Hole, 26°36′, 125°52′, 1 male, 3 females, WAM (M5242/001-003, M13372). *Locality 43* Mount Charles, 25°45′, 126°11′, 1 female, WAM M14640. *Locality 44* Charles' Knob, 25°03′, 124°59′, 2 females, WAM (M14641-42). *Locality 45* Great Sandy

Desert, 20°50′, 127°59′, 2 males, 2 females, WAM (M22843-44, M22846, M22849). *Locality 103* Tennant Creek, 19°39′, 134°00′, 6 males, 4 females, CM M845, WAM B (128-29), NTM (M357-59), WAM (M5844-47). *Locality 104* Peko Mine, 19°41′, 134°17′, 2 males, 4 females, WAM (M6283-88). *Locality 105* Hatches Creek, 20°56′, 135°12′, 3 females, NTM (M4274-76). *Locality 106* 8 km east of Arltunga, 23°28′, 134°43′, 3 females, CM (M5836, M5838, M13218). *Locality 107* Arltunga Gold Mine, 23°30′, 134°50′, 1 female, CAM M175. *Locality 109* Hermannsburg Station, 29°59′, 132°46′, 1 male, NTM M5331. *Locality 110* Tennant Creek, 19°39′, 134°11′, 1 female, CM M4167. *Locality 111* 10 km south-east Mount Leichard, 21°51′, 132°37′, 1 female, CAM M408.

Taphozous kapalgensis

Locality 125

Kapalga, South Alligator River, 12°36′, 132°25′, 2 males, 1 female, CM (M4806 (paratype), 4823), WAM M18580.

Taphozous troughtoni

Locality 139

Ballara, 20°57′, 139°58′, 1 male, CM M4145. *Locality 140* Native Bee Mine, Mount Isa, 20°44′, 139°29′, 3 females, CM (M13213, M13215, M13217).

Saccolaimus flaviventris

Locality 10

Karri Karri Pool, 25°29′, 120°37′, 1 male, WAM M14400. *Locality 11* Mount Salvado, 25°17′, 120°42′, 1 female, WAM M14639. *Locality 12* Durba Spring, 23°45′20″, 122°31′00″, 3 males, 1 female, WAM (M14396-99). *Locality 17* Marillana Homestead, 22°46′00″, 119°13′08″, 2 males, WAM (M18398, M19406). *Locality 18* Pingandy Creek, 23°58′, 117°40′, 1 female, WAM M6622. *Locality 25* Hamersley Range National Park, 22°38′46″, 118°08′03″, 1 female, WAM M18650. *Locality 26* Great Sandy Desert, 22°32′50″, 122°24′20″, 1 male, WAM M22868. *Locality 34* Coongan River, 20°55′, 119°47′, 1 female, WAM M22870. *Locality 46* Great Sandy Desert, 20°17′, 127°26′, 1 female, WAM M22870. *Locality 47* Fossil Downs, 18°08′30″, 125°36′45″, 1 male, WAM M5732. *Locality 52* Barker Gorge, 17°15′20″, 124°43′45″, 1 male, WAM M18500. *Locality 60* Edgar Range, 18°27′45″, 123°40′30″, 2 females, WAM (M15127-28). *Locality 61* Edgar Range, 18°49′20″, 123°17′50″, 2 males, 3 females, WAM (M15037-39, M22265, M22869). *Locality 62* Edgar Range (Hatches Bore) 18°22′45″, 123°03′25″, 7 males, 3 females, WAM (M15040-45, M15131, M17459). *Locality 64* Waterbank Homestead, 17°44′20″, 122°14′52″, 4 males, 2 females, WAM (M24019-21, M24057, M24065, M24071). *Locality 65* Point Coulomb, 17°21′20″, 122°09′20″, 3 males, 1 female, WAM (M8432, M22531, M22535, M22662). *Locality 66* Cocky Well, 16°43′50″, 122°48′30″, 1 female, WAM M22534. *Locality 70* Wotjulum Mission, 16°11′, 123°37′, 1 male, WAM M3001. *Locality 75* Prince Regent River Reserve, 15°48′11″, 125°20′26″, 2 males, 1 female, WAM (M12252-54). *Locality 76* Mitchell Plateau, 14°49′10″, 125°50′20″, 3 males, 7 females, WAM (M21791, M21828-33, M21852-53, M21875). *Locality 77* Drysdale River Crossing, 15°40′30″, 126°23′45″, 1 female, WAM M14359. *Locality 81* Drysdale River National Park, 14°43′, 126°54′, 2 males, WAM (M14022-23). *Locality 83* Drysdale River National Park, 15°09′, 127°06′, 3 females, WAM (M14019-21). *Locality 84* Wyndham, 15°28′, 128°06′, 1 female, AM M6768. *Locality 90* Keep River National Park, 15°58′, 129°02′ 1 female, CAM M602. *Locality 100* Tanami Desert, 20°09′, 130°15′, 1 female, NTM M2779. *Locality 101* Tanami Desert, 20°13′, 131°47′, 1 male, CAM M8. *Locality 102* Banka Banka Station, 18°48′, 134°02′, 1 female, CM M2472. *Locality 103* Tennant Creek, 19°39′, 134°02′, 1 male, SAM M498. *Locality 108* Temple Bar Creek, Alice Springs, 23°45′, 133°44′, 1 female, CM M2426. *Locality 113* Murrayi, 16°50′, 132°48′, 2 females, CAM M57-58. *Locality 114* Dorisvale, 14°10′, 131°00′, 1 female, CM M6660. *Locality 115* Daly River, 14°48′, 131°24′, 1 female, CAM M36. *Locality 116* Daly River, 14°22′, 131°33′, 1 female, CAM M30. *Locality 119* Katherine Gorge, 14°06′, 132°18′, 5 females, CAM (M610-612). *Locality 121* Twin Peaks, 13°45′, 130°43′, 1 male, 1 female, WAM (M8424-25). *Locality 123* 35 km south of Darwin, 12°27′, 130°50′, 1 male, B 190. *Locality 124* Point Charles, 12°23′, 130°37′, 1 male, C 928. *Locality 126* Smith Point, Coburg Peninsula, 11°16′, 132°09′, 3 males, CM (M1896, M1900-01). *Locality 127* Nourlangie Rock, 12°43′, 132°33′, 1 male, CM M4671. *Locality 128* Oenpelli, 12°19′, 133°03′, 1 female, B 190. *Locality 129* Deaf Adder Creek, 13°06′, 132°56′, 1 male, CAM 4702. *Locality 130* Deaf Adder Gorge, 13°03′, 132°52′, 1 female, AM M10352. *Locality 141* Norman River, Normanton, 17°40′, 141°04′, 1 female, JM 2037. *Locality 142* Gulf of Carpentaria, 13°01′, 141°44′, 1 male, C 1482. *Locality 149* Ingham, 18°39′, 146°10′, 1 male, CM M1580. *Locality 153* Thirlstone, Torres Creek, 21°37′, 145°35′, 1 male, the other sex unknown, JM (M8816-17). *Locality 155* Glengalon, south-east of Emerald, 23°31′, 148°10′, 1 female, JM M15531. *Locality 158* Yebna Station 80 km west of Taroomm, 25°41′, 149°11′, 1 female, JM M15813. *Locality 159* Eidsvold, 25°22′, 151°07′, 1 male, JM 3082. *Locality 160* Landsborough, 26°48′, 152°48′, 1 female, JM M10948. *Locality 161* Cowan Cowan, Morton Island, 27°11′, 153°04′, 1 male, JM 4069. *Locality 162* Mount Crosby, 27°32′, 152°48′, 1 male, JM 9797. *Locality 163* Greymere, 28°14′, 151°45′, 2 females, JM (13308-09). *Locality 164* Durikai, 28°12′, 151°37′, 1 male, 1 female, JM (M13337, M13849). *Locality 165* Moree, 29°28′, 149°51′, 1 male, 1 female, AM (M918, M3228). *Locality 166* Mungindi, 28°59′, 149°00′, 2 males, 1 female, AM (M5521, M7920, M7922). *Locality 167* Brewarrina, 29°58′, 146°52′, 1 male, AM M8190. *Locality 168* Killara, Sydney, 31°28′, 150°36′, 1 female, AM M7384. *Locality 169* Frankston, 38°09′, 145°08′, 1 male, C 5130. *Locality 170* St Albans, 37°45′, 144°48′, 1 male, C 5132. *Locality 171* Winchelsea, 38°15′, 143°59′, 1 female, C 5131. *Locality 172* Coombe, 35°58′, 140°13′, 1 male, SAM M5206. *Locality 173* Berri, 34°17′, 140°36′, 1 male, SAM M7698. *Locality 174* Railway Siding, 34°56′, 138°36′, 1 male, SAM M5659. *Locality 175* Meningie, 35°41′, 139°20′, 1 male, SAM M3155. *Locality 176* Salt Creek, 36°08′, 139°39′, 1 female, SAM M7698.

Saccolaimus mixtus

(non-Australian)

Port Moresby, Papua New Guinea, 1 male, Two specimens sex unknown, AM (M3256 (paratype), M3257 (holotype), M3258 (paratype)).

Saccolaimus saccolaimus

Locality 145

Upper Endeavor River, 15°20′, 145°11′, 1 female, C 310. *Locality 146* Cooktown, 15°59′, 145°08′, 1 female, JM M19028. *Locality 151* Jerona Fauna Sanctuary, 19°34′, 147°13′, 1 male, WAM M23334. *Locality 152* Mosman, 1 female, JM M19028 (*S. 'nudicluniatus'*).

Non Australian Specimens Examined

Saccolaimus saccolaimus

Borneo, 1 male, WAM (M26085); India, 1 female, AMNH (27420); Java, 5 males, 1 female, AMNH (101602-06); Solomon Islands, 1 male, FMNH 54806 (*S. 'nudicluniatus'*).

Taphozous longimanus

Bali, 3 males, 1 female, WAM (M16182-85), Madras, India, 1 male, C 2210.

Appendix II Measurements, in mm for holotypes and unique specimens of some Australian emballonurids examined. Body measurements are from alcohol preserved specimens. For code to characters see Figure 2.

Species Catalogue No./ Character	*Saccolaimus mixus* AM M3258 (paratype)	*Taphozous hilli* M18260 WAM (holotype)	*Taphozous kapalgensis* CM M4806 (paratype)	*Taphozous troughtoni* CM M13213	*Taphozous georgianus* Derby W.A. WAM M24032	 Mount Isa Qld CM M13216	 Rockhampton Qld JM M9976
Sex	?	Female	Male	Female	Female	Female	Female
GL	21.7	20.0	20.7	24.3	21.0	22.0	22.6
AOW	6.6	6.0	5.9	6.8	6.1	6.5	6.5
LOW	7.9	6.2	6.4	7.1	6.1	6.6	6.3
ZW	–	13.0	13.0	14.7	13.1	13.3	14.2
ROL	8.6	8.2	8.7	10.2	8.6	9.2	9.6
MW	12.1	10.5	11.2	12.1	10.5	11.0	11.7
BW	11.6	10.6	10.9	11.7	10.0	10.7	10.5
CH	8.0	7.4	7.6	8.4	7.1	7.5	8.1
PL	8.8	7.1	8.0	9.8	8.6	8.8	8.9
PPW	–	3.4		4.7	3.7	3.8	4.1
BL	18.7	16.3	18.4	21.2	18.6	19.1	19.6
BUL	4.9	5.1	5.2	5.6	5.0	5.0	5.1
BB	3.4	2.2	2.3	2.6	2.1	2.0	2.3
OB	11.6	10.2	9.1	11.5	10.0	10.4	10.6
CW	1.8	1.7	2.0	2.2	1.9	2.0	2.1
RC^1-LC^1	4.8	3.5	4.0	4.5	4.0	4.1	4.3
C^1-M^3	10.0	8.8	9.3	11.0	8.8	10.0	10.3
M^1-M^3	5.4	4.8	5.0	5.8	4.9	5.3	5.6
M^2L	2.2	1.9	2.0	2.2	1.9	2.0	2.2
M^2W	2.4	2.4	2.3	2.6	2.5	2.4	2.6
M^3W	2.1	2.0	2.1	2.4	2.1	2.2	2.2
RM^3-LM^3	10.2	8.4	9.1	10.7	9.1	9.2	9.9
LR	12.2	10.7	11.0	13.1	11.4	12.0	12.3
RC	5.7	4.6	5.2	5.8	5.1	5.0	5.4
DL	18.7	16.1	17.1	20.7	17.6	18.8	19.1
SPL	4.0	4.3	3.7	4.6	4.5	3.9	4.0
PBW	1.0	0.3	0.6	0.6	0.5	0.6	0.7
ICD	3.2	2.9	2.9	3.3	2.8	3.0	3.2
HV		75.1	68.8	81.8	72.0	74.7	
TV		30.7	22.8	36.9	26.7	32.3	
EL		22.6	17.6	26.6	20.1	19.2	
EW		14.9	13.2	19.0	15.0	14.8	
TL		6.1	5.6	9.4	7.1	7.1	
RL		68.9	59.2	75.6	65.2	69.6	
MCIII		61.7	60.2	69.1	57.2	64.4	
PI	–	20.4	21.1	24.6	19.2	20.9	
PII	–	25.7	21.4	27.1	23.5	26.0	–
TIB		26.8	23.1	31.7	26.7	27.0	–
PES		12.9	12.4	14.7	12.1	12.6	

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Holocene avian assemblage from Skull Cave (AU-8), south-western Western Australia.

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Abstract

The avian assemblage from Skull Cave is composed of a minimum of 10 species. It is dominated by a single species, *Glossopsitta porphyrocephala*, which comprises up 58% of the total number of individuals recorded from the deposit (68), *Atrichornis clamosus* makes up a further 19%, and the last eight species cover the rest of the total (33%). The species which dominate this assemblage are non-terrestrial/diurnal/gregarious species, which are irruptive in nature. Terrestrial forms are also important to the composition of the assemblage. The assemblage was probably accumulated by *Tyto alba*. A palaeoenvironmental intrepretation based upon this assemblage indicates the presence of forest throughout the period of deposition.

Introduction

Until recently birds have been largely ignored or overlooked in the fossil vertebrate assemblages of Australia although they are useful in determining palaeoenvironments (Baird 1989) and could provide baseline data for biogeography and biostratigraphy (Baird in press a). The fossil material in Skull Cave (AU-8: Matthews 1985) includes one of the few avian assemblages associated with radiocarbon dates of Holocene age in Australia (Baird in press a). Although the Leeuwin/Naturaliste Penninsula has a proponderance of fossil localities (Porter 1979), because of the cavernous limestones in that region (Baird in press b), few have either radiocarbon dates or significant avian assemblages (Baird in press a). Information from the study of this assemblage, combined with the palaeoenvironmental information from the fossil avian assemblage of Devil's Lair (Baird in press e), could provide a hypothesis on a pattern of regional changes in climate over the past 35,000 years for the southwest of Western Australia.

Several studies on fossil vertebrate material from Skull Cave have been published, including mammals (Porter 1979) and frogs (Tyler 1985). This paper will provide identifications and discussion of the significance of the avian assemblage from Skull Cave.

Skull Cave occurs on the Leeuwin/Naturaliste Peninsula approximately 10 km west-north-west of the township of Augusta, Western Australia (115°05'S and 34°17'E). The local topography consists of hills with a relief of 30-90 m composed of sandstone and conglomerate (Laut *et al.* 1975). The vegetation surrounding Skull Cave consists of a forest of *E. diversicolor* to the east and north, open scrub merging to low open scrub to the west and low open woodland to the south (Smith 1973).

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The cave is a collapse doline, whose longest axis is in an east-west direction (approximately 40 m x 25 m) and an apical entrance (Figure 1). There is a pile of rubble which stands 13 m high, whose peak is 10 m below the entrance.

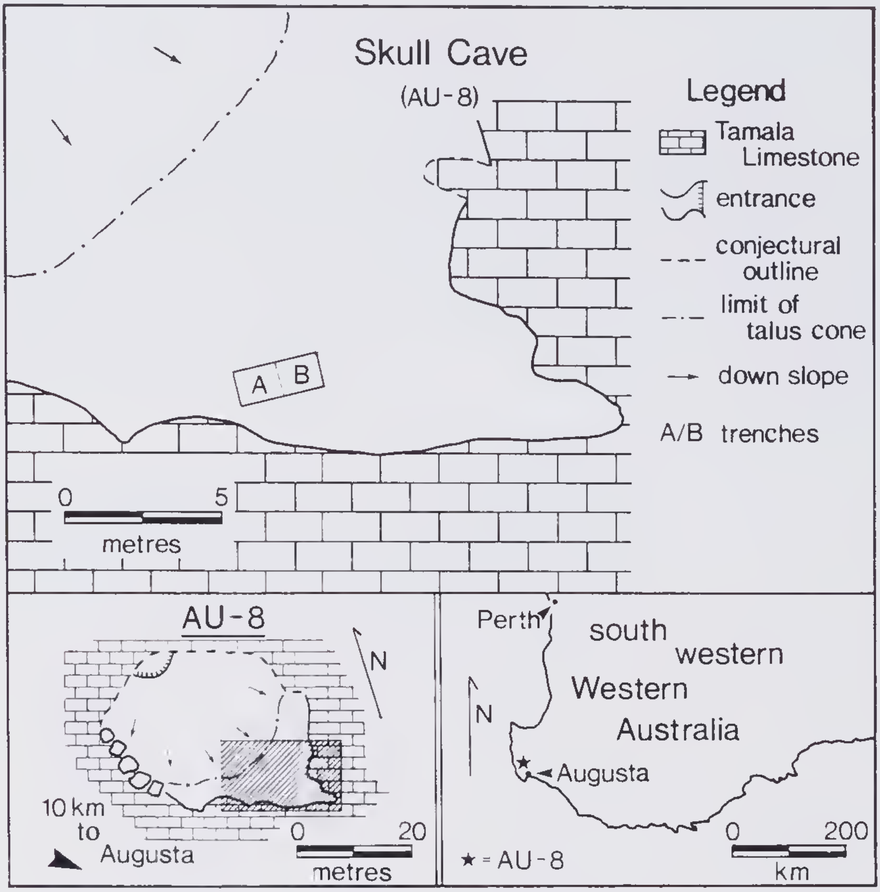

Figure 1. Plan view of Skull Cave demonstrating the position within the feature from which the fossil material was excavated.

The deposits in Trenches A and B consist of "thin interfingering bands of brown, orange and sometimes whitish coloured sediments" Porter (1979). A time transgressive chronology of deposition is corroborated by the radiocarbon dates on charcoal from two different levels within the stratigraphy (see Table 1).

No figure was offered to display the distribution of the layers. The vertebrate remains were labelled by excavation level not sedimentary unit. Therefore, except for the depth of the spits involved, there is no stratigraphic information for the specimens. The minimum number of individuals (MNI) calculated, then, will be lower than that which might have been possible if discrete sedimentological units had been identified.

Table 1. Radiocarbon dates, in y.B.P., completed on charcoal associated with excavations in Skull Cave, accomplished by J.R. Porter between 1969 and 1975 (from Porter 1979). SUA = University of Sydney, Australia.

Trench/Unit	Date	Reference #
B/4	2,900 ± 80	SUA 227
A/12	7,875 ± 100	SUA 228

Porter (1979) stated that the bulk of the small animals (undefined) were brought into the cave by owls, and the large animals, like *Macropus fuliginosus,* were trapped in the cave as a result of falling through the apical opening which created an effective pitfall trap. The evidence for the taphonomic scenario comes from the size and relative complete nature of the elements of smaller animals and the undamaged elements of the larger animals, except for broken limb-bones, which could be effectively argued as evidence for a pitfall origin of the material. There is little evidence for human involvement in the deposit, and no occupational evidence has been uncovered (*e.g.* hearths, shelly fauna, burnt bone, numerous artifacts, etc.).

The proposed palaeoenvironmental sequence for the time period covered by the deposit is as follows (from Porter 1979): that the area surrounding the cave must have been forested for much of the Holocene, based on the presence of *Potorous tridactylus,* whose undamaged remains are interpreted as being pitfall in origin. In addition most of the other animals included in the deposit include forest in their repertoire of habitats. Porter (1979) also suggested that the disappearance of the heath and scrub dwelling animals from the deposits represents the contraction of local pockets of these habitats as a "culmination of trends begun in late Pleistocene times perhaps initially influenced by marine transgression".

Materials and Methods

Material available for study included all avian elements excavated from trenches A and B (Figure 1). Of the available material there is still a moderate amount of passeriform elements which are as yet unidentified (Appendix IV). This is largely due to their fragmentary nature and the uniformity of most postcranial elements across the order, therefore hindering determinations.

All of the material discussed in the section on Skull Cave will be deposited in the palaeontological collection of the Western Australian Museum (WAM).

The scientific names used in each account follow Condon (1975) and Schodde (1975). Minimum numbers of individuals were determined by the standard method of counting the most abundant element from a particular side from each excavation level. This may lead to an overestimate of the MNIs due to mixing of the excavation layers (the levels do not necessarily correspond to discrete stratigraphic layers), although this is considered to by minor, because the deposit is largely time transgressive.

Geographical ranges for each species are here assumed to be the same as the current range, unless otherwise noted. Anatomical terminology follows Baumel *et al.* (1979). All measurements in the text are in millimetres. Standard measurements in the text are indicated in brackets and follow the guidelines in von den Driesch (1976) unless stated otherwise. All measurements were taken with vernier calipers accurate to 0.05 mm and were rounded to the nearest 0.1 mm. Species determination is based upon mensural criteria in every species account except where otherwise stated. Botanical nomenclature follows the guidelines of Specht (1981). Abbreviations used in the text and figures are listed in Appendix I. Material identified as juvenile is based upon the criteria of having a "pitted appearance of the surface of the bone and incomplete ossification of the articular facets" (Campbell 1979: 17). Morphological characters for determinations higher than species level are included in Appendix II, unless only one element is considered, in which case they are included in each species account (see Baird in press c for detailed methods).

Accounts of Species

Family: Phasianidae

Coturnix sp.

Material

Incom. right hum. (74.8.64), 2 huml end left ccd (86.7.398, 86.7.399), com. left tmt. (76.10.83).

Characters

See Baird (in press c) for the suite of characters considered diagnostic for the genus *Coturnix*.

The larger species of *Coturnix* cannot be separated by size or morphology (see Baird 1986).

Remarks

Coturnix pectoralis and *C. australis* are both considered likely for this material, based on biogeographic probability. Both of these species are irruptive, dispersing when food becomes scarce, and *C. pectoralis* will invade inland areas after substantial rains (Frith *et al.* 1977, Frith & Waterman 1977). The range of habitats covered by these species includes EOFF, EWF, HF, MOSF and ATSF.

Family: Columbidae

Phaps elegans

Material

Com. right ulna (76.10.126).

Characters

See van Tets and Rich (1980) for the suite of characters considered diagnostic for the family Columbidae and the genus *Phaps*.

The one specimen referred to *P. elegans* has a total length [GL] of 43.5 mm. This measurement falls within the range of total lengths for *P. elegans* and outside those for its cogeners (van Tets & Rich 1980).

Remarks

"Throughout its [*P. elegans*] range, it maintains this preference for healthland and other vegetation with a heath-like structure" (Frith 1982), particularly around swamps and coastal and near-coastal country. Although this species is not exclusively dependant on heaths, where it is sympatric with *P. chalcoptera* it seems to have a strong preference for this type of habitat.

Family: Loriidae

Glossopsitta porphyrocephala

Material

See Appendix III.

Characters

See Appendix II for the suite of characters considered diagnostic for the genus *Glossopsitta.*

G. porphyrocephala is intermediate in size between *G. pusilla* and *G. concinna* and the fossil material falls within the range of variation for *G. porphyrocephala* (see Baird in press e for an example of this).

Remarks

Mensurally the specimens of *Glossopsitta porphyrocephala* from this deposit are very similar to those from Devil's Lair (Baird in press e). There does not seem to have been any changes in the species, either mensural or morphological, throughout the span of time covered by the deposit.

The species is of little use in palaeoenvironmental interpretation, as it is nomadic and ranges over very large areas. It is considered irruptive and requires flowering plants, mainly eucalypts, for its food.

Family: Platycercidae

Platycercus icterotus

Material

Com. cran. (76.10.45), two dist. end right hum. (76.1.377, 86.7.501), two com. left hum. (75.10.25, 76.1.36), incom. right cmc. (86.7.498), dist. end right tmt. (86.7.500), com. left tmt. (86.7.499).

Characters

See Baird (in press c) and Appendix II for the suite of characters considered diagnostic for the family Platycercidae.

Within the south-west the family can be divided into a large species (*Barnardius zonarius*), a medium sized species (*Purpureicephalus spurius*) and a small species (*Platycercus icterotus*). Within this context, the fossil material falls into the range of variation exhibited by *Platycercus icterotus.*

Remarks

Habitats covered by this species include EOFF and EWF, particularly "open and partly cleared eucalypt woodland and forest but not heath" (Blakers *et al.* 1984).

Family: Aegothelidae

Aegotheles cristatus

Material

Prox. end left fem. (86.7.502), dist. end left tmt. (86.7.503).

Characters

See Appendix II for the suite of characters considered diagnostic for the genus *Aegotheles*.

Remarks

In most deposits *Aegotheles* material is usually considered to have had lived in the caves in which their remains are found but the condition, e.g. their incomplete nature and acute fractures, of the specimens in this deposit, would suggest that they were collected by *Tyto* sp. instead of being part of the autochthonous speleobiocenose fauna.

Aegotheles cristatus inhabits a broad range of habitats including EOFF, EWF, MOSF, and ATSF (Schodde & Mason 1980, Morris *et al.* 1981).

Family: Atrichornithidae

Atrichornis clamosus

Material

Two incom. rost. (76.7.228, 86.7.524), dist. end rost. (86.7.513), com. right hum. (72.8.120), incom. right hum. (74.8.45), dist end right hum. (86.7.507), com. left hum. (75.7.228), two prox. end left hum. (76.1.296, 86.7.508), com. right ulna (86.7.509), com. left ulna (86.7.525), com. right cmc. (86.7.519), com. left cmc. (86.7.520), two com. right ccd (76.10.262, 76.10.263), com. left ccd (86.7.526), incom. stm (86.7.517), incom. right fem. (74.1.70), prox. end right fem. (76.10.25), dist. end right fem. (86.7.510), two com. left fem. (86.7.504, 86.7.521) in com. left fem. (86.7.515), two prox. end right tbt. (86.7.516, 86.7.521), com. left tbt. (86.7.518), incom. left tbt. (86.7.505), two prox. end left tbt. (86.7.506, 86.7.514), com. left tmt. (86.7.523), dist. end left tmt. (86.7.511).

Characters

See Appendix II for the suite of characters considered diagnostic for the genus *Atrichornis* and refer to Rich *et al.* (1985) for plates on all elements.

Species-determination is based on both mensural and morphologic characters. *A. clamosus* is larger than *A. rufescens* (see Table 2, Baird in press d, Baird in press e, and Rich *et al.* 1985). All elements not included in the tables are considered to fall within the range of variation for *A. clamosus*. Unusual among these are the femora, which are considerably smaller than the one specimen of *A. clamosus*, but also far larger than the one specimen of *A. rufescens*. From the table of tarsometatarsal lengths (Baird in press d) it is apparent that the comparative specimen of *A. clamosus* is on the extreme upper end of the range of variation for this species. Therefore, because of the small sample size of fossil material, the difference between the fossil material and the comparative material is considered to be a result of sampling at either end of the range of variation. Extrapolating the size of femora from the fossil sample of tarsometatarsi (Table 2) demonstrates that both modern and fossil samples could fall within the total range of variation for *A. clamosus.*

Remarks

The material from Skull Cave was evenly distributed throughout the deposit. Mensurally, some of the elements have a wider range than would be expected for a single species, but I have no other reason to suspect that there are more than one. Measurements from specimens of this species from Skull Cave, and Devil's Lair versus modern specimens of both *A. clamosus* and *A. rufescens* are shown in Table 2.

Burbidge *et al.* (1986) described the habitat of *A. clamosus* in the following way: "Examination of the habitat at Two Peoples Bay, and other locations where Noisy Scrub-birds are known to have occurred, indicates that they were confined to the wetter area within the distribution of the Jarrah/ Marri (*Eucalyptus marginata*/ *E. calophylla*) forest, in particular to the ecotone between forest and swamp vegetation".

This species apparently requires sedges and/or shrubs in the understorey as well.

Table 2. Length measurements of femora of both species of *Atrichornis* and all referred material. The last set of data is extrapolated from tarsus lengths, from fossil material, multiplied by a factor of 1.0383 (the factor of difference between the femur and tarsus of the comparative specimen) to test the range or variation possible for this material.

	μ	σ -1	OR	N
A. rufescens (M)	>20.4	—	—	1
A. clamosus (M)	27.1	—	—	1
A. clamosus (AU-8)	24.4	0.4	24.0 - 24.9	4
A. clamosus (extrap.)	26.2	1.6	23.7 - 27.2	4

Family: Hirundinidae

undetermined

Material

Dist. end right hum. (86.7.533).

Characters

See Baird (in press c) for the suite of characters considered diagnostic for the family Hirundinidae.

Generic — and specific — determinations are not possible for the Australian members of this family because of their extreme morphological uniformity (Baird 1985).

Family: Maluridae

Malurus sp.

Material

Com. right hum. (76.1.35).

Characters

The suite of characters considered diagnostic for the family Maluridae includes: **Humerus,** (proximal end), 1. *caput humeri* flattened proximally but has a centrally located distal extension (in palmar view), 2. *tub. dorsale* large, 3. *cta bicipitalis* convex proximally, 4. transition from *caput humeri* to *cta pectoralis* is abrupt (90⁰), 5. single *fossa pneumotricipitalis,* 6. *crus dorsale fossae* attaches to shaft distally, 7. *cta pectoralis* proximodistally short, 8. *inc. capitis* broad, deep and extends to, midline of shaft, 9. *fossa pneumotricipitalis* not incised into shaft; (distal end), 1. whole end proximodistally flattened, 2. *proc. flexorius* extends furthest distally, 3. distal end of *proc. flexorius* rounded, 4. *proc. flexorius* forms a smooth transition with curve of shaft. The suite of characters considered diagnostic for the genus *Malurus,* includes: **Humerus,** 1. palmar face of *cta pectoralis* swollen, 2. *cta bicipitalis* not as reduced proximally, 3. sulcus for attachment of *M. pectoralis* not deep, 4. *cta pectoralis* ends abruptly distally, 5. medium size.

The total length of the specimen [G.L. = 11.5] falls within the range of variation for the species *M. elegans* and outside that for *M. splendens,* although there is an additional species of *Malurus* within which this specimen also falls, *M. leucopterus.* Although biogeographic probability suggests that this is referrable to *M. elegans,* the determination will be left at *Malurus* sp. until specimens of *M. pulcherrimus,* which also occur in this region, become available.

Family: Acanthizidae

Dasyornis longirostris

Material

Com. right hum. (86.7.528), com. left hum. (86.7.527), incom. right fem. (76.1.70), incom. left fem. (76.10.192)

Characters

See Baird (in press c) for the suite of characters considered diagnostic for the genus *Dasyornis.*

Dasyornis longirostris is the smallest of the three species in the genus *Dasyornis.* The fossil specimens are considered to fall within the range variation for *D. longirostris* and outside that for fossil specimens of *D. brachypterus* and both fossil specimens and modern material of *D. broadbenti* (see Baird in press c). Assignment only confers the fossil material to *D. longirostris* because of the lack of an adult comparative specimen of *D. longirostris* to confirm the identification.

Remarks

The range of *Dasyornis longirostris* at the time of European contact, as discerned through skins and sightings, has been figured and discussed in Smith (1977). Although it had not been recorded from the Cape Leeuwin/Naturaliste Peninsula, the author did demonstrate that the species was known from the area around Perth, to the north, and extensively around Albany, to the east. Smith (1977) mentions that the habitat in which the species is currently recorded is coastal heath.

Ford (1965) provides a more precise habitat of *D. longirostris* as, "although the Bristlebird frequently occurs in the same habitat as the Noisy Scrub-bird *Atrichornis clamosus*, at Two Peoples Bay, it prefers the margins of swamp heath and the dune valleys where the vegetation is only a few feet high. Sword grass, *Lepidosperma gladiatum* and *augustatum*, and saw grass, *Gahnia trifida*, are common elements of its habitat which is usually overgrown with an entanglement of dodder, *Cassytha racemosa*, and *Agrostis aemula*, mat grass, *Hemarthria uncinata*, spear grass, *Diplogon setaceus* and rushes which often include *Anarthria prolofera*, *Hypolaena gracillima*, *H. fasciculata* and *Loxocarya flexuosa*".

Family: Artamidae

Artamus cyanopterus

Material

Incom. left hum. (76.1.194).

Characters

The suite of characters considered diagnostic for the genus *Artamus* includes: **Humerus,** (proximal end) 1. single *fossa pneumotricipitalis*. 2. *cta bicipitalis* does not extend beyond *tub. ventrale* laterally, 3. *cta bicipitalis* not greatly expanded laterally, 4. *inc. M. supracoracoideus* and *M. pectoralis* restricted to distal end of *cta pectoralis;* (distal end), 1. *fossa M. brachialis* shallow; (whole), 1. element very stout.

The specimen (76.1.194) is referred to the species *A. cyanopterus* based on its total length [T.L.=20.5], which falls within the range of variation for this species and outside that for all other Australian artamid spp. (see Baird 1986).

Remarks

Artamus cyanopterus is largely restricted to EWF and EOFF (Morris *et al.* 1981), but can occur in wetter areas (*i.e.* ETOFF) particularly where dry ridges support a drier vegetation type (*i.e.* EOFF) than the surrounding gullies (Loyn 1980, Smith 1984).

Non-Passeriformes

Family: Undetermined

Material

Dist. end right ulna (76.1.163), incom. right cmc. (86.7.530), shaft frag. right cmc. (86.7.529), incom. left ccd (86.7.532), dist end left fem. (86.7.531).

Passeriformes

Family: Indeterminate

Material

Com. right hum. (74.8.19), incom. right hum. (74.8.20), incom. right fem. (86.7.534), two incom. left fem. (86.7.535).

Aves

Order: Indeterminate

Material

14 vertebrae (86.7.634, 86.7.636, 86.7.637, 86.7.638, 86.7.640), two acet, frag. pel. (86.7.635, 86.7.639).

Table 3. List of avian species identified from the Skull Cave deposit, with both common and scientific names, number of specimens (N), and minimum number of individuals (MNI) based on the total number of elements in the deposit.

	MNI	N
Phasianidae		
Coturnix sp. (Quail sp.)	4	5
Columbidae		
Phaps elegans (Brush Bronzewing)	1	1
Loriidae		
Glossopsitta porphyrocephala (Purple-crowned Lorikeet)	39	161
Platycercidae		
Platycercus icterotus (Western Rosella)	5	8
Aegothelidae		
Aegotheles cristatus (Australian Owlet-nightjar)	1	2
Atrichornithidae		
Atrichornis clamosus (Noisy Scrub-bird)	13	32
Hirundinidae		
indeterminate (Swallow sp.)	1	1
Maluridae		
Malurus sp. (Fairy-wren sp.)	1	1
Acanthizidae		
Dasyornis longirostris (Western Bristlebird)	2	3
Artamidae		
Artamus cyanopterus (Dusky Woodswallow)	1	1

Discussion

The avian assemblage from Skull Cave is composed of a minimum of 10 species. It is dominated by a single species, *Glossopsitta porphyrocephala*, which makes up 58% of the total number of individuals recorded from the deposit (68: Table 3). The MNI from *Atrichornis clamosus* make up a further 19%, and the last eight species cover the rest of the total (33%). The species which dominate this assemblage are non-terrestrial/diurnal/gregarious species, which are irruptive in nature (Figure 4). Terrestrial forms are also important to the composition of the assemblage.

The stratigraphic distribution of the species in the two trenches and their corresponding MNIs are demonstrated in Table 4. There are no extinct taxa currently recognized in the assemblage.

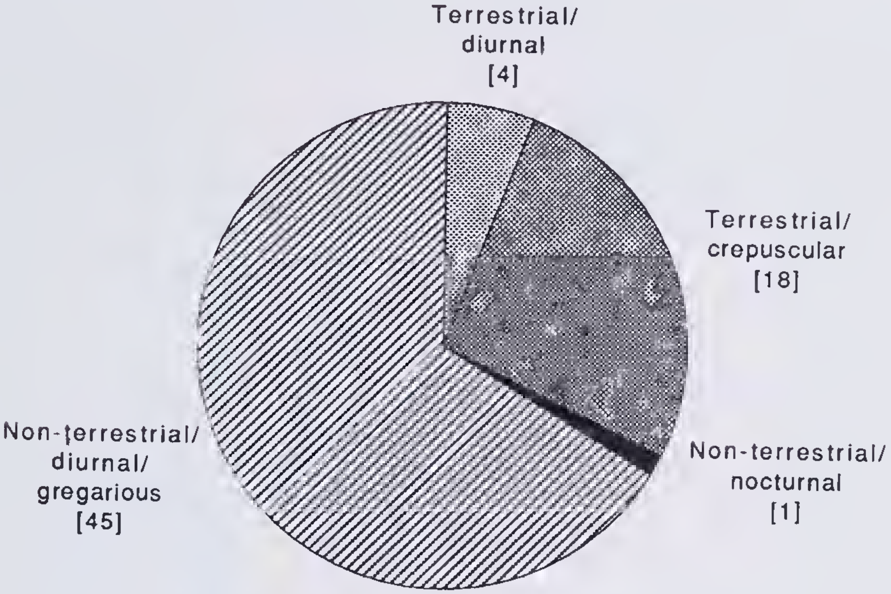

Figure 4. Percentages from total fauna (based on MNI=67) of various avian behavioural groups demonstrating that the non-terrestrial, diurnal, gregarious group dominate this assemblage (figures in brackets are the MNIs for each group).

Taphonomy

The condition of the avian material is good, with large percentages of complete and incomplete elements and crania present. Coloration ranges from white to light brown and increases in intensity with depth.

In the analysis of the distribution of weights of the avian taxa represented in the Skull Cave assemblage I have included all material except the hirundinid material, which is considered to be an allochthonous speleophile (Table 5). Incongruent to the rest of the material is the single specimen of *Phaps elegans*, whose weight of 212 g. is far outside of the mean for the bulk of the other specimens. A summary of the weight distribution can be seen in Figure 2. The bulk of the material (99%) falls below the 100 g level, with the greatest percentages within the 20-40g and 40-60g classes. The mean body weight for this material is 49g.

Sums of complete and incomplete elements barely outnumber those of the terminal ends (Figure 3). The pattern of element abundance for *G. porphyrocephala* is similar to that in Devil's Lair and to those of *Coturnix* and *Turnix* spp. in many of the other

Table 4. Stratigraphic distribution of MNI for avian species identified from sediments excavated from Trenches A and B of Skull Cave.

Depth from Surface (cm)	*Coturnix* sp.	*Phaps elegans*	*Glossopsitta porphyrocephala*	*Platycercus icterotus*	*Aegotheles cristatus*	*Atrichornis clamosus*	Hirundinidae indet.	*Malurus* sp.	*Dasyornis longirostris*	*Artamus cyanopterus*	Non-passerines unident.	Passerines unident.
0 — 7			2	1		1						3
7 — 14	1		2			2			1			4
14 21		1	2									2
*A 21 — 28	1		3	1		1						6
28 — 35			3									3
35 — 42			3			1			1			2
42 — 63			2	1		2						3
63 — 70	1		1			1						2
70 — 80			3								1	3
80 — 90	1		5	2		1		1				2
90 — 100			2			1						1
*B 100 — 115			4								1	2
115 — 127			2		1	1				1	1	2
127 — 137			4			1						5
137 — 144			2			1						1
144 — 150							1					2
150 — 160			1									
160 — 170												
170 — 180												1
180 190												

*A = 2900 ± 80 y.B.P. *B = 7875 ± 100 y.B.P.

deposits across southern Australia, despite the differences in element lengths and structure (Baird in press b). The only aberrant figure for this material is for the number of carpometacarpi, which is unusually low.

The Skull Cave avian assemblage is characterized by relatively good preservation, body size distribution under 100 g, and a large percentage of terrestrial species and gregarious/non- terrestrial/diurnal species which are irruptive in nature (Figure 4). These characters indicate tytonid owls as the accumulators of the avian assemblage (except for *P. elegans*). The tytonid species involved is indicated by the low value for mean body weight (*i.e. T. alba*). This interpretation corroborates the hypothesis of

Table 5. Avian taxa from excavations of Skull Cave and their proposed taphonomic accumulators.

Taphonomic group	Taphonomic agent	Species associated
Autochthonous /speleophiles		Hirundinidae
Allochthonous/avian	*Tyto alba*	All other species
	Unknown	*Phaps elegans*

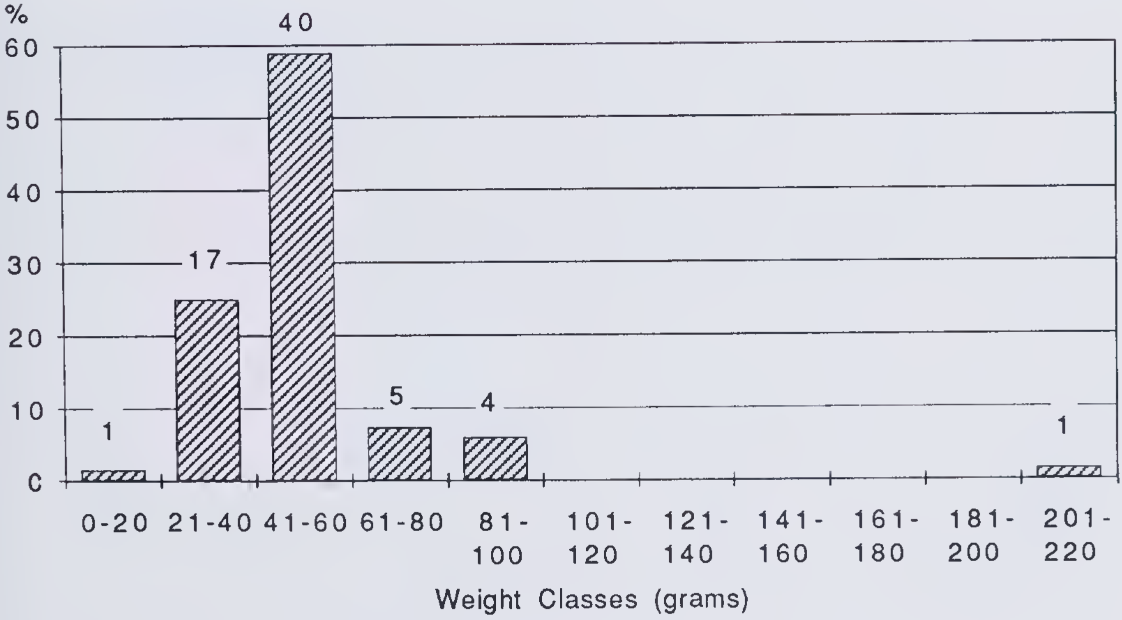

Figure 2. Percentage contribution of weight classes of bird species making up the Skull Cave assemblage (except the hirundinid material) showing the concentration of individuals below the 100 g class. Numbers above the columns represent MNI from a total of 67.

Porter (1979: see Introduction) for an owl accumulated assemblage and is consistant with the microvertebrate assemblage reported to date in that *Tyto alba* includes birds, mammals and amphibians in its diet (Baird in press b, Morgan 1977).

Palaeoenvironmental interpretation.

Although changes in the avian assemblage do not occur throughout the period of deposition, there are some indicators of habitats, which suggest that the environment was largely similar to that of today with a mixture of EOFF and HF, combined with a local wetland dominated by sedges (Table 6). This interpretation corroborates the hypothesis of Porter (1979) for the presence of forest throughout the period of deposition but fails to corroborate the loss of heath or scrub.

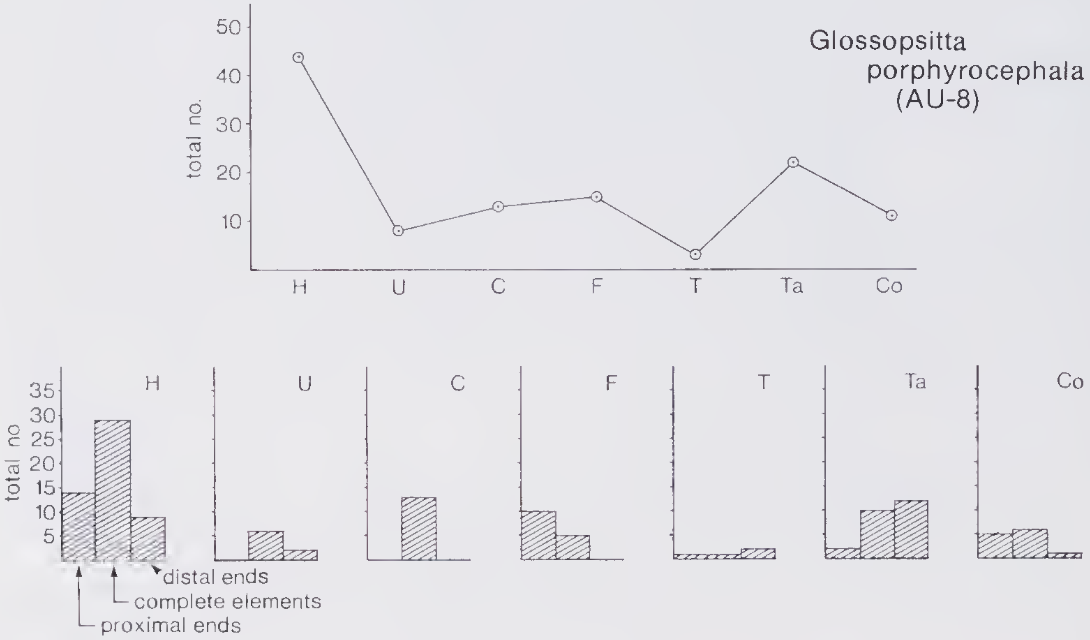

Figure 3. Abundances of seven commonly represented post-cranial elements of *Glossopsitta porphyrocephala* from the excavation of Skull Cave, Western Australia. Included are the sums of complete and most common terminal ends (Top: data points connected to facilitate visual cognition of changes), and the proportions of fragmentary specimens relative to complete (and incomplete) specimens (Bottom). H=humerus, U=ulna, C=carpometacarpus, F=femur, T=tibiotarsus, Ta=tarsometatarsus and Co=coracoid.

Table 6. Groups of avian taxa based on their usefulness in palaeoenvironmental interpretation (habitat specificity (exact/wide ranging)/habitat distribution (patchy/regional)).

- Wide ranging/Regional
  - ETOFF, EOFF, EWF, HF, and MOSF
    - *Coturnix* sp.
    - *Glossopsitta porphyrocephala*
  - EOFF and EWF
    - *Playtcercus icterotus*
    - *Artamus cyanopterus*
  - HF
    - *Phaps elegans*
- Exact/Patchy
  - HF/Wetlands
    - *Dasyornis longirostris*
  - Ecotone between EOFF and Wetlands.
    - *Artichornis clamosus*

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Appendix I

List of abbreviations and contractions used in text, figures and appendices.

acet.	*acetabulum*
ATSF	*Acacia* tall scrub formation
ccd	coracoid
cmc.	carpometacarpus
com.	complete
cond.	*condylus*
cot.	*cotyla*
cran.	cranium
cta	*crista*
dist.	distal
EOFF	*Eucalyptus* open forest formation
ETOFF	*Eucalyptus* tall open forest formation
EWF	*Eucalyptus* woodland formation
fac.	*facies*
fem.	femur
frag.	fragment
HF	heathland formation
hum.	humerus
huml	humeral
imp.	*impressio*
inc.	*incisura*
incom.	incomplete
juv.	juvenile
lig.	*ligamenta*
M.	*musculus*
mand.	mandible
MNI	minimum number of individuals
MOSF	mallee open scrub formation
N	number of elements in the statistical population
OR	observed range
pel.	pelvis
proc.	*processus*
prox.	proximal
rost.	rostum
scap.	scapula
σ	standard deviation
stm	sternum
stnl	sternal
sul.	*sulcus*
symph.	*symphysis*
syn.	synsacrum
tbt.	tibiotarsus
tmt.	tarsometatarsus
troc.	*trochlea*
tub.	*tuberculum*
μ	mean
y.B.P.	years Before Present

Appendix II

Suites of characters considered diagnostic for those taxa included in this study. Only those elements for which representatives occur in the cave deposit are included. The sequence of elements is standardized for ease of reference and includes the following: rostrum, cranium, mandible, humerus, ulna, carpometacarpus, coracoid, scapula, furcula, sternum, pelvis, synsacrum, femur, tibiotarsus and tarsometatarsus. For each of the long bones separate sections are provided for the proximal end, shaft and distal end (except for the coracoid, which is divided into humeral end, shaft and sternal end), and each character is numbered. Not included in the analysis were the vertebrae, costal elements and phalanges.

Order Psittaciformes

See Baird (in press c).

Family: Loriidae

Rostrum, 1. not strongly decurved, 2. culmen a sharp, well defined ridge extending distally, 3. external nares located proximally on rostrum, 4, thin nasal septum (W. Boles, pers. comm.); **Humerus,** (proximal end), 1. broad based *caput humeri,* 2. no distal extension of *caput humeri* on palman face, 3. second *fossa pneumotricipitalis* present, 4. *cta bicipitalis* not greatly expanded laterodistally but gradually slopes to shaft distally; **Ulna,** (shaft), 1. stout, 2. large curvature; (whole), 1. medium to small size (this suite of characters also present in *Lathamus*): **Coracoid,** (humeral end), 1. *proc. acrocoracoid* flattened humerally, not bulbous; (shaft), 1. intermediate between being gracile and stocky; (sternal end), 1. broad sternal base, 2. *imp. M. sternocoracoidei* shallow; **Femur,** (proximal end), 1. *cta trochanteris* does not surpass *caput femoris* proximally, 2. *fac ventralis* excavated; (distal end), 1. medial edge tends strongly distomedially; **Tibiotarsus,** (distal end), 1. very deep *sul. cartilaginis tibialis,* 2. *cond. medialis* much larger than *cond. lateralis,* 3. distal end shaft broad; **Tarsometatarsus,** (proximal end), 1. one large enclosed canal in hypotarsus; (shaft), 1. short and stout; (distal end), 1. *fac. dorsalis* flat, 2. ventral extension of *troc. metatarsi IV* appears further distally due to lack of distal extension of *troc. metatarsi III.*

Glossopsitta

Rostrum, 1. proximodistally short, 2. small size; **Cranium,** 1. area between orbit and proximal end wide (viewed laterally): **Humerus,** (proximal end), 1. *cta pectoralis* lacks medially projecting proc. on distal-most tip; **Carpometacarpus,** (proximal end), 1. facet for insertion of *lig. radiocarpometacarpale* more lateral on *troc. carpalis,* 2. more distally located *proc. pisiformis,* 3. T.L. less than 20mm; **Coracoid,** (proximal end), 1. shallow groove present in anteromedial face of acrocoracoid; **Tarsometatarsus,** (proximal end) 1. *cot. lateralis* not as distorted laterally; (whole), 1. total length less than 15.5 mm.

Family: Platycercidae

Carpometacarpus, (proximal end), 1. *proc. extensiorius* tends proximolaterally, 2. *proc. extensorius* gracile, 3. proximal end, as a whole, relatively small; (shaft), 1. gracile; **Tarsometatarsus,** (proximal end), 1. hypotarsus with one large unenclosed canal, ventrally, and rimmed, dorsally, by numerous small enclosed canals; (shaft), 1. long and gracile; (distal end), 1. *troc. metatarsi III* not greatly expanded distally, 2. *fac. dorsalis* flat (except in *Pezoporus, Geopsittacus* and *Neophema).*

Family: Aegothelidae

Tarsometatarsus, (distal end), 1. troc. with very little splaying laterally, 2. distal foramen in a deep groove extending between *troc. metatarsi III* and *IV,* 3. trochleae laterally compressed with narrow intermetacarpal spaces.

Family: Atrichornithidae

Atrichornis

Humerus, (proximal end), 1. insertion of *M. scapulohumeralis* anterior distally extending and pointed, 2. *caput humeri* flattened and at an angle greater than 90 degrees from shaft (measured internally), 3. *tub. ventrale* reduced, 4. *cta pectoralis* strongly arcuate; **Tarsometatarsus,** (distal end), 1. sulci present on all three *troc. metatarsi,* 2. *tub. M. tibialis cranialis* not pronounced, 3. *inc. intertrochlearis* restricted to extreme distal end (they do not pass middle of *troc. metatarsi* proximally, in dorsal view), 4. outer edges of *troc. metatarsi III* taper together distally, in ventral view, 5. inner edge of *troc. metatarsi II* tends proximomedially, in ventral view, 6. *troc. metatarsi II* and *III* equal in size and larger than *troc. metatarsi IV.*

Appendix III

Loriidae

Glossopsitta porphyrocephala

Material

com. rost. (76.10.227), 3 incom. rost. (71.10.158, 75.10.22, 86.7.480), 2 incom. mand., (71.10.184, 76.10.358), 14 incom. right hum. (74.8.43, 74.8.66, 74.8.122, 74,8,125, 74.8.126, 76.1.254, 76.1.263, 76.7.420, 76.10.392, 86.7.432, 86.7.450, 86.7.463), 7 prox. end right hum. (74.8.44, 74.8.68, 76.1.260, 86.7.409, 86.7.416, 86.7.421, 86.7.451), shaft frag. right hum. (86.7.433), dist. end right hum. (86.7.464), com. left hum. (75.10.26), 16 incom. left hum. (74.8.65, 74.8.145, 74.8.197, 74.8.198, 75.10.28, 76.1.137, 76.1.138, 76.1.191, 76.1.192, 76.10.412, 86.7.400, 86.7.417, 86.7.468, 86.7.482, 86.7.490), 7 prox. end left hum. (74.8.18, 74.8.21, 76.10.311, 76.10.356, 76.10.357, 76.10.414, 86.7.418), shaft frag. left hum. (86.7.452), 2 dist. end left hum. (75.10.29, 86.7.426), 3 incom. right ulna (86.7.453, 86.7.491), 4 incom. left ulna (86.7.434, 86.7.492), dist. end left ulna (86.7.435), 3 incom. right cmc. (86.7.407, 86.7.422, 86.7.483), prox. end right cmc. (86.7.401), 4 dist. end right cmc. (86.7.410, 86.7.436, 86.7.469), 2 com. left cmc. (86.7,427, 86.7.437), 7 incom. left cmc. (76.1.210, 86.7.411, 86.7.419, 86.7.470, 86.7.493), 2 prox. end left cmc. (86.7.412, 86.7.479), 4 dist. end left cmc. (86.7.402, 86.7.428, 86.7.471, 86.7.494), com. right ccd (86.7.481), 3 incom. right ccd (86.7.423, 86.7.438, 86.7.472), 5 huml end right ccd (86.7.440, 86.7.449, 86.7.454), stnl end right ccd (86.7.439), com. left ccd (86.7.484), 2 incom. left ccd (86.7.441), 6 huml end left ccd (86.7.442, 86.7.455, 86.7.486) 3 com. right fem. (76.8.97, 86.7.403, 86,7.456), incom. right fem. (86.7.473), 3 prox. end right fem, (86.7.414, 86.7.429, 86.7.465), incom. left fem. (76.1.69). 7 prox. end left fem. (86.7.404, 86.7.430, 86.7.443, 86.7.474, 86.7.487), 2 dist. end right tbt. (86.7.457, 86.7.477), incom. left tbt. (86.7.424), prox. end left tbt. (86.7.425), 3 dist. end left tbt. (86.7.444, 86.7.458), 12 incom. right tmt. (86.7.405, 86.7.415, 86.7.431, 86.7.445, 86.7.459, 86.7.475, 86.7.478, 86.7.488, 86.7.495), prox. end right tmt. (86.7.476), 3 dist. end right tmt. (86.7.446, 86.7.460), com. left tmt. (86.7.447), 8 incom. left tmt. (86.7.406, 86.7.448, 86.7.461, 86.7.466, 86.7.485, 86.7.489), 7 dist. end left tmt. (86.7.408, 86.7.462, 86.7.467, 86.7.495, 86.7.497).

Appendix IV

Unidentified passeriform material from Skull Cave.

incom. rost. (86.7.536), 2 dist. end rost. (86.7.578, 86.7.599), 2 mand. symph. (86.7.537, 86.7.607), right ramus mand. (86.7.628), left ramus mand. (86.7.620), mand. syph. frag. (86.7.627), com. right hum. (86.7.547), 11 incom. right hum. (74.8.46, 74.8.167, 74.8.178, 74.8.179, 76.1.261, 76.1.262, 86.7.566, 86.7.594, 86.7.597, 86.7.608), 10 prox. end right hum. (74.1.259, 74.8.48, 74.8.49, 76.1.193, 76.1.195, 76.1.257, 76.1.258, 86.7.548, 86.7.559, 86.7.600), prox. end frag. right hum. (74.8.168), shaft frag. right hum. (86.7.560), 6 dist. end right hum. (74.8.47, 74.8.197, 86.7.556, 86.7.567, 86.7,579, 86.7.629), 3 com. left hum. (74.8.144, 76.1.321, 86.7.538), 10 incom. left hum. (74.8.67, 74.8.69, 74.8.70, 74.8.71, 74.8.123, 76.10.125, 76.10.312, 86.7.539, 86.7.580, 86.7.604), incom. left hum (juv.) (74.8.121), 6 prox. end left hum. (74.8.72, 74.8.146, 76.1.136, 86.7.581, 86.7.617), prox. end frag. left hum. (76.1.135), 8 dist. end left hum. (75.10.30, 75.10.31, 76.1.320, 76.10.413, 86.7.540, 86.7.545, 86.7.557, 86.7.582), com. right ulna (86.7.583), 2 incom. right ulna (86.7.618), incom. left ulna (86.7.561), prox. end left ulna (86.7.595), com. right cmc. (86.7.562), 7 incom. right cmc. (86.7.584, 86.7.609, 86.7.621, 86.7.630), 10 incom. left cmc. (76.1.277, 86.7.568, 86.7.585, 86.7.605, 86.7.610, 86.7.619, 86.7.622, 86.7.625, 86.7.631), 2 com. right ccd (76.10.263, 86.7.623), 2 incom. pel. (86.7.549, 86.7.569), acet. frag. pel. (86.7.612), 2 com. syn. (86.7.601, 86.7.611), 2 incom. syn. (86.7.551, 86.7.632), 3 com. right fem. (74.8.95, 74.8.98, 76.1.368), 9 incom. right fem. (74.8.99, 76.1.68, 76.10.46, 76.10.193, 86.7.541, 86.7.552, 86.7.563, 86.7.570, 86.7.586), 2 prox. end right fem. (86.7.587, 86.7.606), shaft frag. right fem. (86.7.588), 2 dist. end right fem. (86.7.558, 86.7.571), com. left fem. (86.7.550), 8 incom. left fem. (86.7.543, 86.7.553, 86.7.554, 86.7.564, 86.7.589, 86.7.613, 86.7.694), prox. end left fem. (86.7.576), 4 dist. end left fem. (86.7.544, 86.7.590, 86.7.598, 86.7.614), 3 prox. end right tbt. (86.7.577, 86.7.596, 86.7.615), 4 dist. end right tbt. (86.7.555, 86.7.565, 86.7.572, 86.7.591), 2 incom. left tbt. (86.7.546, 86.7.573), incom. left tbt. (juv.) (86.7.616), 4 prox. end left tbt. (86.7.542, 86.7.574, 86.7.592, 86.7.602), 6 dist. end left tbt. (86.7.575, 86.7.593, 86.7.626), com. right tmt. (86.7.603), dist. end left tmt. (86.7.633).

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SHORT COMMUNICATIONS

Rec. West. Aust. Mus. 1991, **15**(1): 289

A replacement name for *Lerista concolor* Storr, 1990 (Squamata: Scincidae).

G.M. Shea*

In a recent note, Storr (1990) described as new *Lerista concolor,* from a single specimen from the Maitland River. Unfortunately, *Lerista concolor* Storr is a junior subjective homonym of *Lygosoma (Rhodona) bipes concolor* Werner, 1910, itself a junior subjective synonym (Storr 1971) of *Lerista lineopunctulata* (Duméril and Bibron, 1839), and consequently a replacement name is required while both species remain in *Lerista* (Article 59 of the Code). I propose *Lerista quadrivincula* as a replacement name for *Lerista concolor* Storr. The name, from the Latin *quadr-* (four) and *vinculum* (a chain), alludes to the four lines of dark streaks on the dorsum, one of the diagnostic characters of the species (Storr 1990).

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Grooved australite from the vicinity of Corrigin, Western Australia

W.H. Cleverly*

An australite found in south-western Australia has a groove encircling the extant portion of the anterior surface (Figure 1B, C). The find site of the australite was somewhere within the Shire of Corrigin, which is centered upon the town of that name, located at 32°20′S, 117°52′E.

The specimen was a round or slightly oval core, the original shape now uncertain because of an old, natural, flake loss (Figure 1A, D). Dimensions are (23.7-21.9) mm diameter X 15.6 mm thick, mass 9.67 g, and specific gravity 2.45. All surfaces, including flake scars and the groove, are pitted or otherwise affected by weathering.

The well-rounded rim is in the usual position at the greatest diameter of the core, and the surface profile anterior to it is gently convex (Figure 2A, B). These features contrast with the sharper rim and adjacent concavity of a typical core (Figure 2C). A few very small U-grooves (0.2-0.6 mm wide, 0.4-1.0 mm long) are present immediately anterior to the rim, and are oriented normal to it (Figure 1C). Grooves of that type and orientation, but usually several millimetres long, are commonly developed by weathering anterior to a rim i.e. at the rear edge of a surface created by loss of an aerothermal stress shell.

A much larger groove (>1 mm wide, 0.2 mm deep, with gently concave cross section), is centered 3-4 mm anterior to the rim and sub-parallel with it. This groove encircles the australite except in a gap of *ca.* 90°, where there is a large, deeply-etched, flake scar (Figure 1D). Very small U-grooves (0.2-0.4 mm wide, up to 0.6 mm long) are present in places within the large groove and are oriented transverse to it (Figure 1C). Anterior to the large groove, the profile is again convex. The general form of the anterior surface is thus constricted at the groove but gently bulging on each side of it (Figure 1B; 2A, B).

Primary processes of australite formation can explain the various forms of posterior surface as remnants of the surfaces of spherical or rotating masses of melt, but they cannot explain surface features such as this groove occurring elsewhere. Terrestrial ("tertiary") weathering processes have created pits impartially within the groove and on other parts of the surface, thereby indicating that the groove was present prior to weathering. The origin of the groove therefore needs to be sought in the intervening secondary (aerodynamic) shaping period.

Profiles of the australite as far rearward as the points Q (Figure 2A, B) resemble the complete anterior profile of a typical core (Figure 2C), but no rim is present at Q, and it needs to be assumed that the small U-grooves have the same significance as the usual much larger ones. There appear to have been two separate stages or episodes of spalling of the stress shell, neither leading to development of a typical rim. The only recorded

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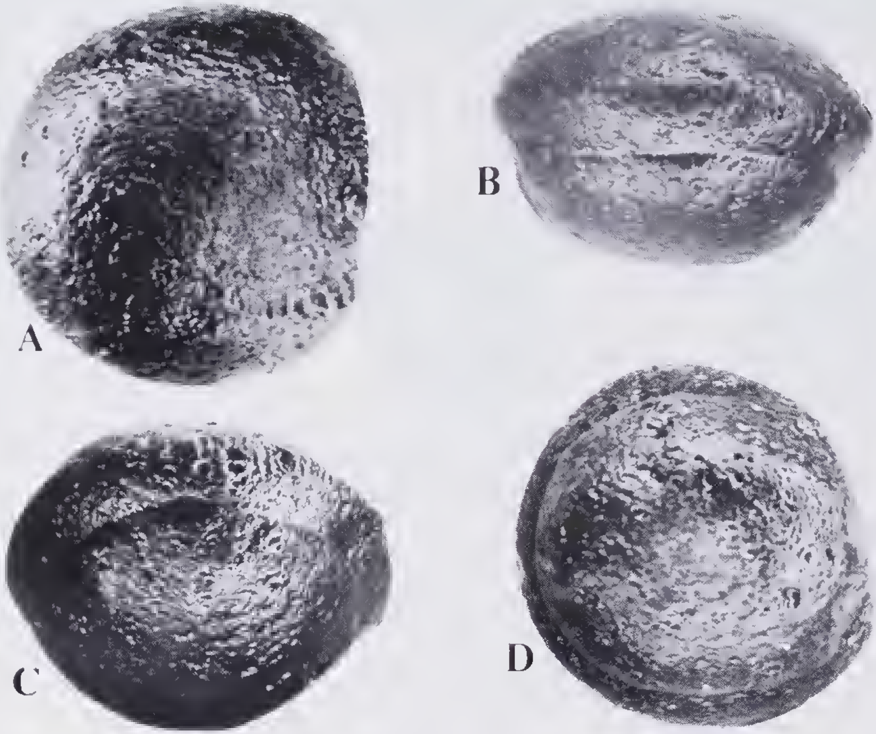

Figure 1. Australite from vicinity of Corrigin, Western Australia. All views x2. A, Posterior surface with large flake loss to right. B. View normal to line of flight which is directed towards bottom of page. In this view, the groove (below centre) may appear to be emphasized as the result of relief inversion. C. View obliquely "upward" showing anterior surface with groove, small U-grooves at rear (upper) edge and minute U-grooves in the large groove towards upper right. Pale, narrow, lunate strip above is posterior surface. D. Anterior surface. Narrow, circumferential, flange-like strip is the part of the anterior surface posterior to the groove, which appears as a pale narrow strip. Flake loss to right.

example of an australite with two rims was found west of Ravensthorpe, 220 km south-east of Corrigin (Cleverly 1987). On that specimen, the rims are only 1 mm apart, but on the Corrigin core, the rim and the more anterior potential rim site are 3-4 mm apart. The more anterior rim is undeveloped (or lost?), and the other is atypical.

Certain other peculiarities of australites found in south-western Australia are already known. One feature is the irregular curvature, or almost faceted shape of the posterior surfaces of certain cores (Chapman 1964). Another peculiarity is the irregular outline of the stress shell detached from very large cores (Cleverly 1981).

A referee of this paper has kindly drawn my attention to his descriptions of composite Ivory Coast microtektites formed by fusion together of two or more individuals, and having encircling V-grooves developed by solution around the junctions (Glass 1974). The Corrigin specimen has been re-examined, and its origin in that way is believed to be

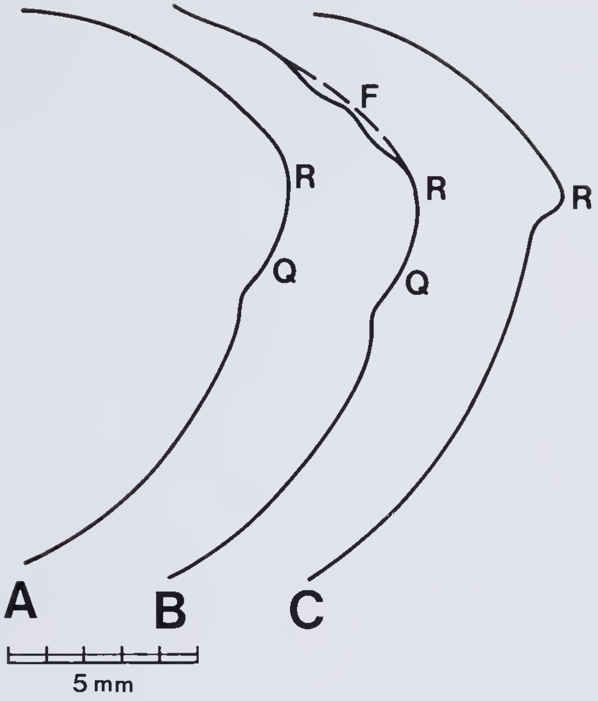

Figure 2. A and B. Partial profiles of australite viewed normal to line of flight. The rim R separates posterior surface above (up page) from anterior surface below. F is a shallow flake loss. Q is the rear limit of the groove. C. Analogous partial profile of typical core. Not to scale.

unlikely. It would need to have occurred in the primary developmental stage during flight. The origin of the groove is thought to be, more probably, related to aerodynamic effects.

The necessary circumstances of formation are evidently rare, as I have seen no other feature comparable with the groove during my examination of an estimated 60 000 australites from numerous and widespread localities. The groove remains with the irregularly curved posterior surfaces of certain cores, the unusual outlines of some stress shells, and the double rim of the Ravensthorpe specimen as one of the peculiarities of australites found in south-western Australia.

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Distribution patterns of Redfin Perch *Perca fluviatilis* Linnaeus and western Pygmy Perch *Edelia vittata* Castelnau in the Murray River System Western Australia

By Michael John Hutchison

Introduction

Various workers including Moyle (1976) and Jackson and Williams (1980) have presented evidence that introduced fish species have a negative impact on native species. Fletcher (1986) summarized what is known about the effects of introduced fish in Australian aquatic environments. One introduced species little known in this regard, is the redfin perch *Perca fluviatilis* Linnaeus. Cadwallader (1978) speculated that this species may have adversely affected some native fishes in the Murray Darling River system.

During research into the distribution of fishes in the Murray River System Western Australia, it was noted that the western pygmy perch *Edelia vittata* Castelnau was apparently absent from most of the main stream. This absence was surprising as *E. vittata* has been easily collected by dip net in 1979 between the mouth of Nanga Brook and Bob's Crossing (A and B Figure 1). Large numbers of pygmy perch were also noted in the Murray River in 1951 (Anonymous 1952). A recent addition to the fish fauna of the Murray River below Driver Road Ford (Figure 1) is the redfin perch *Perca fluviatilis.* A survey of anglers which commenced in 1987 (Hutchison unpublished), revealed that redfin first began to appear in anglers' catches in the early 1980's near Yarragil and the Baden Powell Water Spout. By 1986 anglers were capturing redfin from the vicinity of Coolup and Pinjarra. Previously redfin had only been known from near Driver Road Ford and further upstream (see Figure 1 for localities). Redfin were introduced to the upper Murray System early this century (Coy 1979), probably before 1912, by which time many perch were established in dams between York and Cranbrook (Braysich 1966). This paper documents the distribution of *E. vittata* and *P. fluviatilus* in the Murray River system and suggests that it represents circumstantial evidence for the possible elimination of *E. vittata* by *P. fluviatilis.*

Methods

Seventeen sites were used in this study (see Figure 1) to test the null hypothesis of independence of redfin perch *P. fluviatilis* and western pygmy perch *E. vittata* in the Murray River. Sites one to eight were located on the main stream and nine to 14 were located on the lower reaches of tributary streams below potential barriers (gauging weirs and major waterfalls) that might interfere with the distribution of western pygmy perch. It would have been better if all sites could have been located on the main stream, but

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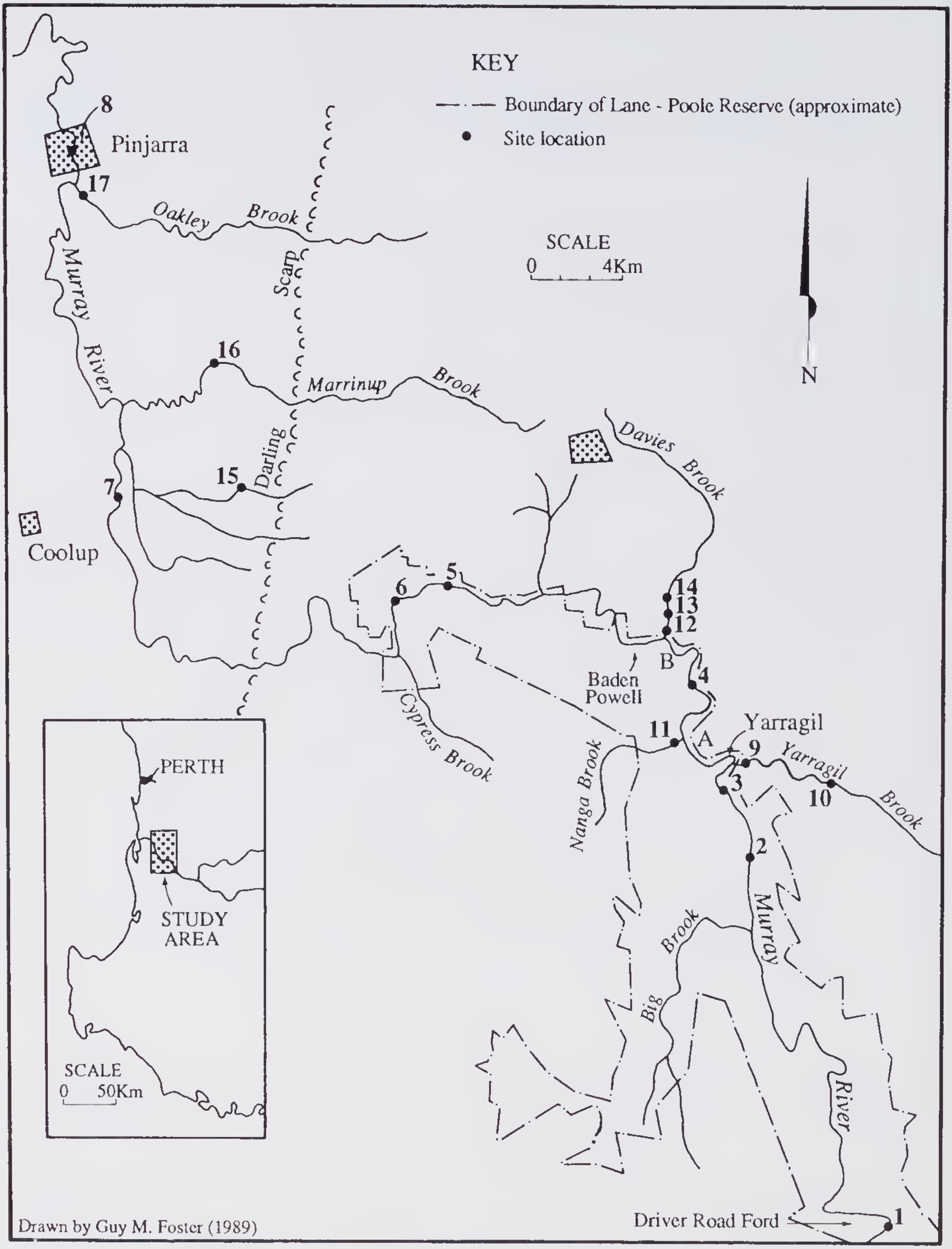

Figure 1. Location of study sites and localities mentioned in the text.

according to reports from anglers, most of the river, had been colonised by perch. Sites one to eight were all large perennial pools 70 to 200 metres in length, with maximum depths in excess of 1.5 metres and bounded at each end by cascades or riffles, runs or flats (the type varying according to seasonal flow variations) as classified by Jackson (1978). These Sites were chosen because each provided a range of habitats and were spaced as evenly as access allowed along the main river. Site 1 was not linked by flow to any other pools during February and March in 1988. Sites one to six were all located on the Darling plateau, whilst sites seven and eight were located on the coastal plain.

Sites nine to 17 were located on the tributary streams and although smaller in area than the sites located on the main stream, also provided a range of habitats. Each of these sites was approximately 25 metres in length and consisted of a pool up to 1.5 metres in depth bounded at either end by a cascade or a riffle, run or flat according to seasonal flow variations. All sites, except nine and 10 contained permanent water. Sites nine and 10 flowed only between May and January inclusive and as such aquired fish fauna as migrants from the river. These two sites therefore could be expected to reflect the situation in the adjacent main stream. Sites nine to 14 were located in valleys on the Darling Plateau and 15 to 17 on the coastal plain. All sites were sampled at least five times between January 1988 and October 1989.

Table 1 Captures and/or observations of *Edelia* and *Perca.*

Capture and observation rates

	Obs/torch survey		Fish/seining unit	Fish/trap set	Fish/angling hour	Fish/polaroiding unit	
Sites	P	E	P	E	P	P	E
1	1.1	0.0	1.7	0.0	3.6	0.7	0.0
2	X	X	X	0.0	0.4	4.9	0.0
3	0.8	0.0	4.3	0.0	1.4	0.4	0.0
4	X	X	X	0.0	0.9	0.3	0.0
5	X	X	X	0.0	0.0	0.2	0.0
6	0.0	0.0	0.0	0.0	1.6	2.8	0.0
7	X	X	X	0.1	0.2	0.0	0.0
8	X	X	X	0.7	0.0	0.0	0.0

Key: E = *Edelia vittata* P = *Perca fluviatilis* X = Method not used

Sites in the tributary streams were sampled using baited fine mesh plastic fish traps (which have been successfully employed to capture *E. vittata*) (Pen* pers. comm.), set for 24 hours, and fifteen minutes of electrofishing using charges between 300 and 400 volts. Since the main stream sites all had salinities in excess of 1%, the electrofishing technique could not be used. In the main stream, fish traps were used at all sites to detect western pygmy perch. Angling was used at all main stream sites to verify the presence of redfin perch. Seine netting at night with 12 mm mesh was used at suitable sites to capture small (<10cm) redfin. On each occasion two sweeps were made with the seine net (one seining unit), covering a total area of approximately $160m^2$. At these same locations a torch survey of $20 \times 0.1m^2$ grids at four metre intervals, followed by a general search of 80 metres of shoreline was used to record the presence of Edelia and Perca. At all main stream sites, prior to angling, a reconaissance of 50 metres of shoreline was made with the aid of polaroid sun glasses. Observed fish were dip netted for positive identification.

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The presence or absence of Edelia and Perca at each site was recorded and put into the form of a 2 x 2 contingency table. Fisher's exact probability test (Fisher 1941)

Formula $$p = \frac{(a+b)!\,(c+d)!\ \ (a+c)!\,(b+d)!}{n!a!b!c!d!}$$

was applied to the data to test the null hypotehsis of independence.

Fisher's test was used rather than a χ^2 test because of the small number of sites (n=17) involved.

Table 2 2 x 2 contingency table for association of *Perca* and *Edelia*.

	Fish/15 minutes electrofishing		Fish/trap set
	P	E	E
Sites			
9	0.2	0.0	0.0
10	0.0	0.0	X
11	0.0	0.0	0.0
12	0.0	2.3	3.0
13	0.0	4.9	1.5
14	0.0	5.2	X
15	0.0	2.8	1.0
16	0.0	2.9	X
17	0.0	7.2	14.6

Key: E = *Edelia vittata* P = *Perca fluviatilis* X = Method not used

Results and Discussion

The presence or absence of *P. fluviatilis* and *E. vittata* at each of the study sites is shown in Table 1. This data is presented in the form of a contingency table in Table 2. It should be noted that there was only one site from which *Perca* and *Edelia* were both recorded. Based on Fisher's exact probability test, the probability of obtaining a result as in Table 2, or a more extreme result in which *Edelia* and *Perca* do not co-occur at any site is 0.0021.

Table 3 Mean capture and observation rates of *Perca* and *Edelia* by different methods at main stream sites.

	Perca fluviatilis		
	present	absent	
Edelia vittata			
present	a 1	b 7	a + b = 8
absent	c 7	d 2	c + d = 9
	a + c = 8	b + d = 9	n = 17

Although this result does not indicate a casual relationship, and evidence of the effect of *P. fluviatilis* on *E. vittata* is only circumstantial, there is good reason for suspecting *P. fluviatilis* of having eliminated *E. vittata* from much of the Murray River, particularly when *E. vittata* is known to have occurred in the Murray River prior to its invasion by redfin.

Perca fluviatilis is known to be a piscivore and Baxter *et al.* (1985) considered it unwise to release trout fingerlings into a redfin dominated water owing to heavy predation of fingerlings by redfin. Popova (1978, 227) presented a table showing an average absolute prey size of approximately 2.5cm for 10cm perch, 4cm for 20cm perch and 7cm for 30cm perch. Western pygmy perch fall within this general prey size range and Pen (personal

Table 4 Mean capture rates of *Edelia* and *Perca* by different methods at tributary stream sites.

Site	*Edelia*	*Perch*
1	*yes*	*no*
2	*yes*	*no*
3	*yes*	*no*
4	*yes*	*no*
5	*yes*	*no*
6	*yes*	*no*
7	*yes*	*yes*
8	*no*	*yes*
9	*yes*	*no*
10	*no*	*no*
11	*no*	*no*
12	*no*	*yes*
13	*no*	*yes*
14	*no*	*yes*
15	*no*	*yes*
16	*no*	*yes*
17	*no*	*yes*

communication) has found western pygmy perch to be the main fish species taken by juvenile redfin perch in the Collie River. *Edelia vittata* is diurnal and slow moving. Therefore unless it has adequate cover, probably presents itself as an easy prey item for the diurnal *P. fluviatilis.*

The only site where *P. fluviatilis* and *E. vittata* were recorded together in the Murray System was Site seven near Coolup. This site was one of the most recently invaded by redfin and densities of *P. fluviatilis* appear to be low (Table 3). Even so the capture rate of *E. vittata* from fish traps at this site is between seven and 146 times lower than the capture rates at sites with *E. vittata,* but from which *P. fluviatilis* was not recorded during this study (Tables 3 and 4).

P. fluviatilis and *E. vittata* occur together in the Collie River, South Western Australia, (Pen, pers. comm.). However different environmental circumstances are known to produce different outcomes in interactions between species (e.g. Zaret 1979) and as suggested above, cover may be important to the survival of *E. vittata* in the presence of *P. fluviatilis.*

Conclusion

The disappearance of *E. vittata* from the Murray River should be treated with concern. Sites one to six and sites nine to 11 occur within the Lane—Poole Conservation and Recreation Reserve (see Figure 1), and yet none yielded *E. vittata.* All sites where *E. vittata* were recorded, were outside the boundaries of the reserve. If it is considered desirable for the reserve to contain representatives of all of the Murray System's native fish species, then the boundaries of the reserve will probably need to be extended*. A logical step would be to include Davies Brook in the reserve as it lies only just outside the reserve's boundaries. If redfin are responsible for the disappearance of pygmy perch, the tributaries containing *Edelia* offer a source for future recolonization of the main stream should redfin ever decline, or some steps be taken to eliminate them. Although the two species may be able to coexist in some situations, it would be prudent to consider *P. fluviatilis* as a potential threat to *E. vittata* and its introduction to other waters containing this native fish should be discouraged.

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*The perennial Big, Cypress and Kyabram Brooks which occur in the Lane-Poole Reserve have not yet been extensively surveyed. Preliminary investigations have not yet located western pygmy perch in the latter 2 streams which have very steep gradients and may be unsuitable habitats. Low densities occur in Big Brook.

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The identity of *Lygosoma (Rhodona) goerlingi* Ahl, 1935 (Squamata: Scincidae)

G.M. Shea*

After *Ctenotus,* the scincid lizard genus *Lerista* is the most species-rich genus of Australian lizards, with over 50 species currently recognised. Recent work has identified several radiations within the genus, including the *L. wilkinsi* group of north-east Queensland (Greer *et al.* 1983), the *L. bipes* group, centred over north-west Australia (Greer 1986), and the *L. nichollsi* complex of the central west coast and hinterland (Storr 1984, 1986; Kendrick 1989). Within these groups, the species are often only subtly different, and may have very restricted distributions.

With the number of such species continuing to grow, it is relevant to reconsider the status of early names, placed in synonymy by Storr (1971) at a time when minor differences were given less importance.

One such species is *Lygosoma (Rhodona) goerlingi* Ahl, 1935, described from a single specimen from Wurarga, Marloo Stn, W.A. Since its description, it has been mentioned only four times: Greer (1967), who transferred the species to *Lerista,* and Glauert (1961) treated it as distinct, while Storr (1971) and Cogger *et al.* (1983) tentatively placed it in the synonymy of *L. muelleri* (Fischer, 1881), although none of these authors indicated that they had examined the holotype (Zoologisches Museum, Berlin 35352).

As described by Ahl (1935), *L. goerlingi* has the following unique combination of character states for *Lerista*: fingers two, toes three, frontoparietals fused, supraoculars four, supraciliaries five, midbody scale rows 20. In addition, while it was not explicitly noted by Ahl, the placement of the species in the subgenus *Rhodona* rather than the genus *Ablepharus* implies the presence of a moveable lower eyelid. In most respects, the description of coloration and scalation given by Ahl is similar to *L. muelleri.* However, two fingers, four supraoculars and a presumably moveable lower eyelid are characters not known for *L. muelleri* (Storr 1971; Greer 1987). Kendrick (1989) recently described *L. allochira,* a species similar to *L. muelleri,* but having only two fingers, but did not compare it with *L. goerlingi,* possibly following Storr's synonymy.

During a recent visit to the Berlin collection, I was able to locate the holotype of *L. goerlingi* and subsequently borrow it for examination. The specimen is in most respects typical of south-western populations of *L. muelleri.* The eye is ablepharine, and the fourth "supraocular" appears to be what can be either termed the last supraciliary (Taylor 1935) or a single pretemporal (Greer 1986). The reduction to two fingers described by Ahl appears to be due to injury: the right forelimb is largely missing (represented by a healed-over humeral stump), while on the left forelimb are two digits of

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equal length (comparable to the axial and lateral digits of *L. muelleri*), bordered medially by a scarcely distinct tubercle. The palm of the manus is extended medially to support this tubercle.

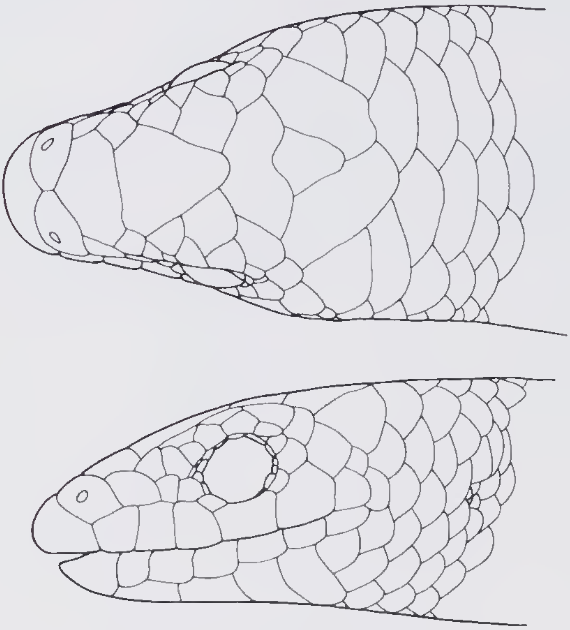

Figure 1. Dorsal and left lateral views of head of holotype of *Lygosoma goerlingi*.

The holotype (Figure 1) has the following combination of character states: nasals enlarged, in moderate contact; prefrontals present, broadly separated; frontoparietals fused into a single shield; interparietal distinct; parietal eyespot present, just caudal to centre of interparietal; parietals in broad contact behind interparietal; nuchals two/three [four pairs *vide* Ahl]; supraoculars three, first two contacting frontal, first smallest; supraciliaries six; first supraciliary short, tall, contacting prefrontal and first supraocular, narrowly separated from frontal; second supraciliary small, bordering first supraocular; third supraciliary subequal to first, strongly projecting between first and second supraoculars; fourth supraciliary subequal to first, strongly projecting between second and third supraoculars; fifth supraciliary low, bordering third supraocular; sixth supraciliary subequal to first, moderately projecting between third supraocular and frontoparietal; loreals two, first larger; presuboculars two; postsuboculars two; eye ablepharine; primary temporal single, moderate; secondary temporals two, upper much the larger, overlapped by lower; ear small, slightly larger than nostril; supralabials six, fourth below centre of eye; infralabials six, first two contacting postmental; three pairs of transversely enlarged chin shields, first pair contacting medially, second pair separated by one scale, third pair separated by three scales.

Midbody scales 20; paravertebral scales (from caudal edge of parietals to level of hind edge of thigh) 78; toes three; subdigital lamellae of longest toe 15/16 [13 *vide* Ahl]; supradigital scales of same toe 11.

Snout-vent length 43mm; tail length 38mm; [total length 80mm *vide* Ahl]; hindlimb length 10mm.

Coloration in preservative grey-brown dorsally, more brown on tail. Dark streaks centrally on paravertebral scales aligned to form a pair of narrow dark paravertebral stripes from nape to tail base, more diffusely onto tail. A dark brown upper lateral stripe from eye, over ear, to tail base, more diffusely onto tail, formed by dark lateral edge of third and dorsal edge of fourth scale rows from midline. Flanks yellow cranially, grey with fine brown flecks caudally. Venter yellow with fine brown flecks over vent and on tail.

All characters are within the range of variation of *L. muelleri,* and consequently I confirm the tentative actions of Storr (1971) and Cogger *et al.* (1983) in synonymising *L. goerlingi* with *L. muelleri.*

Acknowledgements

I thank G.M. Storr for drawing my attention to the problem prior to my visit to Berlin, and for providing a translation of Ahl's description; R. Günther and his assistant Mr Tetzlaff for assistance in Berlin and for the loan of the type, and A. Greer, L. Smith and G. Storr for reading the manuscript.

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Guide to Authors

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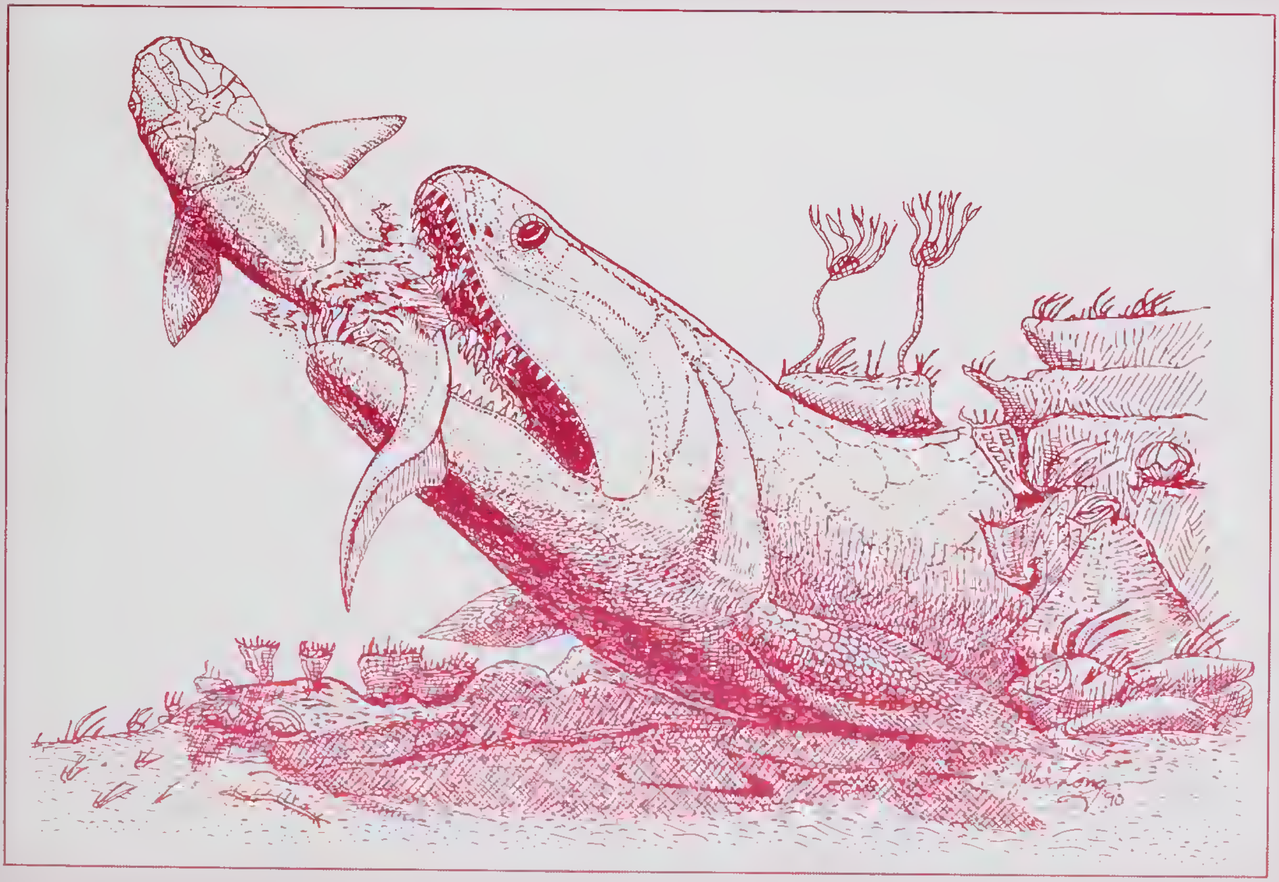

RECORDS of the Western Australian Museum

Volume 15, Part 2.
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Cover
Restoration of an *Onychodus* catching a placoderm fish. Illustrated by John Long.

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Description of a new species of *Cynopterus* (Chiroptera: Pteropodidae) from Nusa Tenggara, Indonesia.

D.J. Kitchener* and Maharadatunkamsi†

Abstract

The taxonomy of small (forearm length <75 mm) members of the '*Cynopterus* Section' of Andersen (1912) is examined. *Cynopterus nusatenggara* sp. nov. is described from Lombok, Sumbawa, Moyo and Komodo Is. *C. minutus* Miller, 1906 is a species from Nias I., Sumatra, Java, Borneo and Sulawesi. *C. luzoniensis* (Peters, 1861) is from Sulawesi, Philippines and adjacent small islands; *C. brachyotis* (Müller, 1838) is redefined; its distribution includes Sri Lanka, Peninsula Malaysia, Penang I., Singapore I., Sumatra, Borneo, Pulau Laut (I.), Bunyu I., Java, Pulau Dua (I.), Madura I., and Bali I. *C. sphinx* is widely distributed from Sri Lanka, India, through Burma, Malaya, Sumatra, Borneo, Java, Sulawesi and many small islands. Within these species are recognisable geographic forms requiring further clarification.

Introduction

Recent vertebrate biological surveys in Nusa Tenggara, Indonesia, carried out by us, in conjunction with colleagues from the Western Australian Museum and Museum Zoologicum Bogoriense, resulted in the collection of an undescribed form of *Cynopterus* on Lombok, Sumbawa, and Moyo islands. Specimens of this form are also present in collections from Komodo I., Nusa Tenggara. The determination of the taxonomic status of this form is the substance of this paper.

According to Tate (1942), morphological differences, apart from overall size, between members of *Cynopterus* are not clearly definable. He stated that even in size, considerable overlap exists between every species in Andersen's (1912) listing of the dimensions of *Cynopterus* spp. Further, he notes that within a series from one locality, pelage colour is frequently variable. Tate (1942) does, however, allow that Andersen's (1912) separation of his '*Cynopterus* Section' and '*Niadus* Section' within this genus is based on seemingly consistent characters. Members of the '*Cynopterus* Section' were seen to differ from those in the '*Niadus* Section' by the oval rather than squarish outline of their cheek teeth, but more particularly by the absence or poor development of surface cusps on P_4 and M_1. Only *C. archipelagus* Taylor, 1934 was considered by Tate (1942) to be difficult to place in these 'Sections' because from its description it appeared to be somewhat intermediate between the 'Cynopterus' and 'Niadus' Sections.

The new form from Nusa Tenggara is clearly a member of the '*Cynopterus* Section' and as such is compared to members of this group in this paper. While this comparison is based on morphology, because the traditional approach has resulted in unsatisfactory diagnoses (Tate 1942), and not withstanding Hill (1983: 118), we have used a

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multivariate statistical approach to assist the diagnosis of this new form and its morphologically close congeners. As a result of these comparisons this new form is herein described as a new species.

Members of the *'Cynopterus Section'* of Andersen (1912)

Andersen (1912: 596) lists 30 proposed names for *Cynopterus* — of which he recognised only 16 as taxonomically valid forms. Since then six new forms have been named: *Cynopterus sphinx babi* Lyon, 1916; *C. archipelagus* Taylor, 1934; *C. terminus* Sody, 1940; *C. brachyotis concolor* Sody, 1940; *C. b. altitudinis* Hill, 1961; and *C. sphinx serasani* Paradiso, 1971.

There has been no comprehensive review of *Cynopterus* since Andersen (1912) whose classification of this group was followed by both Chasen (1940) and Tate (1942), except for the following: the placement of *C. major* Miller, 1906 as a subspecies of *C. sphinx* Vahl, 1797 by Chasen (1940) and the removal of *C. pagensis* Miller, 1906 from synonymy with *C. s. angulatus* and its placement as a subspecies of *C. brachyotis* by both Chasen (1940) and Tate (1942).

Hill (1983) briefly stated his classification of a number of forms of *Cynopterus* in the Indo-Australian region which took into consideration his earlier treatment of some members of this genus (e.g. Hill and Thonglongya 1972). Hill's (1983) classification offers some considerable departures from previous ones. For example, he considered *titthaecheilus* a species and removed it from its placement as a subspecies of *C. sphinx* where it had been placed by earlier workers. He also removed *angulatus, scherzeri, babi* and *pagensis* from *C. brachyotis,* where they had been placed as a subspecies by Chasen (1940) and Tate (1942), and listed them instead as a subspecies of *C. sphinx.* Hill (1983) also lists *major* as a subspecies of *C. titthaecheilus* rather than of *C. sphinx.* He also recognised *C. terminus* as a possible valid species rather than a subspecies of *C. sphinx* as it was considered by Sody (1940).

We largely follow the classification of Hill (1983) except we consider *C. minutus* Miller, 1906 is a species and not a subspecies of *C. brachyotis. C. luzoniensis* (not treated by Hill (1983)), is considered a species and not a synonym of *C. b. brachyotis* as listed by Andersen (1912).

We consider the '*Cynopterus* Section' to now comprise the following members:

'*Cynopterus* Section' (Andersen, 1912)

Cynopterus sphinx sphinx (Vahl, 1797)	Sri Lanka, peninsular and N.E. India, Burma
C. s. scherzeri Zelebor, 1869	Car Nicobar I.
C. s. serasani Paradiso, 1971	Serasan I., Natuna I.
C. s. babi Lyon, 1916	Babi I.
C. s. gangeticus Andersen, 1910	C., N.W. India
C. s. pagensis Miller, 1906	Mentawai Is

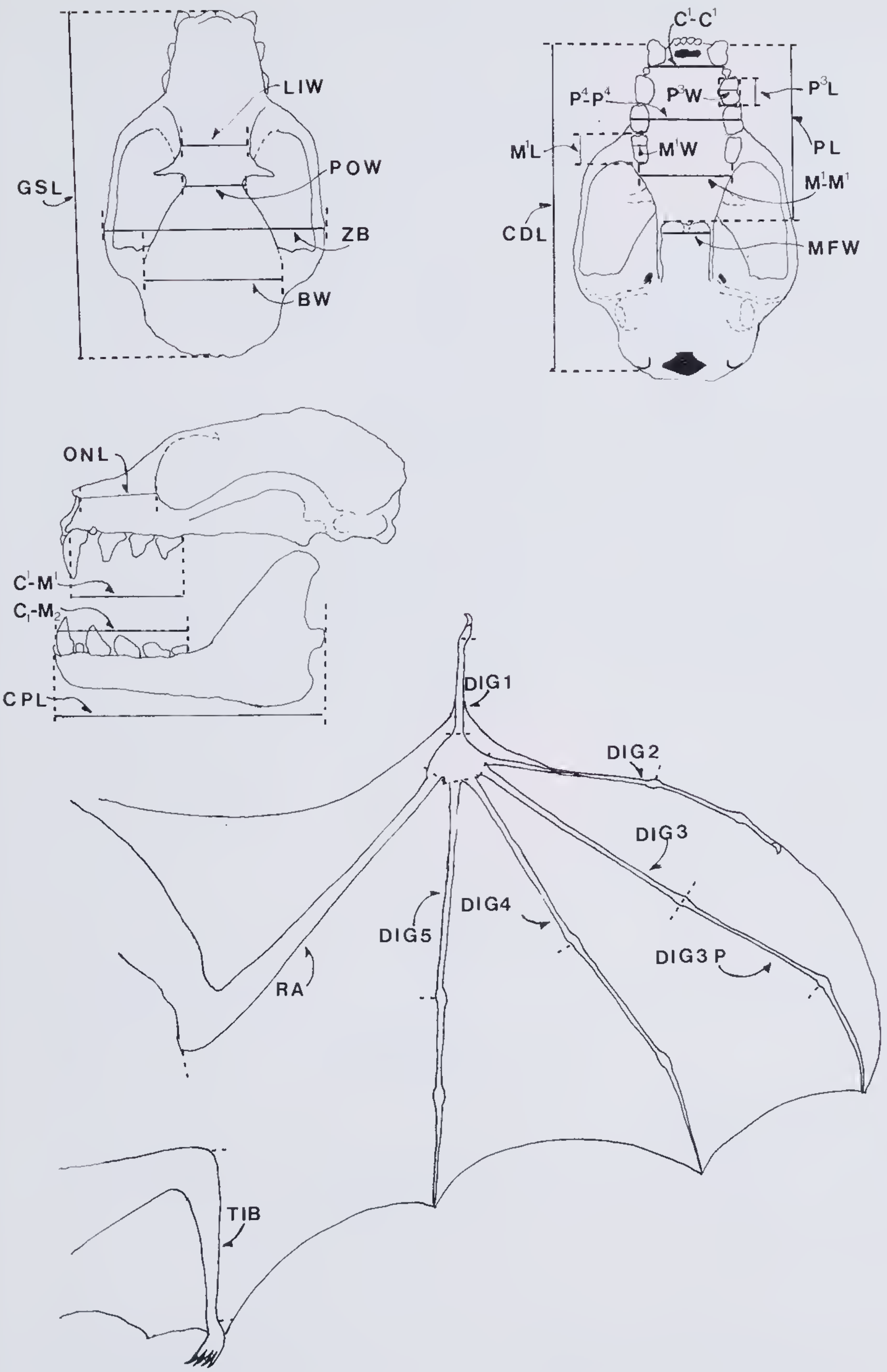


Figure 1 Measurement points for skull and externals of *Cynopterus* spp.
BW, braincase width; CDL, condylobasal length; CPL, dentary condyle to tip of dentary; GSL, greatest skull length; PL, palate length; POW, postorbital width; LIW, least interorbital width; MFW, mesopterygoid fossa width; ONL, orbit to nasal length; ZB, zygomatic breadth; C^1-C^1, outside upper canine breadth (alveoli); P^4-P^4, outside fourth upper premolar breadth (alveoli); M^1-M^1, outside fourth upper molar breadth (alveoli); C^1-M^1, upper canine to first molar length (alveoli); C_1-M_2, lower canine to second lower molar length (alveoli); P^3W, third upper premolar width (crown); P^3L, third upper premolar length (crown); M^1L, first upper molar length (crown); M^1W, first upper molar width (crown); C^1-M^1 upper canine to first upper molar length (alveoli); C_1-M_2, lower canine to second lower molar length (alveoli); DIG1, digit 1 length; DIG2-DIG5, metacarpal length of digits 2 to 5; DIG3P, digit 3, phalanx 1 length; RA, radius length; TIB, tibia length.

C. s. angulatus Miller, 1898	N. Burma to S. China, Hainan I., Vietnam, Lankawi I., N. Malaya, Sumatra, Krakatau Is, Verlaten I. (?), Borneo, Sulawesi, Sangeang I. (?)
Cynopterus brachyotis brachyotis (Müller, 1838)	S. Burma to Vietnam, Malaya, Sumatra, Borneo and many small associated islands, Bawean I.
C. b. altitudinis Hill, 1961	Malayan highlands
C. b. concolor Sody, 1940	Enggano I.
C. b. insularum Andersen, 1910	Kangean I., Mata Siri I.
C. b. javanicus Andersen, 1910	Java, Madura I., Bali I.
C. b. ceylonensis Gray, 1870	Sri Lanka
C. b. brachysoma Dobson, 1871	Andaman Is
Cynopterus minutus Miller, 1906	Nias I., Sumatra, Java, Borneo, Sulawesi
Cynopterus luzoniensis (Peters, 1861)	Philippines, Sulawesi, Peleng I. (?), Talaud I. (?)
Cynopterus titthaecheilus titthaecheilus (Temminck, 1825)	Sumatra; Krakatau I., Sebesi I., Lombok I.
C. t. major Miller, 1906	Nias I.

Other named forms placed in synonomy with above taxa are as follows:

Cynopterus duvaucelii (E. Geoffroy, 1828)	Sumatra
C. brevicaudatum (E. Geoffroy, 1828)	Sumatra
C. diardi (E. Geoffroy, 1828)	Sumatra
C. marginatus philippensis Gray, 1870	Philippines
C. m. cumingii Gray, 1870	Philippines
C. montanoi Robin, 1881	Malacca (Kessang)
C. pusillus (E. Geoffroy, 1803)	India
C. marginatus (E. Geoffroy, 1810)	India (Bengal)
C. m. ellioti Gray, 1870	India (Dharwar, S. Bombay)
C. fibulatus (Vahl, 1797)	India (Tranquebar)
C. minor Revilliod, 1912	S.E. Sulawesi
C. archipelagus Taylor, 1934	Philippines (Polillo I.)

The forms *duvaucelii* and *brevicaudatum* were described (as *Pachysoma*) from specimens collected in Sumatra by Diard and Duvaucel. According to Andersen (1912: 619) they are "both absolutely indeterminable from the descriptions; they may be any one of the four forms of *Cynopterus* occurring on Sumatra, though judging only from the published measurements" . . . "are most probably either *C. b. angulatus* or *C. b. brachyotis.* Types probably not in existence." The forms *philippensis, cumingii* and *montanoi* were considered by Andersen (1912) to be synonymous with *C. b. brachyotis.* He further synonymised *pusillus, marginatus, ellioti,* and *fibulatus* with *C. s. sphinx* and *C. diardi* with *C. titthaecheilus.*

Cynopterus minor is known only from the holotype from Lambuja, S.E. Sulawesi. Hill (1983) considered that with a forearm of 53 mm it may be a young adult or an unusually small *C. brachyotis,* a view supported by Bergmans and Rozendaal (1988).

Cynopterus archipelagus from the Philippines is known only from the holotype which is a juvenile and is probably only an aberrant specimen of the more common *Cynopterus* sp. on Luzon *(C. luzoniensis* (see also Heaney *et al.* 1987)).

Some members of the '*Cynopterus* Section' are clearly distinct from the new species from Nusa Tenggara. *Cynopterus titthaecheilus* occurs sympatrically with it but it is much larger. This restricted the comparison of the new species in this study to members of *C. sphinx* and *C. brachyotis.* However, investigation of *C. brachyotis* (*s.l.*) from Sumatra, Java and Borneo indicated its occurrence at several localities with a distinct form, attributed by us to *C. minutus* (previously known only from Nias I.). Because the form *minutus* retained morphological distinctness from both *C. b. javanicus* and *C. b. brachyotis* in approximate sympatry, it is considered a species. Further, the small form of *Cynopterus* examined from the Philippines is not considered conspecific with *C. brachyotis* but is *C. luzoniensis.*

Consequently the new species of *Cynopterus* from Nusa Tenggara is herein diagnosed against *C. sphinx, C. brachyotis, C. minutus* and *C. luzoniensis.*

Materials and Methods

Specimens Examined

These specimens came from the following institutions (the abbreviations of which prefix specimen numbers listed in Appendix I):

WAM = Western Australian Museum, Perth
MZB = Museum Zoologicum Bogoriense, Bogor
ZRC = Zoological Reference Collection, University of Singapore
BMNH = British Museum (Natural History), London
AMNH = American Museum, Natural History, New York

Measurements (in mm)

Twenty measurements of skull, dentary and dental characters (hereafter referred to as skull characters) and 8 of external characters and weight, where it was available (in gms), were recorded from adult specimens listed in Appendix I. Measurement points for skull and external characters are shown in Figure 1.

Specimens were judged adult if the skull basioccipital suture was closed and phalangeal joints of wing bones were not swollen.

Pelage and skin colour

These colours were determined using Ridgway (1912). Where Ridgway's terms are used the colours are capitalised. However, some of these terms are not immediately recognisable and are translated (in brackets) into simpler words.

Morphometric analyses

Only adults with complete data sets were included in the statistical appraisal. Means, standard deviations and ranges were computed for skull and external body (wing and tibia) characters. Sexual dimorphism was examined using a two factor MANOVA of each of the skull and external characters for the factors, species and sex.

Principal component analysis, based on a correlation matrix of all measured characters using varimax rotation, was performed. The first three principal component scores were examined. This *a priori* clustering procedure did not produce any definable species group clusters so the data are not presented. Canonical variate (discriminant) analysis was then performed on all measured characters for the species as recognised by us.

Measured characters important in discrimination between these *Cynopterus* spp. using both stepwise discriminant function analysis and examination of characters in the canonical variate analysis which weigh heavily on one or more functions. Univariate plots of all combinations of characters seen as important were examined to detect single combinations of characters to discriminate between species.

In the case of individual *Cynopterus* that cannot be classified to species using the diagnostic descriptions supplied, they may be classified by calculating their canonical variate coefficients using Table 2 and plotting their coefficients on Figures 24 and 25.

All the above analyses were performed using both z-values and unscaled values, but because results were very similar only those from unscaled data are presented. All analyses were performed on a COMPAQ computer using SPSS/PC+.

Cynopterus nusatenggara sp. nov.

(Table 1: Figures 2-15)

Holotype

WAM M31335 (field number S222); currently the holotype is in the Western Australian Museum, but its final lodgement will be the Museum Zoologicum Bogoriense, Bogor, Indonesia. Adult female, teats enlarged but not lactating; skull and mandible separate; carcass with tongue intact, fixed in 10 percent formalin and preserved in 70% ethanol; skin prepared as a cabinet specimen. Blood and liver samples held in ultrafreezer at Western Australian Museum.

Type Locality

Desa Belo, Jerewah, West Sumbawa Island, Nusa Tenggara Barat, Indonesia (8°52′S, 116°50′E); mist netted by D.J. Kitchener, R.A. How and Maharadatunkamsi on 15 May 1988 from the boundary between dense, tall, mixed evergreen lowland rainforest and ricefields at an altitude of ± 40 m (Figure 2).

Paratypes

Listed in Appendix I.

Diagnoses

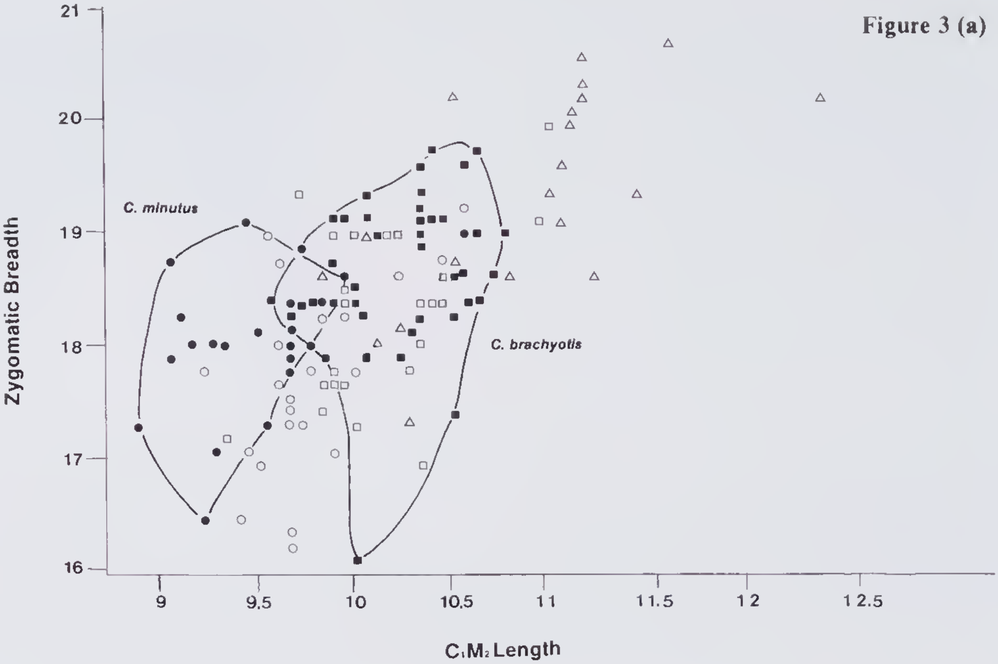
Cynopterus nusatenggara differs from *C. sphinx, C. brachyotis, C. minutus* and *C. luzoniensis* in having margin of ear without white or light coloured edge — this white trim is particularly noticeable on anterior margin of ear of these other species, (except for


Photo: R. How

Figure 2 Photograph of type locality of *Cynopterus nusatenggara*. Capture site was at boundary of rice fields and lowland rainforest near Desa Belo, West Sumbawa.

Sangeang I. population, tentatively attributed to *C. sphinx*); it differs in that the surfaces of metacarpals and phalanges are not strikingly lighter than patagia colour and so do not form such contrasting lines against wing membranes; hair of head contrastingly darker than hair of back, whereas these other species have hair of head the same colour or only slightly darker; it differs in that P^3 lingual cusp connected to base of taller labial cusp by a commissure than runs at right angles to axis of molar row, or slightly forward of this angle (Figure 13a) (except for the Sangeang I. population, tentatively attributed to *C. sphinx*). In these other *Cynopterus* spp. this commissure is angled posterior of this right angle (Figure 13b). It also differs in having P^4 with low lingual cusp separated from its labial cusp by a basin that is frequently raised between these cusps and slopes gently from this raised surface both anteriorly and posteriorly but not forming a definite ridge between these cusps (Figure 13a) as in these other *Cynopterus* spp. (Figure 13b).

It also differs from *C. sphinx* in that it averages smaller for all measurements except P^3W and M^1L in females (Table 1): e.g., ♀♀-GSL 28.1 (26.0-29.9) *v.* 30.3 (28.1-32.9), C_1-M_2 9.9 (9.3-10.6) *v.* 11.0 (9.9-13.1), RAD 59.9 (55.1-64.8) *v.* 65.7 (58.1-75.8); ♂♂-GSL 28.3 (27.2-29.7) *v.* 30.4 (28.7-33.7), C_1-M_2 10.1 (9.3-10.6) *v.* 11.1 (10.1-12.8), RAD 59.3 (54.7-61.9) *v.* 65.1 (59.2-75.0). This size difference is illustrated by the plot of ZB *v.* C_1-M_2 (Figure 3); BW smaller relative to M^1W (Figure 4); GSL shorter relative to DIG 1 (Figure 5); and posterolabial corner of P4 generally much more square.



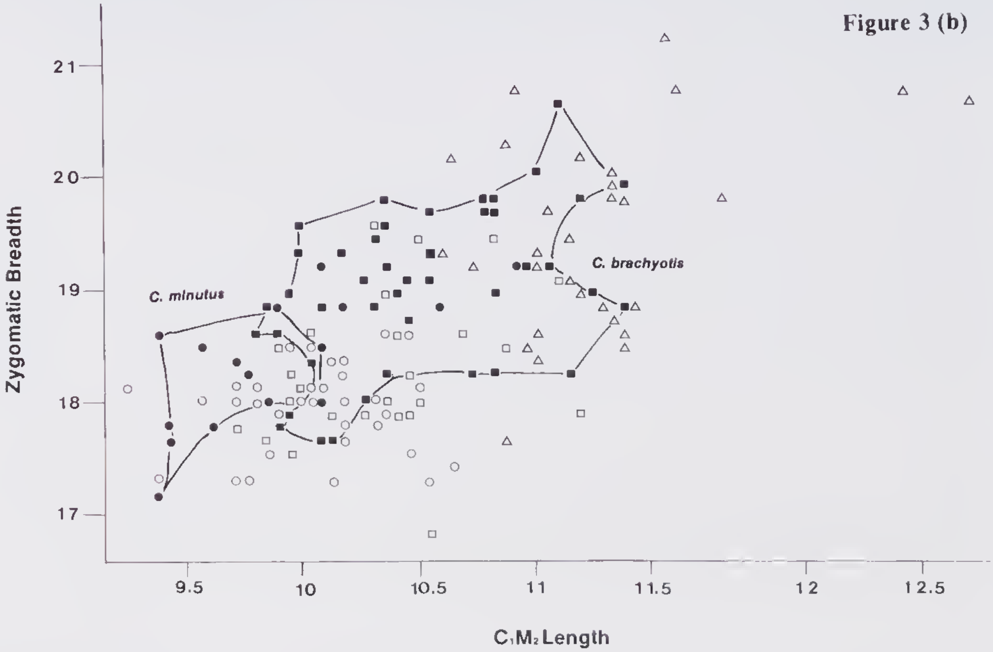


Figure 3-11 Bivariate plots of selected skull and body measurements for five species of *Cynopterus* (a) females, (b) males. O, *C. nusatenggara*; △, *C.* sphinx; ■, *C. brachyotis*; ●, *C. minutus* and □, *C. luzoniensis.*

Figure 4 (a)

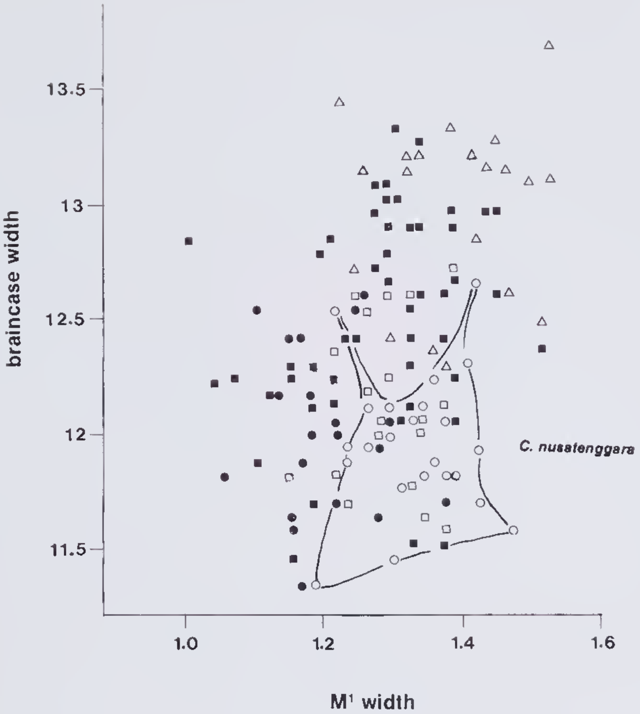


Figure 4 (b)

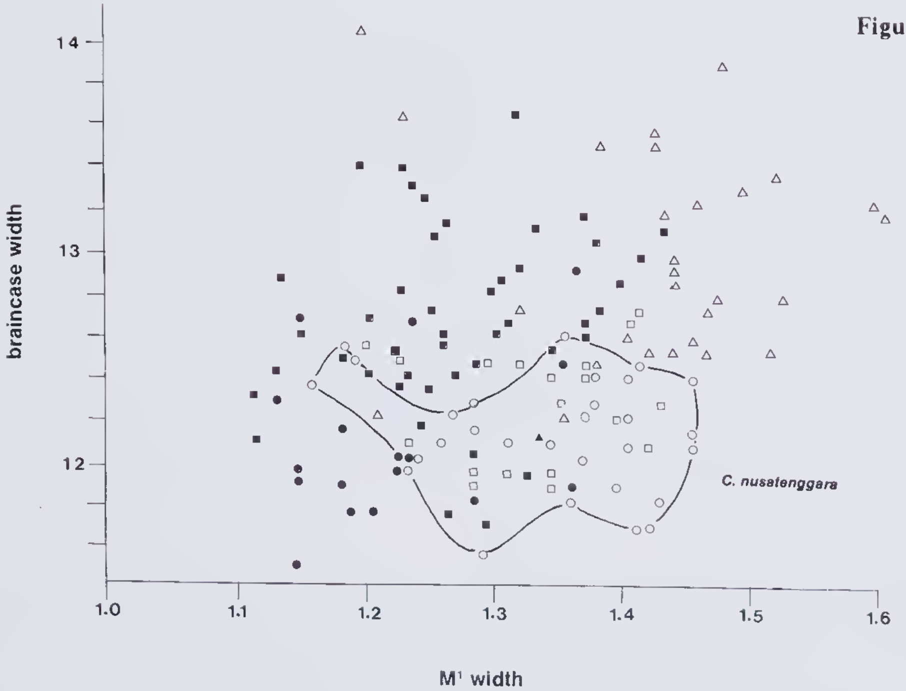


Figure 5 (a)

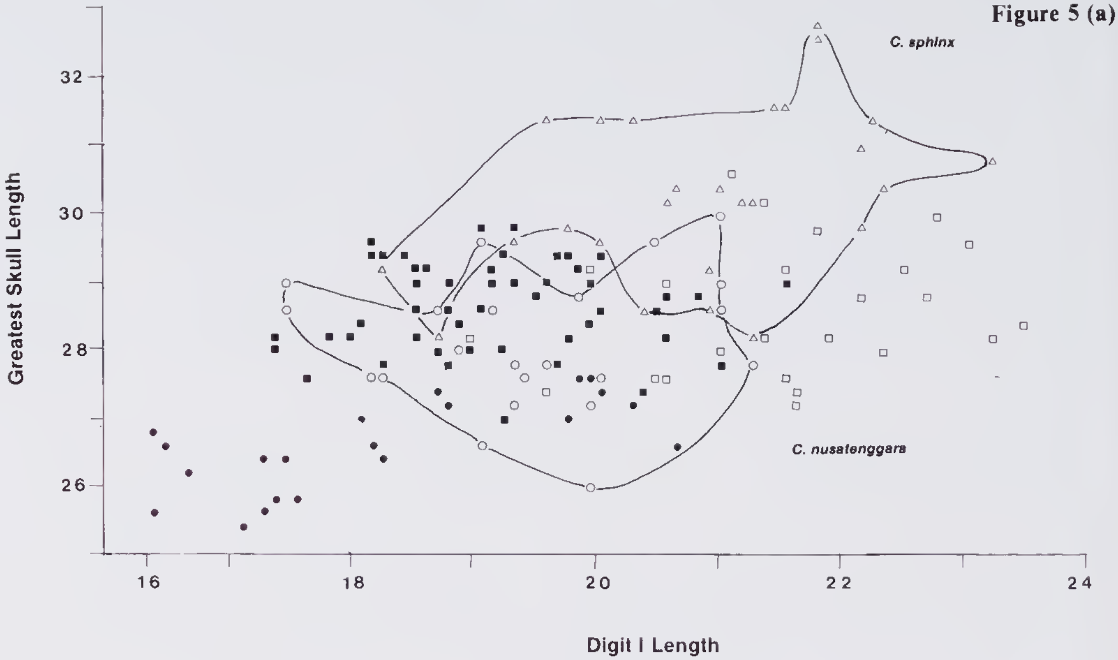


Figure 5 (b)

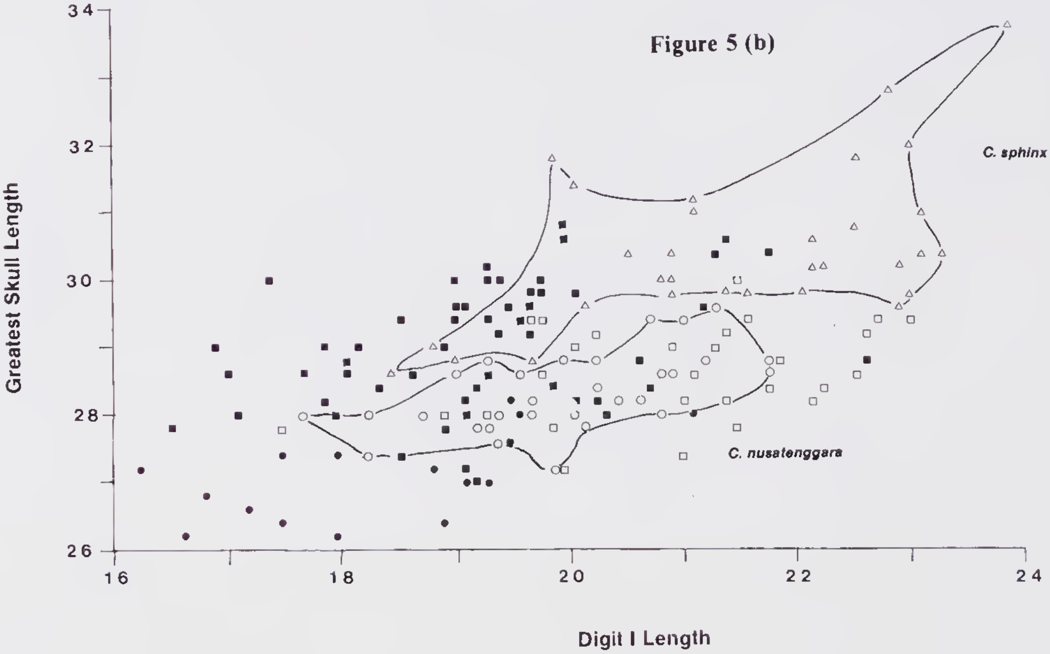


Figure 6 (a)

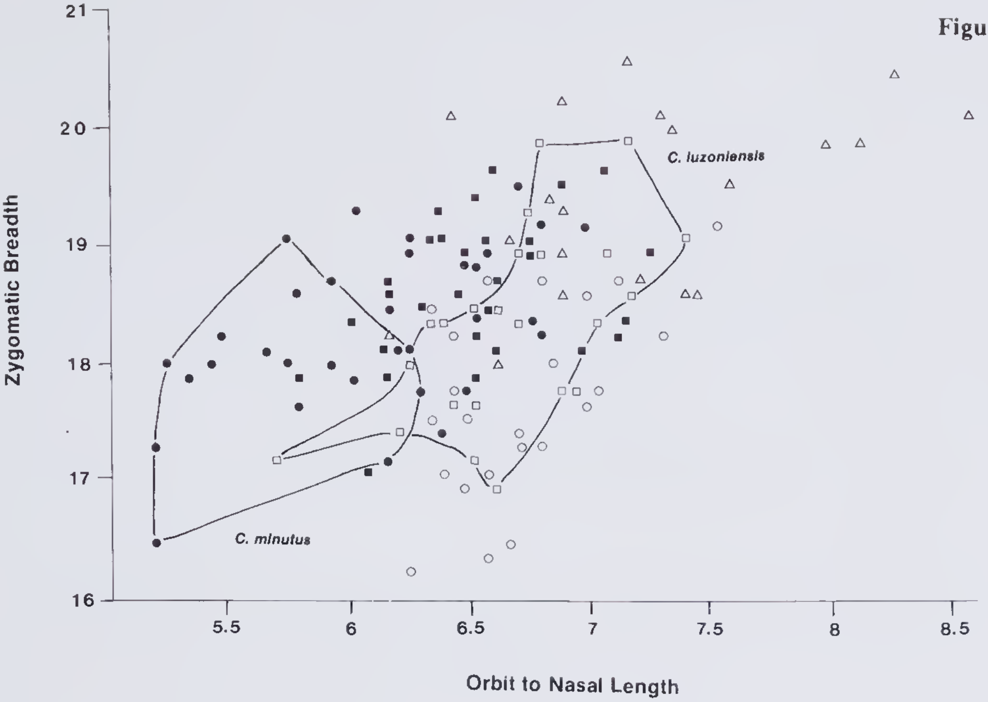
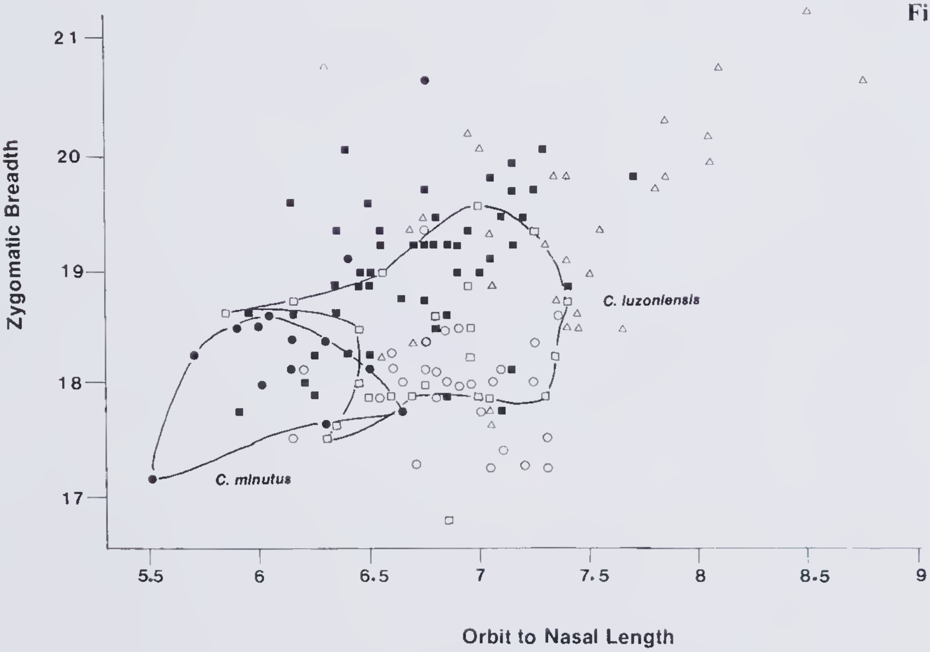


Figure 6 (b)



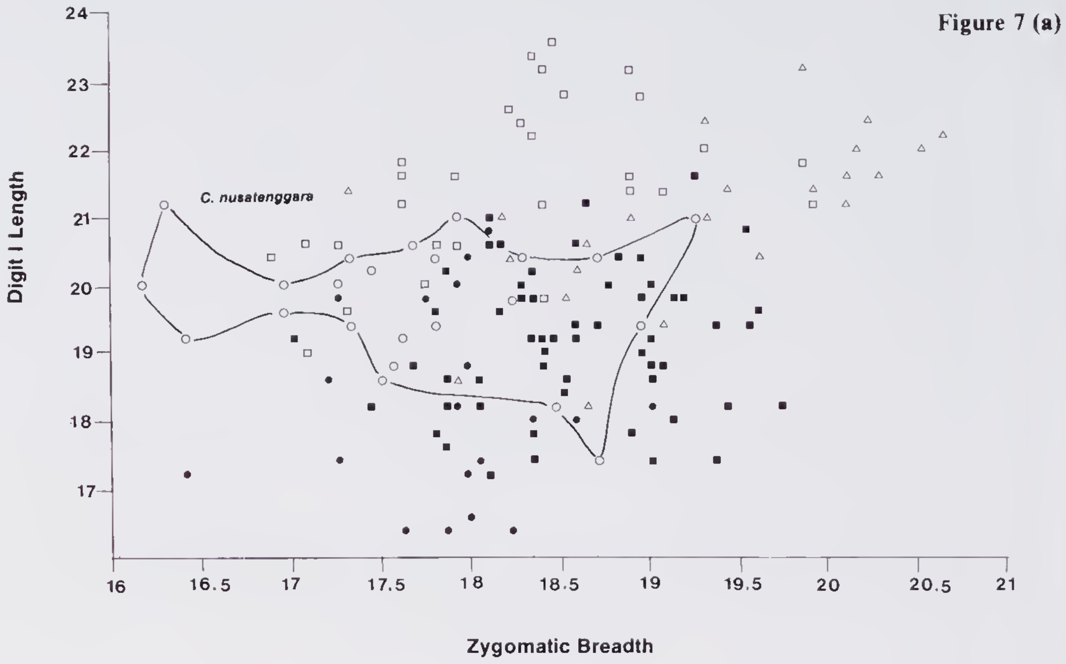


Figure 7 (a)
Digit I Length
Zygomatic Breadth
C. nusatenggara
24
23
22
21
20
19
18
17
16
16.5
17
17.5
18
18.5
19
19.5
20
20.5
21


Figure 7 (b)
Digit I Length
Zygomatic Breadth
C. nusatenggara
24
23
22
21
20
19
18
17
16
17
18
19
20
21

Figure 8 (a)

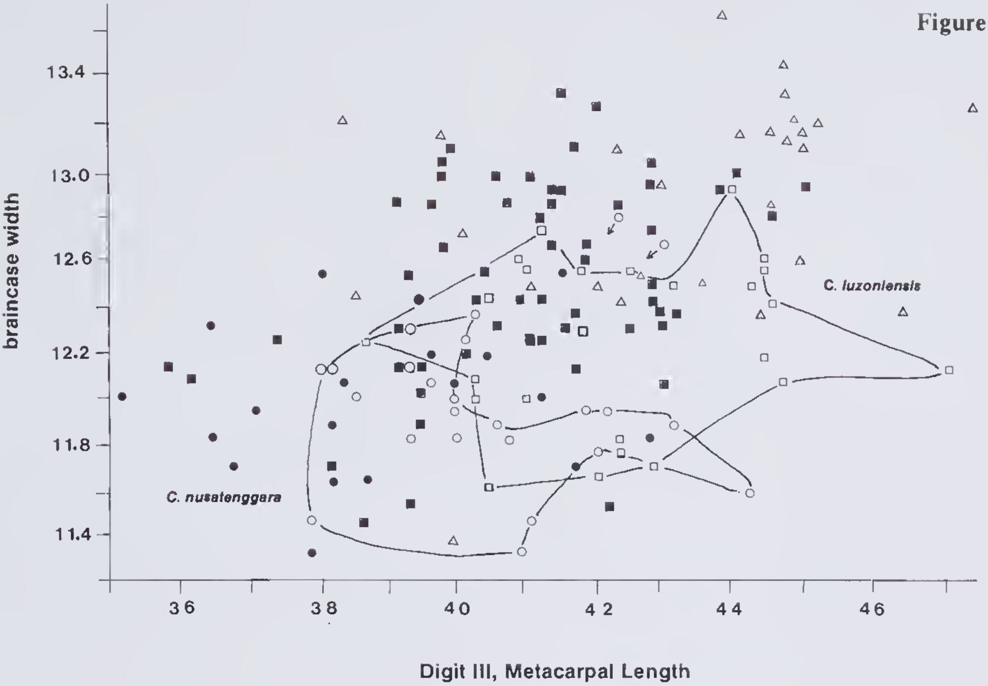


Figure 8 (b)

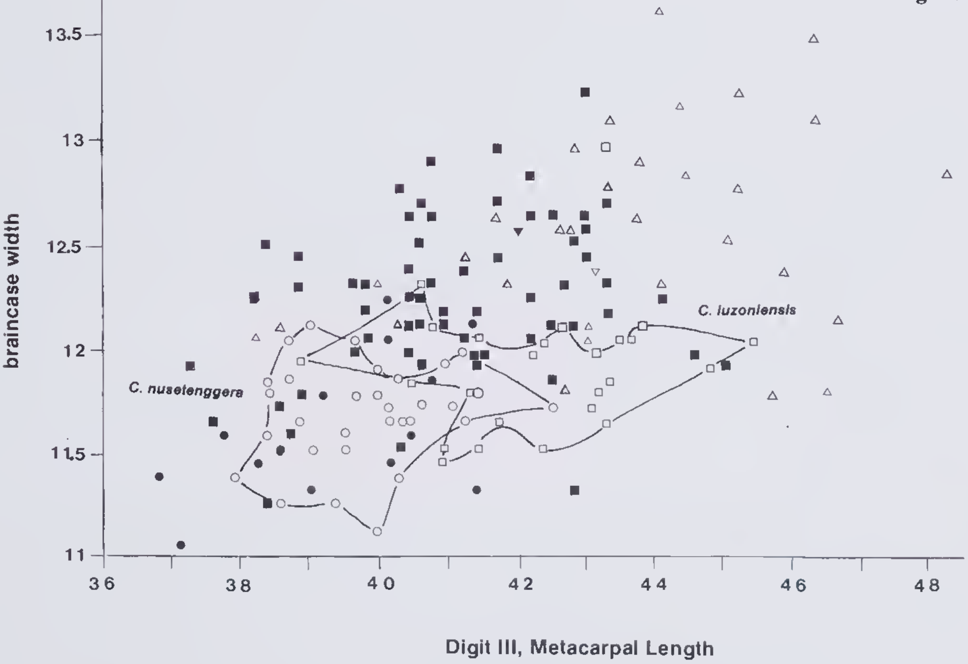


Figure 9 (a)

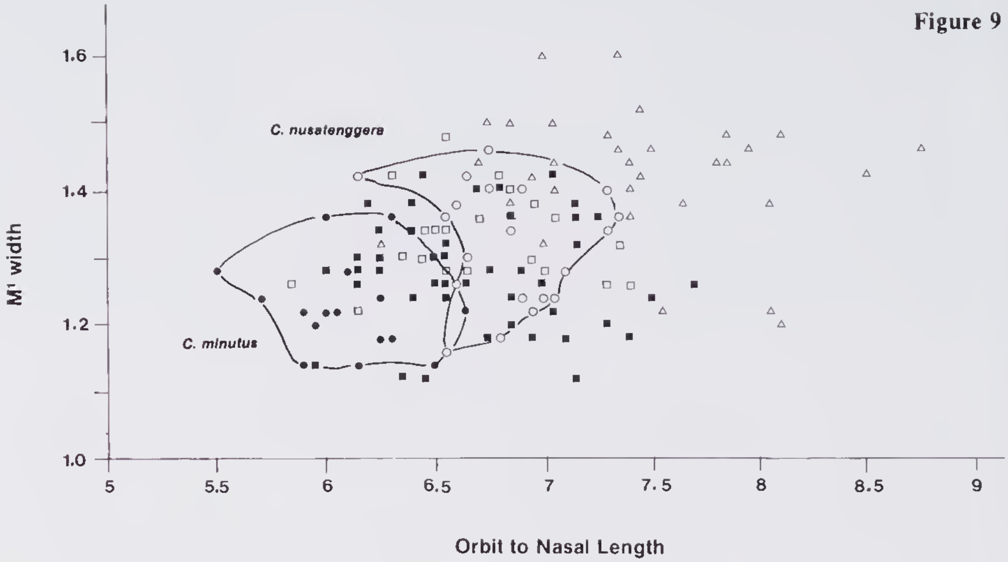


Figure 9 (b)

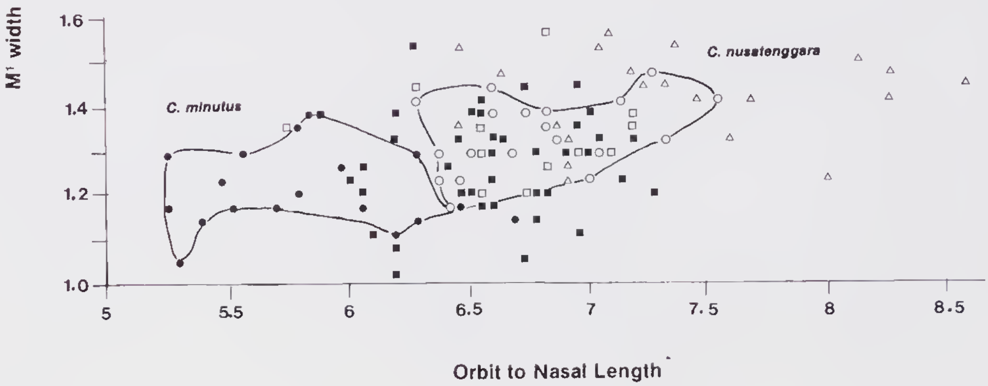


Figure 10 (a)

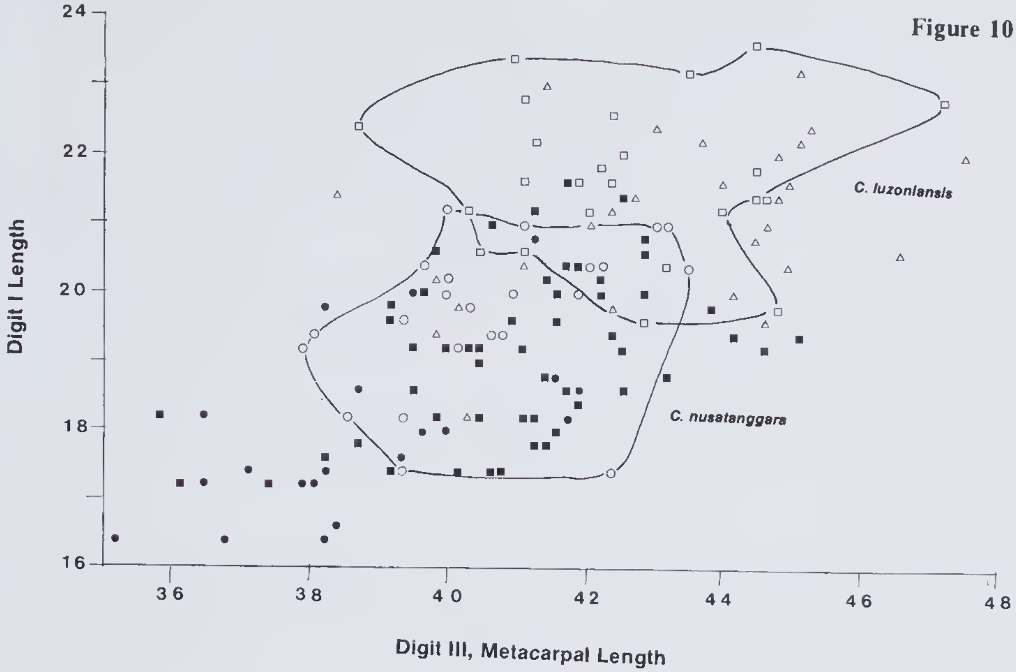


Figure 10 (b)

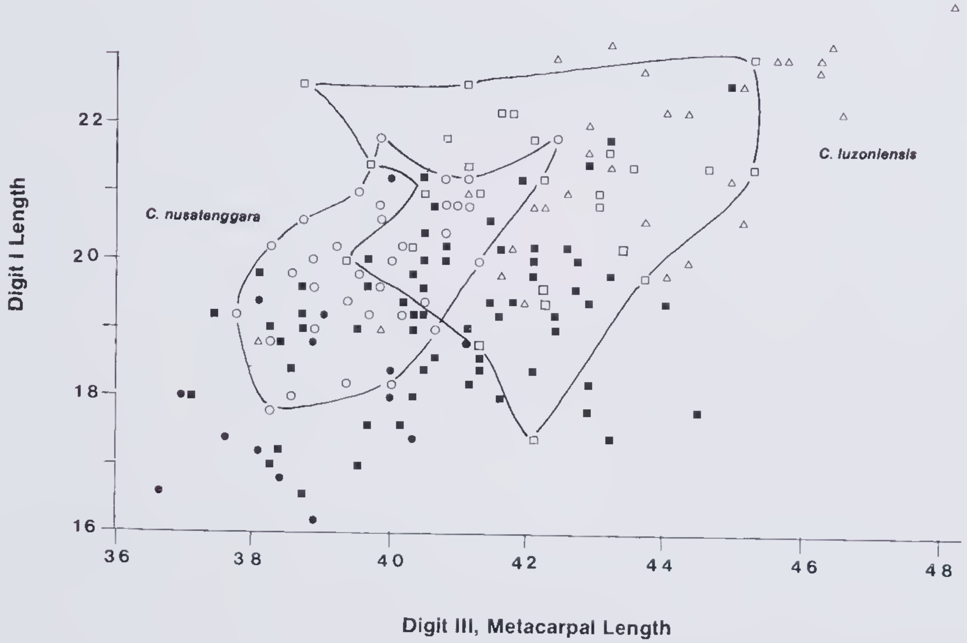


Figure 11 (a)

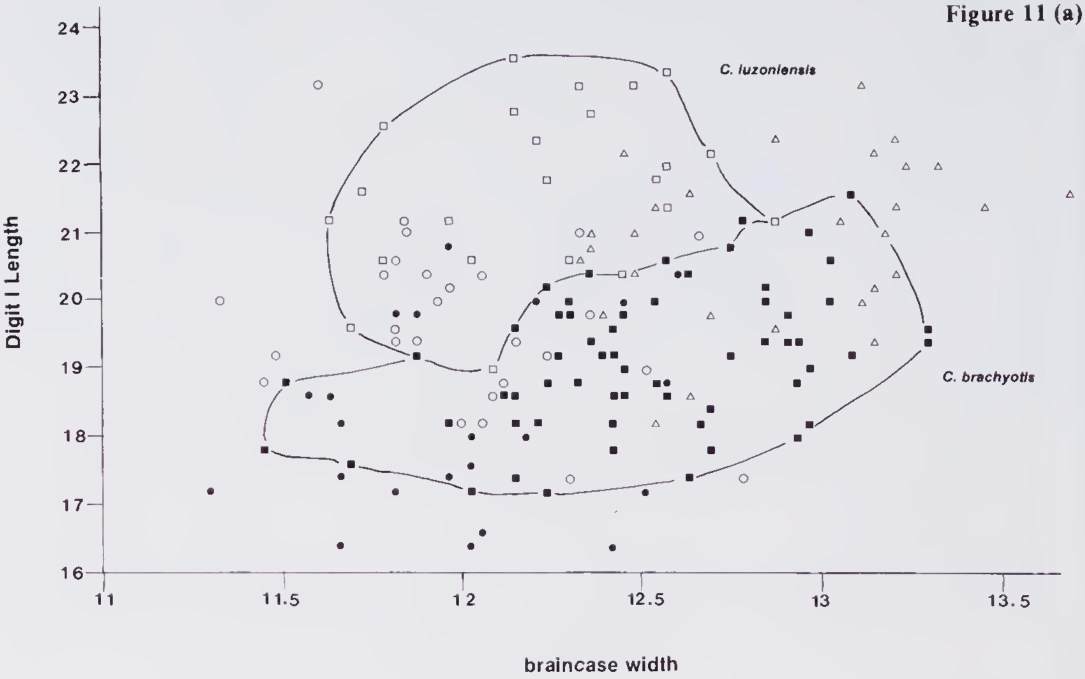
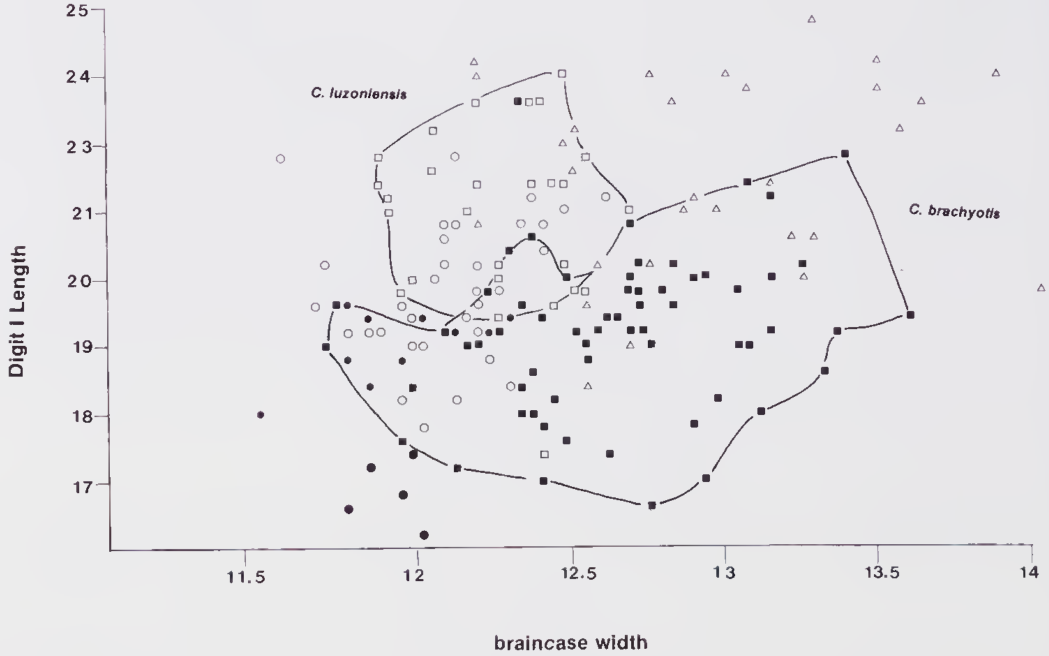


Figure 11 (b)



It also differs from *C. brachyotis* in that it averages slightly smaller in many measurements (Table 1): e.g., ♀♀ -GSL 28.1 (26.0-29.9) *v.* 28.6 (27.0-29.7), ZB 17.8 (16.2-19.2) *v.* 18.6 (17.0-19.7); ♂♂ -GSL 28.3 (27.2-29.7) *v.* 29.0 (27.6-30.7), ZB 18.0 (17.2-19.4) *v.* 18.9 (17.7-20.6); ZB generally narrower relative to ONL and DIG I (Figures 6 and 7, respectively); BW smaller relative to M^1W (Figure 4); ZB generally smaller relative to C_1M_2 (Figure 3); BW generally smaller relative to DIG 3 (Figure 8); P^4 posterolabial corner generally much more square.

It differs from *C. minutus* in averaging larger in all measurements except ZB, BW and C^1-C^1 in females and in males (Table 1. e.g. ♀♀ -GSL 28.1 (26.0-29.9) *v.* 26.6 (25.4-27.6), C_1-M_2 9.9 (9.3-10.6) *v.* 9.6 (9.0-10.2), RAD 59.9 (55.1-64.8) *v.* 57.5 (54.2-61.9) and ♂♂ -GSL 28.3 (27.2-29.7) *v.* 27.2 (26.2-28.3), C_1-M_2 10.1 (9.3-10.6) *v.* 9.8 (9.4-10.2), RAD 59.3 (54.7-61.9) *v.* 57.3 (52.9-60.9); ONL generally longer relative to ZB and M^1W (Figures 6 and 9, respectively); P4 posterolabial corner generally much more square; pelage darker generally Olive Brown on back compared to Wood Brown (brown fawn) or Buffy Brown.

It also differs from *C. luzoniensis* in having all wing measurements averaging slightly shorter (Table 1); DIG 1 shorter relative to DIG 3 (Figure 10); DIG 1 generally shorter relative to ZB (Figure 7); DIG 3 generally shorter relative to BW (Figure 8); pelage darker — generally Olive Brown on back compared to lighter Drab (cinnamon fawn) to Hair Brown (grey brown).

Description

Skull, dentary and dentition

Typical *Cynopterus* skull (Figure 12) of moderate length; cranium dorsal view oval, maximum height and inflation in posterior half of frontal bone — *c.* 4 mm posterior to base of postorbital process; posterior outline of cranium bulges slightly again dorsally and considerably laterally in midparietal region; interparietal region flatter and narrows evenly to a sharp and moderately high lambdoidal ridge; sagittal ridge absent in juveniles, barely perceptible in young adults and forms a low (*c.* 1.5 mm), wide (*c.* 3 mm) ridge in old adults; postorbital width wider in juveniles than adults *c.* (7.4 *v.* 6.3 mm), while interorbital width less affected by age and remains approximately the same; lateral frontal anterodorsal tubular swellings more inflated and median frontal sulcus more concave in adults; postorbital lateral processes triangular shaped, facing slightly posteriorly, short in juveniles (*c.* 1 mm) and longer in adults (*c.* 2.2 mm), base penetrated by small foramen; nasal narrowly triangular, constricted posteriorly to a blunt point which penetrates *c.* 3.5 mm from frontal — premaxillary anterior junction, distal end slightly flared laterally but without any constriction midlength; lacrimal foramen size moderate, lacrimal forms part of anterior edge of orbit; frontal posterior to postorbital lateral process broadly circular, not square; infraorbital foramen subequal in size to lacrimal foramen, separated from latter by low ridge from orbit; rostrum lateral profile slopes gently from frontal to distal tip of nasal in juveniles but rostrum becomes square in shape in recent adults and old specimens; nasal distal end in some specimens slightly uptilted; optic foramen circular, separated from its immediately posterior and larger

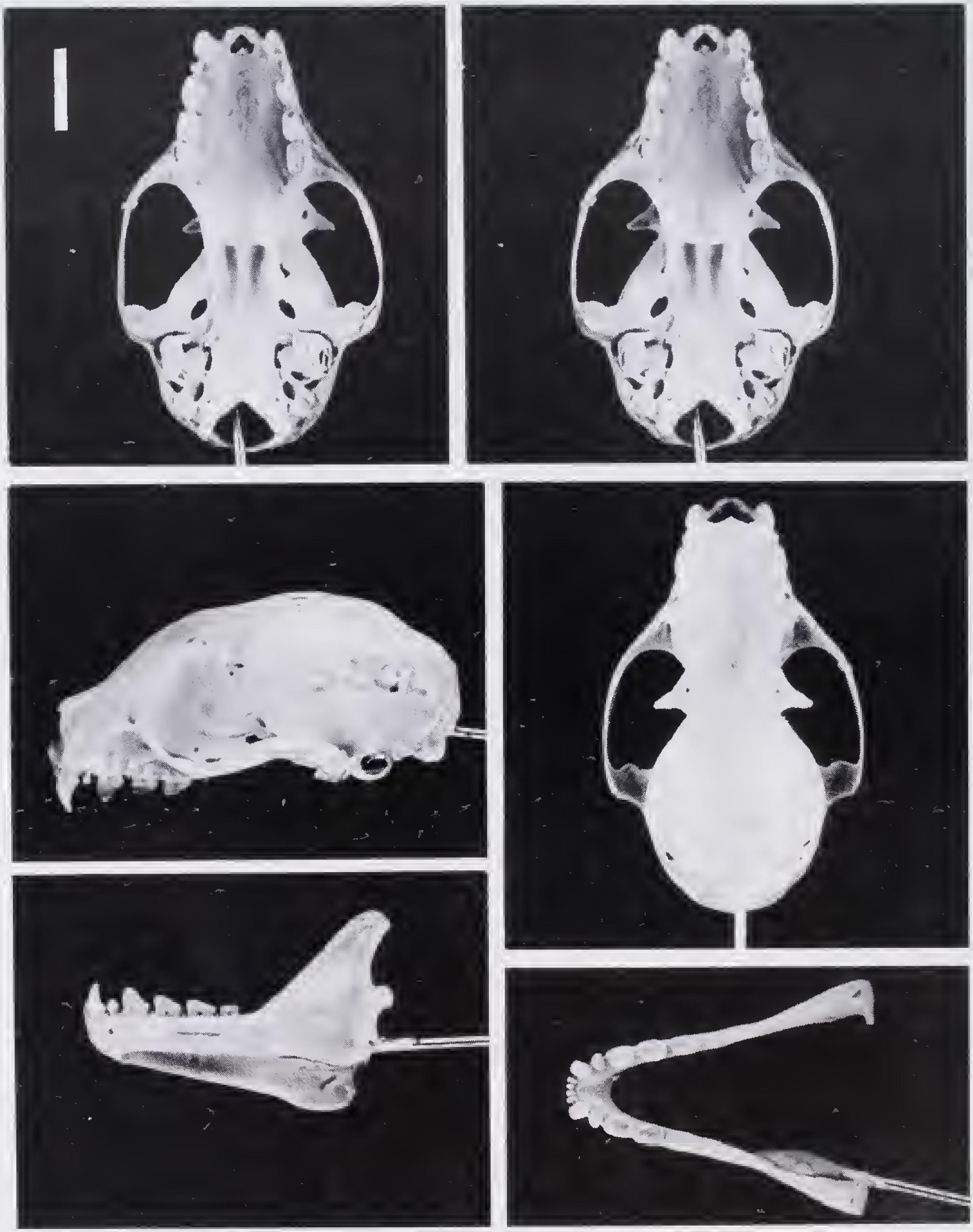


Figure 12 Skull, dentary and dentition of *Cynopterus nusatenggara* holotype. Ventral view as stereopair. Scale line 5 mm.

foramen (? sphenoidal fissure) by stout broad strut connecting alisphenoid with dorsal lateral margin of presphenoid; foramen oval moderately large, with posterior edge formed by slight ridge from glenoid fossa posterior margin; postdental palate length subequal to distance between P^4-P^4 lingual faces; mesopterygoid fossa wide, subequal to distance between P^3-P^3 lingual faces, anterior margin shape variable but usually straight or gently curved; pterygoid ridges merging slightly posteriorly with low posterobasal ridge curving towards bulla anteromedial edge; bulla small, robust, close to glenoid fossa, in lateral view external auditory meatus subcircular; lambdoidal ridge from immediately posterior to bulla to crest almost straight or gently curved; paraoccipital process moderately long but not reaching as far as occipital condyle posterior edge; zygomatic squamosal part robust with postsquamosal ridge immediately dorsal to bulla usually terminates prior to lambdoidal crest; zygomatic arches gently curved and not squarish; zygomatic breadth moderate (*c.* 17.9 mm); incisive foramen heart shaped, small, terminates posteriorly before a point level with C^1 posterior face; dentary coronoid process gently sloping dorsoposteriorly, apex blunt and occasionally with slight posterior hook, posterior margin gently concave or almost straight; angular process gently rounded, without ventrointernal shelf, ventral edge only slightly convex against long axis of ventral surface of dentary. I^{1-2} subcircular in cross-section, simple crown, usually loosely adpressed to each other, occasionally crossed; distal one-third slightly flattened anteroposteriorly, worn posterior face usually produces spade shaped distal end; I^2 slightly shorter than I^1; diastema between I^2 and C^1 wide, approximately equal to combined widths of I^1 and I^2; C^1 upper stout, anterior face smooth and evenly convex such that apex faces slightly posteriorly, secondary cusp in middle of lingual edge, one-third to one-half principal cusp height; P^1 small, rod-like, crown simple, occlusal area varies from slightly larger to twice that of incisors, height approximates C^1 cingulum, rarely vestigial or absent; P^3 large, basal area subequal or slightly larger than that of C^1, labial cusps tall, threequarters C^1 height, lingual cusp from cingulum half labial cusp height and connected to base of labial cusp by commissure running almost at right angles to axis of molar tooth row or slightly forward of this angle (Figure 13a); vestigial cusplet visible on anterolingual cingulum in some juveniles; P^4 occlusal area slightly larger than P^3, antero- and postero-lingual margins more developed than in P^3 to produce a more square occlusal surface, lingual and labial cusps much lower than in P^3; P^4 anterolabial cusp prominent and about half height P^3 principal cusp — posterior ridge with secondary cusplet; lingual cingulum with small anterior cusplet and occasionally with secondary cusplet at midpoint; P^4 with low lingual cusp separated from its labial cusp by gently sloping basin that is frequently raised between these cusps and sloping downwards both anteriorly and posteriorly — but not forming a definite ridge or commissure (Figure 13a); M^1 oblong, slightly longer and narrower than P^3 and P^4, anterolabial cusp three-quarters height of this cups on P^4 and with only a trace of secondary cusplet on posterior ridge, low cusplet on anterolingual cingulum; surface cusps absent on P^3, P^4 and M^1.

I_1 occlusal surface subtriangular; I_2 more oblong, anterior face with faint median notch; I_1 occlusal area one-half to three-quarters that of I_2, noticeably shorter than I_2;

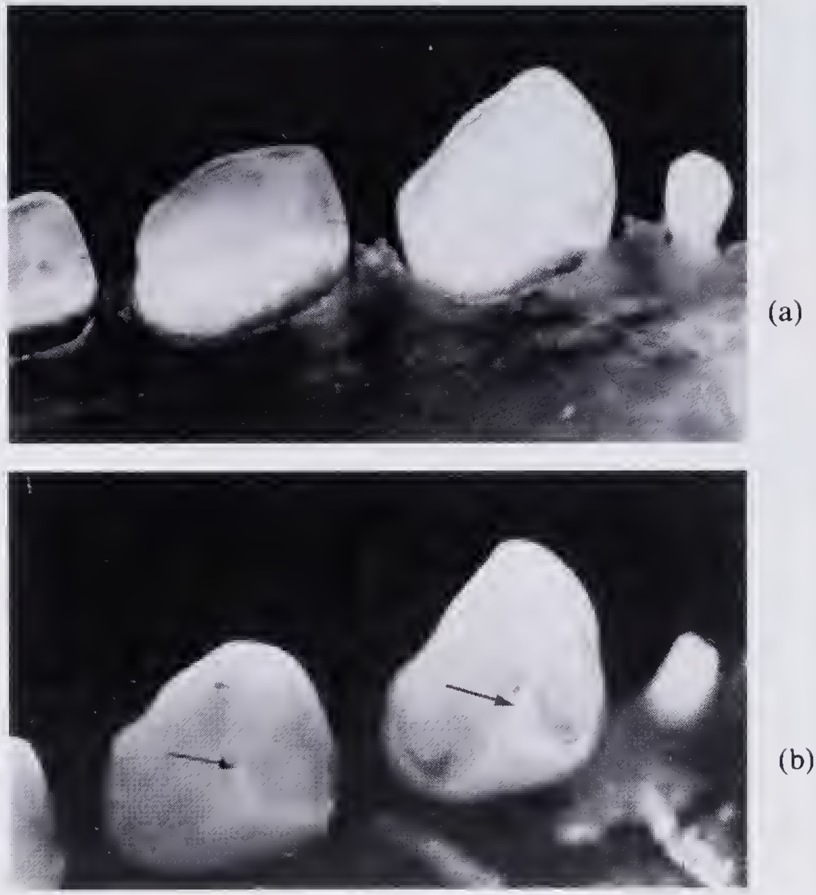


Figure 13 Upper second and third premolars; occlusal view (a) *Cynopterus nusatenggara* (holotype) from West Sumbawa and (b) *Cynopterus brachyotis* WAM M16163 from Bali. Arrow on P^3 and P^4 indicating commissure (see text for discussion).

incisors usually not in contact but occasionally loosely adpressed to each other; diastema between I_2 and C_1 usually approximately equal to I_2 width but occasionally much narrower; C_1 anterior face smooth, gently curving dorsoposteriorly such that apex partly faces posteriorly, moderately sharp posterolabial ridge from apex of cusp to contact with posterior cingulum at its most outside (labial) point, this contact marked by small circular cusplet (often not visible in worn teeth); lingual cingulum produces larger cusps at its midpoint which reaches to approximately half height of principal cusp; P_1 occlusal area moderately large, slightly smaller than M_2, oval shaped with long axis at right angle to dentary, labial cusp about one-third height of that of P_3; P_3 with prominent labial cusp to four-fifth height of C_1, lingual cingulum rises to cusp — partly fused to taller labial cusp below its apex, labial cusp posterior ridge usually with cusplet at midlength; P_3 posterolabial corner sharp and square, occasionally marked by faint cingular cusplet; P_4

anterolabial and anterolingual cusps separate, not connected by commissure, produces a squarer occlusal surface than P_3, slight internal ridge from apex of principal cusp to its base, posterolabial corner as in P_3; M_1 occlusal surface oval shaped, longer and narrower than P_3 and P_4, similar cusp morphology to P_4 but with ridges lower and posterolabial corner rounded rather than square, slight internal ridge from labial cusp apex to its base; M_2 occlusal surface area about one-third that of M_1, anterior edge very gently curved with low cusp on anterolabial corner, posterior edge gently curved; P_4 and M_1 with low but obvious occlusal surface cusps.

Externals

Moderate sized *Cynopterus* averaging 27.9 ± 1.52 (24.5-30.5) (N = 27) and 29.9 ± 3.94 (21.5-37.5) (N = 21) gm for adult males and adult females, respectively. Nostrils short, *c.* 4 mm, subtubular and diverging anterolaterally at an angle of *c.* 70^0, such that they open slightly laterally with ventrolateral nasal slit lateral on muzzle; ear narrowly rounded, *c.* 16 mm long, antitragal lobe small, narrowly rounded (see Kitchener *et al.* (1990a: 40) for photograph of *C. nusatenggara*, described as *C. brachyotis*). Tail and calcar about one-half length of foot and claw; plagiopatagia widely separated, from sides of back, insert at distal end of digit 1 metatarsal; index finger clawed; relative lengths of radius, metacarpals and phalanges indicated in Table 1; penis short with external sheath short, *c.* 5 mm, skin thick, darkly pigmented, particularly so ventrally, moderately haired, up to 5 mm long; penis cigar shaped with obvious low dorsal ridge raised *c.* 0.3 mm above surrounding surface with low median groove; this ridge terminates just before distal end of penis; urethral groove dorsoventral slit at penis distal end opening directly to a ventral groove for some 1.3 mm, this groove closes posterior to this point but continues posteriorly along the midventral surface of length of penis as a closed groove. This groove medially on slightly raised 'keel' of tissue which laterally joins the dorsal ridge at its distal end only and projects slightly anterior to dorsal ridge, particularly the anterobasal point of keel.

Palatal ridges

Ten prominent palatal ridges in interdental region and immediately postdental; anterior ridge almost straight; ridges posterior to this become progressively more sharply curved as illustrated in Andersen (1912: 591); usually last two of these ridges divided but sometimes the last three and occasionally only the last one divided. Near posterior margin of palate are two flattened and divided 'ridges'.

Pelage and skin colour

Adult males have a collar of lighter coloured Sayal Brown (fawn cinnamon) to Snuff Brown (cinnamon brown) fur around throat and extending to base of chin, chest, and side of neck. This colour usually connects behind neck, frequently forming a mantle on shoulders and occasionally colouring fur to rump; ventrally it usually also extends along sides to rump flanking pale Neutral Gray to Neutral Gray venter. Top of head from rhinarium to occiput, face and lips Fuscous (cinnamon black) to Fuscous Black; chin a mixture of Light Olive-Buff and Pale Payne's Gray (pale blue grey) hairs; back Olive

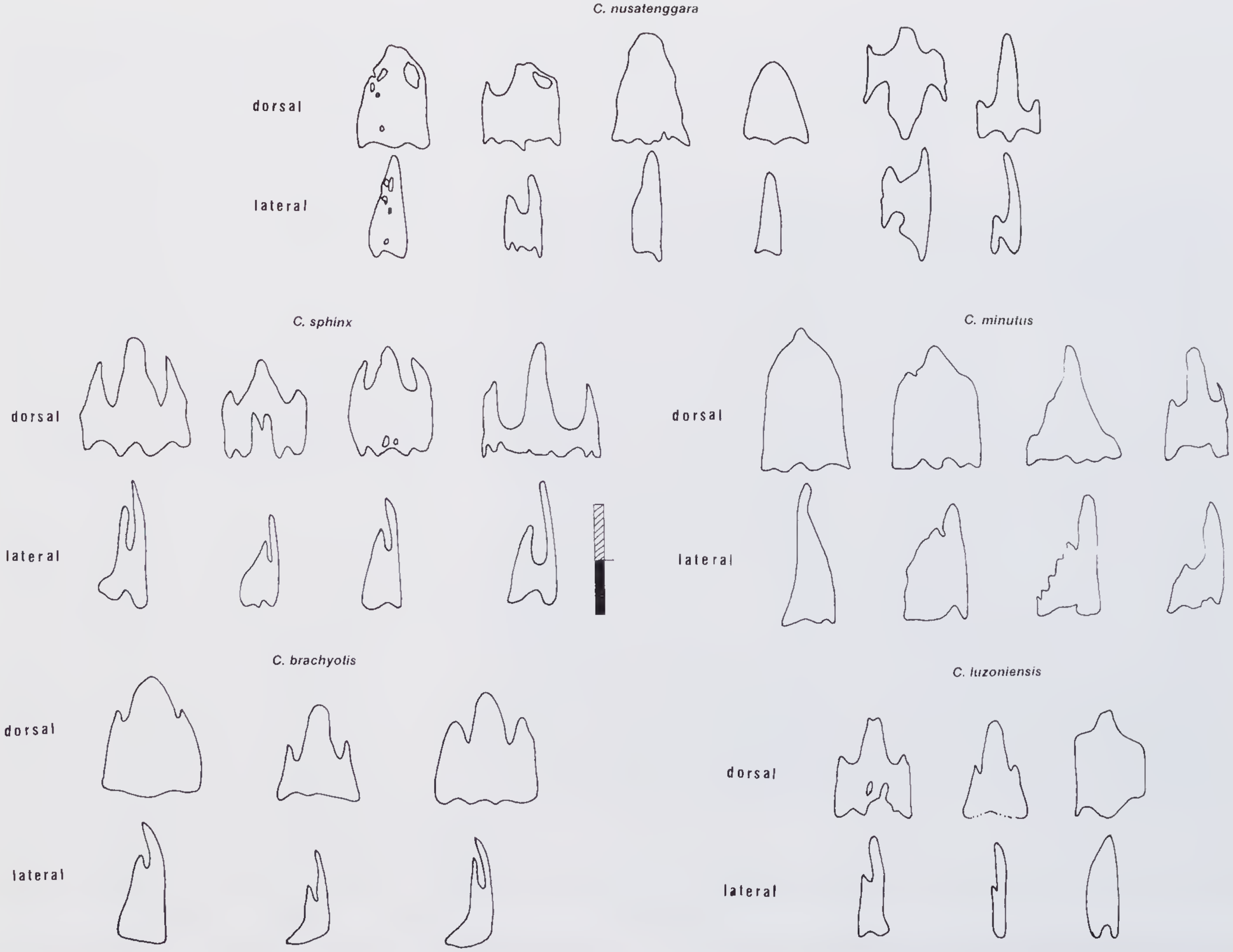


Figure 14 Shape of bacula of five species of *Cynopterus (nusatenggara, sphinx, brachyotis, minutus* and *luzoniensis)* from dorsal and lateral views. Scale line 2 mm.

Figure 15 Localities of *Cynopterus nusatenggara* examined in this study.

Brown to Dark Olive, frequently tipped with Sayal Brown to Snuff Brown of shoulder mantle; plagiopatagium ventral surface adjacent to body and forearm thinly furred with Buckthorn Brown (golden brown); uropatagium ventral and dorsal surfaces lightly furred with Drab (cinnamon fawn), except near tail where there is a tuft of hairs up to *c.* 5 mm long; radius proximal half to two-thirds furred (frequently densely) on dorsal surface with same colour as on rump; ear naked, apart from base. Skin of ear, lip, feet and patagia Fuscous to Chaetura Black (dark olive black). Margin of ear same colour as other surfaces of ear — not contrastingly lighter as in other *Cynopterus* spp. considered. Surfaces of metacarpals and phalanges same colour as patagia or occasionally a slightly lighter Drab but not contrasting with colour of patagia as in other *Cynopterus* spp. considered.

Table 1a females Sample size (N), mean (x), Standard deviation (SD), minimum (Min) and maximum (Max) values of skull, dental and external measurements (in mm) of *Cynopterus nusatenggara, C. sphinx, C. brachyotis, C. minutus* and *C. luzoniensis* for (a) females, and (b) males. For explanation of character codes see Figure 1 caption.

SPECIES/CHARACTER		GSL	CDL	PL	MFW	ONL	LIW	POW	ZB	BW	CPL	C^1C^1	P^4-P^4	M^1-M^1	C^1-M^1
C. nusatenggara	N	29	29	30	30	30	30	30	28	30	30	30	30	29	30
	x	28.1	26.0	14.3	4.0	6.8	5.8	6.3	17.8	12.0	20.9	5.7	8.1	8.4	9.0
	SD	0.94	0.83	0.48	0.23	0.33	0.34	0.40	0.80	0.34	0.62	0.26	0.35	0.35	0.28
	Min	26.0	24.4	13.4	3.5	6.3	5.2	5.5	16.2	11.4	19.9	5.3	7.5	7.9	8.4
	Max	29.9	27.6	15.2	4.5	7.6	6.5	7.2	19.2	12.8	22.1	6.3	8.9	9.3	9.5
C. sphinx	N	27	28	27	25	29	28	28	23	28	28	28	29	28	29
	x	30.3	28.0	15.6	4.3	7.2	6.1	6.8	19.3	12.9	23.0	6.2	8.6	8.9	9.8
	SD	1.23	1.13	0.69	0.30	0.59	0.34	0.52	0.91	0.38	1.19	0.32	0.47	0.50	0.57
	Min	28.1	25.7	14.3	3.9	6.2	5.3	5.8	17.3	12.3	20.9	5.6	7.8	7.9	8.7
	Max	32.9	30.5	17.5	5.0	8.6	6.7	7.8	20.7	13.7	26.9	7.1	9.9	10.1	11.6
C. brachyotis	N	62	65	65	66	68	70	70	64	69	70	67	62	62	67
	x	28.6	26.3	14.6	4.1	6.6	5.8	6.6	18.6	12.5	21.4	5.9	8.2	8.4	9.1
	SD	0.60	0.71	0.43	0.22	0.32	0.28	0.53	0.56	0.40	0.56	0.24	0.35	0.40	0.35
	Min	27.0	24.4	13.5	3.6	5.8	5.2	5.2	17.0	11.5	19.9	5.3	7.3	7.5	7.4
	Max	29.7	28.8	15.3	4.5	7.3	6.4	8.0	19.7	13.3	22.4	6.4	8.8	9.4	9.7
C. minutus	N	22	22	22	22	23	23	23	22	23	23	22	23	22	23
	x	26.6	24.5	13.4	3.8	5.9	5.5	6.2	18.0	12.0	20.0	5.7	7.9	8.1	8.6
	SD	0.67	0.69	0.49	0.19	0.41	0.34	0.51	0.57	0.35	0.58	0.23	0.30	0.30	0.29
	Min	25.4	23.0	12.5	3.4	5.3	4.7	5.5	16.4	11.3	18.8	5.3	7.4	7.7	8.1
	Max	27.6	25.6	14.5	4.1	6.7	6.2	7.2	19.0	12.6	21.3	6.3	8.8	8.9	9.1
C. luzoniensis	N	30	30	30	29	30	30	30	30	30	30	30	30	30	30
	x	28.6	26.2	14.5	4.0	6.7	6.0	6.5	18.3	12.3	21.2	5.9	8.2	8.3	9.2
	SD	0.91	1.05	0.57	0.23	0.36	0.40	0.36	0.77	0.35	0.78	0.32	0.36	0.38	0.37
	Min	27.3	23.1	13.5	3.5	5.7	5.4	5.8	16.9	11.6	20.0	5.1	7.3	7.5	8.6
	Max	30.5	28.2	16.0	4.4	7.4	6.9	7.3	19.9	12.9	23.1	6.5	8.8	9.0	10.1

Table 1a cont.

SPECIES	CHARACTER	C_1-M_2	P^3L	P^3W	M^1L	M^1W	RAD	DIG 1	DIG 2	DIG 3	DIG 3P	DIG 4	DIG 5	TIB
C. nusatenggara	N	30	30	30	30	30	29	29	29	29	29	29	29	29
	x	9.9	1.9	1.5	2.0	1.3	59.9	19.8	27.4	40.7	26.7	38.1	39.8	23.2
	SD	0.34	0.10	0.06	0.12	0.15	2.00	1.22	1.32	1.65	1.04	1.38	1.42	1.05
	Min	9.3	1.7	1.4	1.8	1.2	55.1	17.4	25.6	38.0	24.2	35.8	36.5	21.1
	Max	10.6	2.1	1.6	2.2	1.5	64.8	23.2	30.6	44.3	29.6	41.1	41.7	25.7
C. sphinx	N	28	29	29	29	29	29	29	29	29	29	29	29	28
	x	11.0	2.1	1.5	2.0	1.4	65.7	21.0	29.1	43.0	28.5	40.9	42.2	24.7
	SD	0.67	0.11	0.08	0.16	1.10	4.28	1.22	1.87	2.50	1.65	2.63	2.70	1.08
	Min	9.9	1.9	1.4	1.6	1.2	58.1	18.3	23.6	36.8	25.3	35.9	36.0	21.4
	Max	13.1	2.3	1.7	2.3	1.6	75.8	23.3	31.4	47.6	33.0	45.9	47.0	29.6
C. brachyotis	N	65	69	69	67	67	70	70	70	70	70	70	69	69
	x	10.2	2.0	1.4	1.9	1.3	61.7	19.2	27.8	41.0	27.0	38.7	40.1	22.9
	SD	0.33	0.11	0.09	0.11	0.10	2.86	1.08	1.56	1.82	1.29	1.85	1.88	1.56
	Min	9.4	1.7	1.0	1.7	1.0	54.7	17.2	23.3	35.8	23.8	34.4	35.3	19.4
	Max	10.8	2.2	1.6	2.1	1.5	66.2	21.6	31.0	45.2	29.9	42.8	43.9	25.5
C. minutus	N	23	23	23	23	23	23	23	23	23	23	23	23	23
	x	9.6	1.8	1.4	1.8	1.2	57.5	18.2	26.2	39.1	25.3	36.6	37.5	21.0
	SD	0.32	0.09	0.06	0.14	0.08	2.13	1.36	1.41	2.02	1.45	1.84	1.34	1.19
	Min	9.0	1.6	1.2	1.6	1.1	54.2	16.4	24.0	35.1	22.9	33.0	33.3	19.0
	Max	10.2	2.0	1.5	2.1	1.4	61.9	20.7	28.8	42.8	28.5	39.4	41.7	23.3
C. luzoniensis	N	30	30	30	30	30	30	30	30	30	30	30	30	30
	x	10.2	2.0	1.5	2.0	1.3	61.4	21.4	28.6	42.3	27.7	39.5	41.0	22.7
	SD	0.39	0.16	0.10	0.11	0.08	2.81	1.34	1.69	1.94	1.57	1.81	1.99	1.34
	Min	9.4	1.6	1.2	1.7	1.2	57.2	19.0	24.7	38.5	25.2	35.8	36.2	19.2
	Max	11.2	2.4	1.7	2.3	1.6	68.9	23.6	31.6	47.2	30.7	43.5	46.7	25.2

Table 1b males

SPECIES/CHARACTER		GSL	CDL	PL	MFW	ONL	LIW	POW	ZB	BW	CPL	C^1-C^1	P^4-P^4	M^1-M^1	C^1-M^1
C. nusatenggara	N	36	36	39	39	39	39	39	39	38	39	38	39	38	39
	x	28.3	26.0	14.3	3.9	6.9	5.9	6.3	18.0	12.2	21.0	5.9	8.2	8.5	9.1
	SD	0.54	0.43	0.36	0.17	0.46	0.30	0.30	0.45	0.24	0.37	0.20	0.23	0.24	0.25
	Min	27.2	25.1	13.5	3.6	6.2	5.3	5.7	17.2	11.6	20.2	5.5	7.6	8.0	8.4
	Max	29.7	27.2	15.2	4.2	9.2	6.5	7.0	19.4	12.6	21.9	6.4	8.6	8.9	9.6
C. sphinx	N	34	35	34	37	37	38	38	35	37	38	36	34	34	36
	x	30.4	28.2	15.7	4.3	7.3	6.1	6.5	19.4	12.9	22.8	6.4	8.8	9.0	9.9
	SD	1.14	1.05	0.72	0.33	0.60	0.40	0.43	0.89	0.47	0.95	0.30	0.38	0.39	0.50
	Min	28.7	26.1	14.5	3.7	6.2	5.2	5.5	17.7	12.2	21.1	5.9	8.1	8.4	9.0
	Max	33.7	31.0	18.2	5.0	8.7	6.9	7.4	21.3	14.0	25.5	7.2	9.8	10.0	11.7
C. brachyotis	N	68	72	66	71	71	71	72	67	72	72	71	70	70	72
	x	29.0	26.7	14.7	4.0	6.7	5.9	6.6	18.9	12.7	21.9	6.1	8.3	8.5	9.6
	SD	0.85	0.78	0.56	0.23	0.37	0.36	0.48	0.65	0.38	0.92	0.23	0.34	0.29	2.14
	Min	26.9	25.4	13.3	3.5	5.9	4.9	5.4	17.7	11.7	20.5	5.5	7.6	7.7	8.4
	Max	30.7	28.6	16.2	4.6	7.7	6.7	7.9	20.6	13.6	27.1	6.6	9.9	9.2	10.8
C. minutus	N	18	18	18	17	18	18	18	15	18	18	18	18	18	18
	x	27.2	24.9	13.7	3.8	6.1	5.5	6.2	18.2	12.0	20.3	5.7	7.9	8.1	8.7
	SD	0.67	0.67	0.40	0.20	0.64	0.39	0.59	0.44	0.27	0.53	0.27	0.28	0.26	0.24
	Min	26.2	23.3	13.0	3.4	5.7	4.8	4.8	17.2	11.5	19.4	5.4	7.6	7.7	8.2
	Max	28.3	26.1	14.2	4.2	6.6	6.2	7.0	18.9	12.7	21.3	6.2	8.4	8.6	9.0
C. luzoniensis	N	29	32	31	31	31	32	32	30	32	32	30	31	31	32
	x	28.6	26.4	14.7	4.0	6.7	6.1	6.4	18.3	12.3	21.0	6.0	8.2	8.4	9.2
	SD	0.69	0.64	0.50	0.20	0.35	0.38	0.45	0.58	0.24	0.78	0.32	0.28	0.27	0.29
	Min	27.2	25.1	13.8	3.6	5.9	5.5	5.6	16.8	11.9	22.1	5.6	7.6	7.9	8.7
	Max	30.0	27.8	15.8	4.4	7.4	7.3	7.5	19.5	12.7	22.5	6.5	8.8	9.0	9.7

Table 1b cont.

SPECIES/CHARACTER		C_1-M_2	P^3L	P^3W	M^1L	M^1W	RAD	DIG 1	DIG 2	DIG 3	DIG 3P	DIG 4	DIG 5	TIB
C. nusatenggara	N	38	39	39	39	39	39	39	39	39	39	39	39	39
	x	10.1	1.9	1.5	2.0	1.3	59.3	19.9	27.2	39.8	26.3	37.3	38.9	23.0
	SD	0.30	0.10	0.06	0.10	0.10	1.48	1.01	1.04	1.06	1.02	0.99	1.26	0.88
	Min	9.3	1.7	1.4	1.7	0.9	54.7	17.7	25.2	37.7	23.7	35.2	34.9	19.8
	Max	10.6	2.1	1.6	2.2	1.5	61.9	1.8	29.2	42.4	29.1	39.1	41.4	24.7
C. sphinx	N	37	37	37	36	36	38	37	38	38	38	38	38	38
	x	11.1	2.1	1.6	2.1	1.4	65.1	2 .2	29.3	43.2	28.6	40.6	41.8	24.1
	SD	0.51	0.13	0.09	0.16	0.09	3.19	1.47	1.75	2.28	1. 5	2.19	2.07	1.67
	Min	10.1	2.0	1.4	1.8	1.2	59.2	8.4	25.6	38.1	25.9	34.9	37.1	20.1
	Max	12.8	2.4	1.8	2.5	1.6	75.0	23.8	32.6	48.2	33.0	45.0	45.5	27.6
C. brachyotis	N	68	72	72	72	72	71	72	72	72	72	72	72	72
	x	10.5	2.0	1.5	1.9	1.3	61.8	19.3	27.8	41.0	27.0	38.5	39.9	23.0
	SD	0.41	0.14	0.10	0.14	0.08	2.49	1.13	1.54	1.71	1.37	1.63	1.82	1.61
	Min	9.8	1.7	1.3	1.6	1.1	55.9	16.6	22.7	37.1	23.8	34.7	36.2	18.7
	Max	11.4	2.4	1.7	2.3	1.4	66.7	22.6	30.7	45.0	30.6	42.0	43.8	26.3
C. minutus	N	18	18	18	18	18	18	18	18	18	18	18	18	18
	x	9.8	1.8	1.4	1.8	1.2	57.3	18.4	26.6	39.2	26.2	36.7	37.8	20.7
	SD	0.25	0.08	0.07	0.10	0.07	2.30	1.26	1.50	1.38	2.35	1.36	1.34	1.21
	Min	9.4	1.6	1.2	1.6	1.1	52.9	16.3	24.8	36.6	23.7	34.5	35.4	19.4
	Max	10.2	1.9	1.5	2.0	1.4	60.9	21.1	29.0	41.3	34.4	38.9	40.1	23.4
C. luzoniensis	N	32	32	32	32	32	32	32	32	32	32	32	32	32
	x	10.4	2.0	1.5	2.0	1.3	60.9	20.9	28.2	42.0	27.6	38.8	40.5	22.5
	SD	0.37	0.09	0.08	0.13	0.07	2.26	1.24	1.36	1.59	1.32	1.97	1.39	0.98
	Min	9.7	1.7	1.3	1.8	1.2	56.0	17.5	25.6	38.8	25.4	31.0	37.9	20.8
	Max	11.1	2.1	1.7	2.2	1.5	65.9	23.0	30.9	45.3	30.3	41.6	43.9	24.5

Adult females generally lighter coloured than males, although pattern of colour similar. Neck collar ranges from Deep Olive Buff to Isabella Color (fawn olive) and contrasts less with Light Grayish Olive stomach and inguinal region than is the case in males; head, face and chin similar colour to males, except females generally have the darker hair projecting further to nape of neck; back Hair Brown (grey brown) tipped on shoulders with same colour as neck collar; rump and legs Drab; plagiopatagium furred with Light Ochraceous Buff.

Baculum

Shape of baculum very variable (Figure 14) with its shape and incomplete ossification seemingly independent of size of skull and extent of tooth wear.

The maximum length and maximum width of bacula are 1.92 ± 0.29 (N = 11) and 1.43 ± 0.30 (N = 11), respectively.

Natural History

Kitchener *et al.* (1990a) report that *C. nusatenggara* (as *C. brachyotis*) on Lombok I. is common in both natural rainforest and disturbed situations such as native gardens. Females were pregnant in September and October just before the monsoon rains with a single foetus (in either the left or right uterine horn). They suggest the species is seasonally polyoestrous. Kitchener *et al.* (1990b) report that (as *C. brachyotis*) at near coastal sites on Lombok I. it has a pollen dietary niche breadth approaching the nectarivorous species *Eonycteris spelaea, Macroglossus minimus* and *Rousettus amplexicaudatus,* but that this niche breadth decreased at more inland and upland sites. *C. nusatenggara* also eats substantial amounts of plant epidermis.

Distribution

At the time of this study the species was known from only Lombok, Sumbawa and Komodo islands (Figure 15). More recently we have collected *C. nusatenggara* from Sumba, Flores, Adonara and Lembata Is, Nusa Tenggara.

Etymology

This species is named after the Indonesian island group to which it is restricted.

Cynopterus sphinx (Vahl, 1797)

(Table 1; Figures 3-11, 14, 16, 17)

Vespertilio sphinx Vahl, 1797, Skr. Nat. Selsk. Copenhagen 4 (1): 123

Vespertilio fibulatus Vahl, 1797, Skr. Nat. Selsk. Copenhagen 4 (1): 124

Pteropus pusillus E. Geoffroy, 1803, Cat. Mamm. Mus. Nat. d'Hist. Nat. p. 49

Pteropus marginatus E. Geoffroy, 1810, Ann, Mus. d'Hist. Nat. 15: 97

Cynopterus marginatus var. *scherzeri* Zelebor, 1869, Reise 'Novara', Säug. p. 13

Cynopterus marginatus var. *ellioti* Gray, 1870, Cat. Monkeys Lemurs, and Fruit-eating Bats in the Collections of the British Museum, Lond. p. 122

Cynopterus angulatus Miller, 1898, Proc. Acad. Nat. Sci. Philad. p. 316

Cynopterus sphinx gangeticus K. Andersen, 1910, Ann. Mag. nat. Hist. (8) 6: 623

Cynopterus pagensis Miller, 1906, Proc. Biol. Soc. Wash. 19: 62

Cynopterus babi Lyon, 1916, Proc. U.S. Nat. Mus. 42: 438

Cynopterus sphinx serasani Paradiso, 1971, Proc. Biol. Soc. Wash. 84: 293-300

Holotype

Andersen (1912) states that "the (two) cotypes, once in the Museum of Copenhagen Natural History Society ("Naturhistorie-Selskabet"), are probably now no longer in existence".

Type Locality

Tranquebar, Madras, India.

Diagnoses

C. sphinx differs from *C. nusatenggara* in that it averages larger for all measurements (except P^3W and M^1L in females (Table 1): e.g., ♀♀ — GSL 30.3 (28.1-32.9) *v.* 28.1 (26.0-29.9), C_1-M_2 11.0 (9.9-13.1) *v.* 9.9 (9.3-10.6), RAD 65.7 (58.1-75.8) *v.* 59.9 (55.1-64.8); ♂♂ — GSL 30.4 (28.7-33.7) *v.* 28.3 (27.2-29.7), C_1-M_2 11.1 (10.1-12.8) *v.* 10.1 (9.3-10.6), RAD 65.1 (59.2-75.0) *v.* 59.3 (54.7-61.9). This size difference is illustrated by the plot of ZB *v.* C_1-M_2 (Figure 3); BW wider relative to M^1W (Figure 4); GSL longer relative to DIG 1 (Figure 5). P_4 posterolabial corner generally much less square, P^3 lingual and labial cusp commissure slopes slightly posteriorly and P^4 lingual and labial cusps connected by low ridge or distinct commissure. White or light coloured edge to margin of ear present. Pelage on head not markedly darker than that of back; and surface colour of metacarpals and phalanges markedly lighter and contrasting with wing membrane.

It differs from *C. brachyotis* in that it averages larger in all measurements except P^3L in females and LPW in males (Table 1): e.g., ♀♀ -GSL 30.3 (28.1-32.9) *v.* 28.6 (27.0-29.7), C_1-M_2 11.0 (9.9-13.1) *v.* 10.2 (9.4-10.8), RAD 65.7 (58.1-75.8) *v.* 61.7 (54.7-66.2); ♂♂ -GSL 30.4 (28.7-33.7) *v.* 29.0 (26.9-30.7), C_1-M_2 11.1 (10.1-12.8) *v.* 10.5 (9.8-11.4), RAD 65.1 (59.2-75.0) *v.* 61.8 (55.9-66.7); ONL generally longer relative to M^1W (Figure 9); DIG 1 generally longer relative to GSL and ZB (Figures 5 and 7). Pelage on dorsum a darker Chaetura Drab (olive black) compared to Snuff Brown (cinnamon brown) to Wood Brown (brown fawn).

It differs from *C. minutus* in averaging larger in all measurements (Table 1). It is absolutely larger in the following: ♀♀ -CDL 28.0 (25.7-30.5) *v.* 24.5 (23.0-25.6); DIG 2 29.1 (23.6-31.4) *v.* 26.2 (24.0-28.8) and ♂♂ -GSL 30.4 (28.7-33.7) *v.* 27.2 (26.2-28.3); CDL 28.2 (26.1-31.1) *v.* 24.9 (23.3-26.1); PL 15.7 (14.9-18.2) *v.* 13.7 (13.0-14.2); P^3L 2.1 (2.0-2.4) *v.* 1.8 (1.6-1.9), RAD 65.1 (59.2-75.0) *v.* 57.3 (52.9-60.9) [♀♀ RAD 65.7 (58.1-75.8) *v.* 57.5 (54.2-61.9)]; BW greater relative to M^1W (Figure 4); canines much more robust. Pelage on dorsum a darker Chaetura Drab compared to Wood Brown to Buffy Brown.

It differs from *C. luzoniensis* in averaging larger in most measurements (except P^3L, P^3W, M^1L and DIG 1 in females and LIW in males) (Table 1); e.g.: ♀♀ -GSL 30.3 (28.1-32.9) *v.* 28.6 (27.3-30.5), C_1-M_2 11.0 (9.9-13.1) *v.* 10.2 (9.4-11.2), RAD 65.7

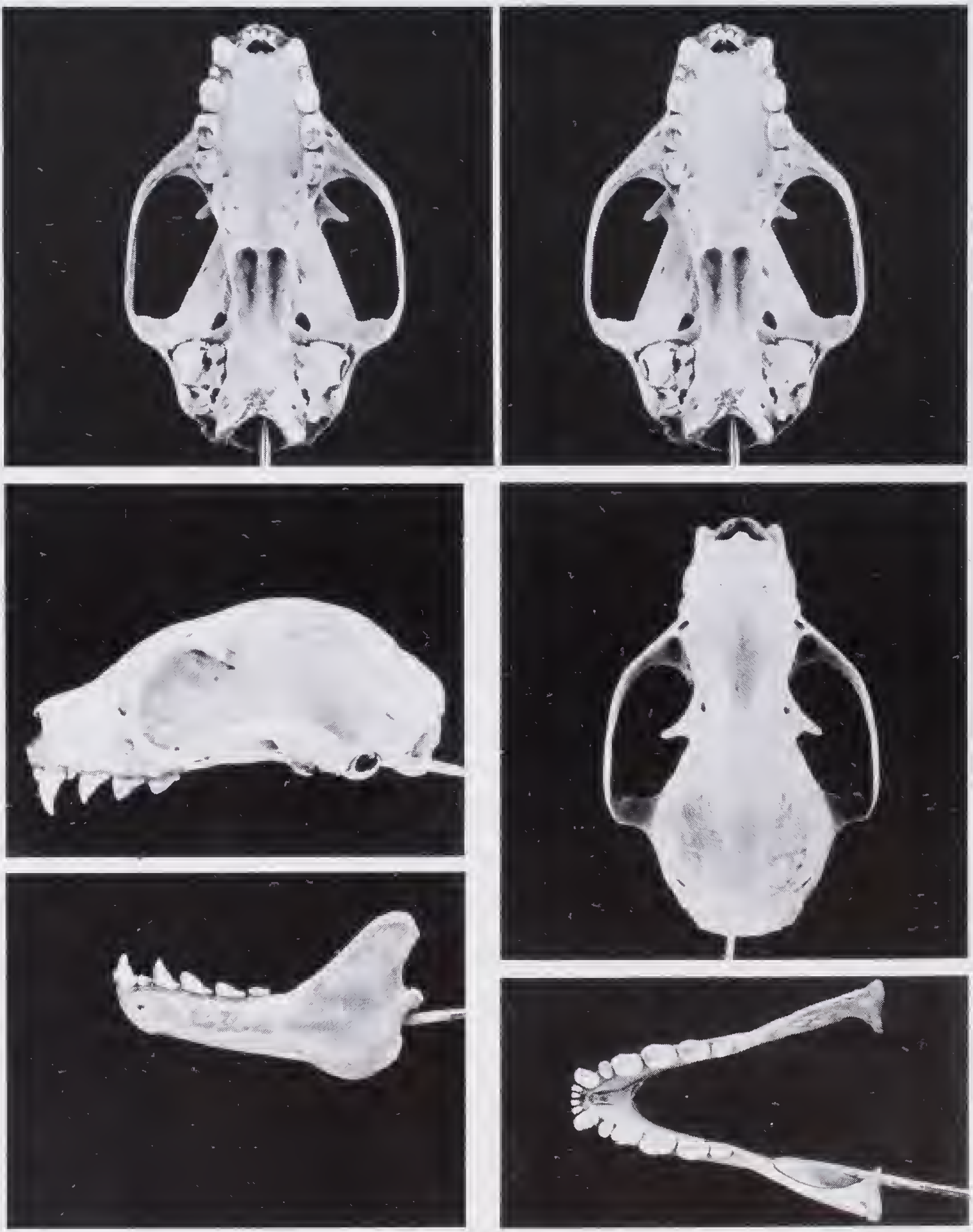


Figure 16 Skull, dentary and dentition of *Cynopterus sphinx* WAM M26362 from Krakatau I. Ventral view as stereopair. Scale line 5 mm.

(58.1-75.8) *v.* 61.4 (57.2-68.9); ♂♂ -GSL 30.4 (28.7-33.7) *v.* 28.6 (27.2-30.0), C_1-M_2 11.1 (10.1-12.8) *v.* 10.4 (9.7-11.1), RAD 65.1 (59.2-75.0) *v.* 60.9 (56.0-65.9); ZB generally wider relative to ONL (Figure 6); BW larger relative to M^1W (Figure 4); GSL generally longer relative to DIG 1 (Figure 5). P^4 posterolabial corner generally much less square. Pelage on dorsum a darker Hair Brown to Chaetura Drab compared to Grayish Drab (cinnamon fawn) to Hair Brown.

Description

The description is generally as for *C. nusatenggara* except for the following:

Skull, dentary and dentition (Figure 16).

Cynopterus sphinx is considerably larger in most measurements (Table 1). Shape of rostrum in lateral profile changes with age as in *C. nusatenggara* and many specimens can be found of these two species with a similar shape rostrum; however, in juveniles of *C. sphinx* rostrum dorsal surface in lateral profile straighter (e.g. WAM M23785) rather than gently concave in the middle; some juveniles of *C. sphinx* with rostrum distal end projecting slightly further than in *C. nusatenggara* to almost level with premaxilla distal point; nasal narrowly triangular, constricted posteriorly to a blunt point, occasionally in juveniles appears constricted at midpoint by overlapping flange of maxilla (e.g. WAM M23315); frontal bone posterior to postorbital lateral process in juveniles narrower and squarer than in *C. nusatenggara;* basioccipital process tends to be more vertical and less angled towards occipital condyle than in *C. nusatenggara;* foramen oval posterior margin tends to form a more pronounced lip such that its outline is usually narrower than in *C. nusatenggara;* P^3 and P^4 (particularly P^4) lingual edge straighter without gentle curve of *C. nusatenggara;* this is reflected in measurements (Table 1) where P^3 width averages the same (1.5) but P^3 length longer in *C. sphinx* then in *C. nusatenggara* (2.1 *v.* 1.9). P^3 lingual cusp connected to base of taller labial cusp by a commissure that angles slightly posterior of the right angle to axis of molar row (Figure 13b); P^4 with lingual cusp connected to its labial cusp by a definite low ridge (obscure in worn teeth). Teeth in some *C. sphinx* (e.g. from Java and Krakatau) more robust than in *C. nusatenggara,* in others (e.g. Thailand) of subequal size; P_1 occlusal area subequal to or slightly larger than M_2; P_3 posterolabial corner more curved or widely angled rather than square as in *C. nusatenggara;* M_1 usually with very low occlusal surface cusps P_4 with such cusps only occasionally present and less obvious.

Externals and palatal ridges

The largest of the *Cynopterus* spp. considered. Weight 38.5 ± 6.43 (34.5-53.0) (N = 10) and 46.5 ± 16.06 (28.0-70.0) (N = 5) gm for adult males and adult females, respectively; external measurements presented in Table 1; overall shape as for *C. nusatenggara.*

Pelage and skin colour

Adult pelage colour of males and females differ principally in colour of collar of fur in region of neck and adjacent parts: both sexes have a collar of of lighter coloured hairs around throat and extending to chin, chest, side of neck to behind ears — occasionally this collar is complete behind neck, often colour of collar extending to fur of lateral

Figure 17 Localities of *Cynopterus sphinx* examined in this study.

aspect of chest and venter. In adult females overall colour of pelage on top of head, neck, and face Hair Brown (grey brown), but occasionally a darker Mummy Brown (charcoal brown) (in specimens from Bengkulu, Sumatra); a collar of Drab (cinnamon fawn) to Dresden Brown (olive brown) usually joined across back of neck and shoulders; on throat; chin and flanks of venter a lighter Marguerite Yellow (lemon cream), occasionally Chamois (yellow tan), Dresden Brown or Sulphine Yellow (pale lemon yellow). The back Isabella Color (fawn olive) to Mummy Brown but occasionally lighter near tail to Tawny Olive. Venter generally Pale Drab Gray merging to Deep Olive Buff near tail. Plagiopatagium ventral aspect adjacent to body and forearms with scattered Sulphine Yellow hairs; uropatagium dorsal and ventral surfaces very lightly haired, except at margin where hairs slightly denser, and Deep Olive Buff to Buckthorn Brown (golden brown); proximal half of radius furred on dorsal surface with same colour as dorsum; base of ear furred with same colour as neck collar, remainder naked. Skin of ears, lips, feet and patagia Deep Mouse Gray (dark lilac grey); inner and outer margins of ear a contrasting Light Buff to Warm Buff, except in specimens from Sangeang I. near

Sumbawa, where the margins of ear are slightly more lightly coloured on antero-proximal margins of ear only. Surfaces of metacarpals and phalanges a light Tilleul-Buff (pale tan cream) contrasting with colour of patagia.

Adult males have similar colours to females except that neck collar is usually a deeper colour, frequently Dresden Brown.

Baculum

A range of baculum shapes occur in adult *C. sphinx* from Krakatau I. (Figure 14). These shapes appear unrelated to age of adults as judged by extent of tooth wear and skull size.

The maximum length and width of bacula are 2.08 ± 0.26 (N = 7) mm and 1.80 ± 0.24 (N = 7) mm, respectively.

Distribution

The locality of *C. sphinx* South East Asian specimens examined by us are shown in Figure 17. They are from Thailand, Sumatra, Siberut I., Pagai I., Krakatau Is, Java, Bali I., Sangeang I., Sulawesi, Salayar I., as well as from Central India.

We have not examined specimens from Sri Lanka, Peninsula and North East India and Burma (*C. s. sphinx*), Car Nicobar I. (*C. s. scherzeri*), Serasan and Natuna Is (*C. s. serasani*), Babi I. (*C. s. babi*) or specimens of *C. s. angulatus* from North Burma, South China, Hainan I., Vietnam and Langkawi I., North Peninsula Malaysia, Verlaten I., but from available descriptions these forms are considered to be *C. sphinx*.

Remarks

Cynopterus sphinx differs from *C. brachyotis* principally on overall size and some other minor characters, particularly occlusal outline and general shape of molars and shape of rostrum.

Specimens WAM (M16160, M16162) were judged on balance to be more like *C. sphinx* than *C. brachyotis*, particularly on morphology of molars. These specimens were also allocated to *C. sphinx* by the discriminant function analysis — although they are located at the boundary of the *C. sphinx* and *C. brachyotis* discriminant function clusters. The allocation of these two specimens to *C. sphinx* is tentative. Previously these specimens were allocated to *C. brachyotis* by Kitchener and Foley (1985).

Allocation of some of the Sangeang I. specimens to *C. sphinx* is similarly tentative. These specimens have some characters typical of *C. nusatenggara*. For example, absence of white margins on ears and angle of commissure connecting P^3 low lingual and taller labial cusp (at right angles to axis of tooth row or slightly anterior to that angle). However, they are much larger specimens than *C. nusatenggara* and have other aspects of the teeth and skull that resemble *C. sphinx*. Further, their discriminant function coefficients place them clearly in the *C. sphinx* cluster.

Cynopterus sphinx is a very variable species, with specimens from India and Thailand clustering somewhat apart in the discriminant function analysis while specimens from Sulawesi and Java clustered closely with those from elsewhere in Indonesia. Characters used to distinguish *Cynopterus sphinx* from some other species in this paper, and by other researchers, are considered to a degree to be inadequate. Clearly other character sets, particularly genetic ones, need to be applied to clarify the taxonomy of this group.

***Cynopterus brachyotis* (Müller, 1838)**

(Table 1; Figures 3-11, 13, 14, 18, 19)

Pachysoma brachyotis S. Müller, 1838, Tijd. Nat. Gesch. 5 (1): 146

Cynopterus marginatus var. *ceylonensis* Gray, 1870, Cat. Monkeys, Lemurs and Fruit-eating Bats in the Collections of the British Museum, London p. 122.

Cynopterus brachysoma Dobson, 1871, J. Asiat. Soc. Beng. p. 260

Cynopterus brachyotis javanicus K. Andersen, 1910, Ann. & Mag. nat. Hist. (8) 6: 624

Cynopterus brachyotis insularum K. Andersen, 1910, Ann. & Mag. nat. Hist. (8) 6: 624

Cynopterus brachyotis concolor Sody, 1940, Treubia 17: 391-401

Cynopterus brachyotis altitudinis Hill, 1961, Proc. Zool. Soc. Lond. 136: 629-642

Holotype

Andersen (1912: 619) states that the cotypes are in Leyden Museum: four as mounted specimens (Cat. Syst. *a-d*, two male adults, one female adult and one juvenile); and six odd skulls (Cat. Ost. *b-g*). Skull of specimen *a* extracted, those of *b-d in situ*; all seven skulls adult except *f*; the lower jaw of *c* missing.

Type Locality

"eene diepe kalksteen — spelonk, aan den oever van de rivier Dewej" (= Dewei River, South Central Borneo).

Diagnoses

Cynopterus brachyotis differs from *C. nusatenggara* in averaging slightly larger in many measurements (Table 1): e.g., ♀♀-GSL 28.6 (27.0-29.7) *v.* 28.1 (26.0-29.9), ZB 18.6 (17.0-19.7) *v.* 17.8 (16.2-19.2); ♂♂-GSL 29.0 (26.9-30.7) *v.* 28.3 (27.2-29.7), ZB-18.9 (17.7-20.6) *v.* 18.0 (17.2-19.4); ZB generally wider relative to ONL and DIG 1 (Figures 6 and 7, respectively); BW larger relative to M^1W (Figure 4); ZB generally larger relative to C_1M_2 (Figure 3); BW generally larger relative to DIG 3 (Figure 8); P4 posterolabial corner generally much less square; P^3 lingual and labial cusp commissure slopes gently posteriorly and P^4 lingual and labial cusps connected by low ridge or distinct commissure. White or light coloured edge to margin of ear. Pelage on head not markedly darker than on back and surface of metacarpals and phalanges markedly lighter and contrasting with colour of wing membrane.

It differs from *C. sphinx* in that it averages smaller in all measurements except P^3L in females and POW in males (Table 1): e.g., ♀♀-GSL 28.6 (27.0-29.7) *v.* 30.3 (28.1-32.9), C_1-M_2 10.2 (9.4-10.8) *v.* 11.0 (9.9-13.1), RAD 61.7 (54.7-66.2) *v.* 65.7 (58.1-75.8); ♂♂-GSL 29.0 (26.9-30.7) *v.* 30.4 (28.7-33.7); C_1-M_2 10.5 (9.8-11.4) *v.* 11.1 (10.1-12.8); RAD 61.8 (55.9-66.7) *v.* 65.1 (59.2-75.0); ONL generally shorter relative to M^1W (Figure 9); DIG 1 generally shorter relative to GSL and ZB (Figures 5 and 7, respectively).

It differs from *C. minutus* in averaging larger in all measurements (except P^3W in females (Table 1): e.g., ♀♀-GSL 28.6 (27.0-29.7) *v.* 26.6 (25.4-27.6), C_1-M_2 10.2 (9.4-10.8) *v*. 9.6 (9.0-10.2), RAD 61.7 (54.7-66.2) *v*. 57.5 (54.2-61.9) and ♂♂-GSL 29.0 (26.9-30.7) *v*. 27.2 (26.2-28.3), C_1-M_2 10.5 (9.8-11.4) *v*. 9.8 (9.4-10.2), RAD 61.8 (55.9-66.7) *v*. 57.3 (52.9-60.9); ONL generally longer relative to ZB and M^1W (Figures 6 and 9, respectively); and C_1-M_2 generally longer relative to ZB (Figure 3).

It is similar in size to *C. luzoniensis* in most skull and dental measurements but averages shorter in metacarpals 1 to 5 length (Table 1): e.g. ♀♀-DIG 3 41.0 (37.1-45.0) *v*. 42.0 (38.8-45.3); ♂♂-DIG 3 40.7 (39.2-42.6) *v*. 42.2 (40.5-44.0); DIG 1 shorter relative to both DIG 3 and BW (Figures 10 and 11, respectively). P4 posterolabial corner generally much less square; P^3 lingual and labial cusps commissure slopes slightly posteriorly and P^4 lingual and labial cusps connected by low ridge or distinct commissure. Pelage on dorsum a darker Snuff Brown (cinnamon brown to Wood Brown (brown fawn) compared to a Drab (cinnamon fawn) to Hair Brown (grey brown).

Description

The description is generally as for *C. nusatenggara* except for the following:

Skull, dentary and dentition (Figure 18)

The greatest length of skull averages slightly longer (28.6 *v*. 28.1 and 29.0 *v*. 28.3 for females and males, respectively); zygomatic breadth averages wider (18.6 *v*. 17.8 and 18.9 *v*. 18.0 for females and males, respectively); and dentary length from condyle averages longer (21.4 *v*. 20.9 and 21.9 *v*. 21.0 for females and males, respectively); P3 and P4 occlusal surfaces generally less square, particularly posterolabial corner of P4, e.g., in females, on average, P^3 longer (2.0 *v*. 1.9) but narrower (1.4 *v*. 1.5); P^3 lingual cusp connected to base of labial cusp by commissure that angles slightly posterior of the right angle to axis of molar row; P^4 with low commissure (sometimes obscure in worn teeth) linking lingual cusp to base of labial cusps (particularly prominent in Bali specimens: e.g., WAM M16163 (Figure 13b), this commissure is absent in *C. nusatenggara*).

Externals and palatal ridges

Moderate sized *Cynopterus;* external measurements presented in Table 1. Overall shape of externals and palatal ridges as described for *C. nusatenggara*.

Pelage and skin colour

Colour of Javan and Sumatran specimens broadly similar and generally lighter than those from Borneo.

Adult males from Java and Sumatra have a collar of lighter coloured fur varying from Pale Orange Yellow, Capucine Orange (fawn orange) or Isabella Color (fawn olive) around throat extending to chin, chest and side of neck, but not forming a distinct mantle on shoulders, ventrally it also extends along sides of rump flanking the Pallid Mouse Gray (pale lilac-grey) to Olive Gray venter — occasionally this flanking colour deepens to Tawny Olive. Top of head from rhinarium to occiput, face, lips, Hair Brown (grey brown); chin Chamois (yellow tan) to Honey Yellow; back Hair Brown; plagiopatagium ventral surface adjacent to body and forearms thinly furred with Hair Brown; uropatagium ventral and dorsal surfaces lightly furred with Hair Brown except near tail where there is a tuft of hairs; radius proximal one-third lightly furred on dorsal

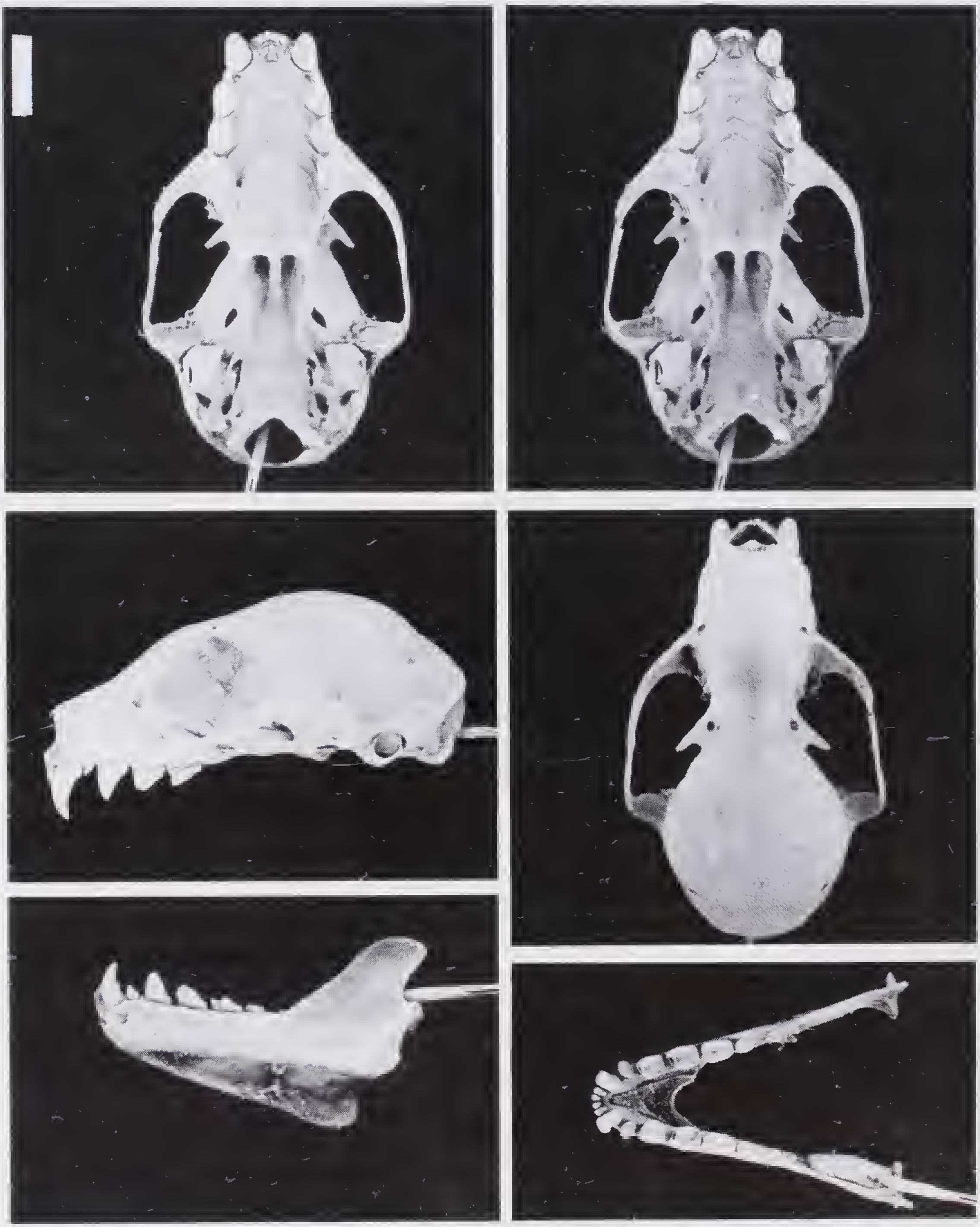


Figure 18 Skull, dentary and dentition of *Cynopterus brachyotis* WAM M16163 from Bali. Ventral view as stereopair. Scale line 5 mm.

Figure 19 Localities of *Cynopterus brachyotis* examined in this study, excluding specimens from Sri Lanka.

surface with colour of back; ear naked apart from base; skin of ear, lips, feet and patagia Fuscous Black; margins of ear, both externally and internally, Tilleul Buff (pale tan cream) contrasting with rest of ear; metacarpals and phalanges Vinaceous Buff (cinnamon cream), contrasting with colour of patagia.

Adult females from Java and Sumatra generally a lighter colour than adult males, although the pattern of colour similar. Neck collar ranges from Deep Colonial Buff (light yellow tan) to Honey Yellow — colours which weakly splash flanks of stomach and contrast less with the Grayish Olive stomach and inguinal region than with males; head, face and chin similar colour to males. Other colours as in males.

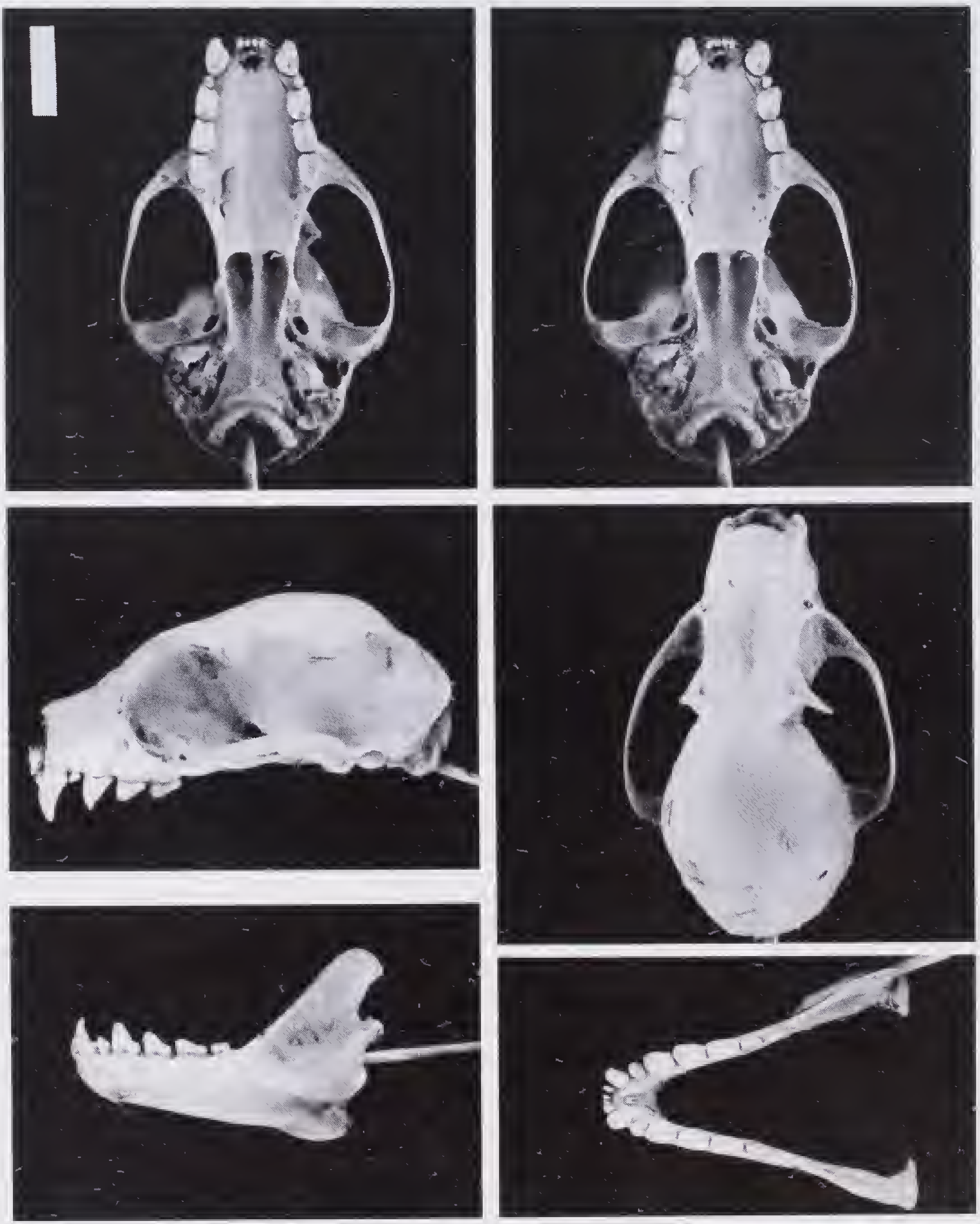


Figure 20 Skull, dentary and dentition of *Cynopterus minutus*, MZB 13446. Topotype from Nias I. ventral view as stereopair. Scale line 5 mm.

Figure 21 Localities of *Cynopterus minutus* examined in this study.

Adult males from Borneo have a collar of Sayal Brown (brown cinnamon) to Mikado Brown (orange brown) around throat and extending to chin, chest and flanks of abdomen almost to inguinal region, and dorsally behind ears and on lateral aspects of shoulders — it does not form a united band behind head; top of head from rhinarium to nape of neck Olive Brown tipped on back and rump with Snuff Brown (cinnamon brown); ventral surface adjacent to body and forearm thinly furred with Cinnamon Buff; uropatagium ventral and dorsal surfaces lightly furred with Buckthorn Brown (golden brown) except near tail where there is a tuft of hairs; radius proximal one-third lightly furred on dorsal surface with colour of back. Other colours as for Javan and Sumatran specimens.

Adult females from Borneo a lighter colour and pattern of colour slightly different. The neck-collar less pronounced and ventrally indistinct lateral to stomach, dorsally also less distinct, particularly on shoulders. The major difference between sexes of Bornean specimens is the neck-collar of females which ranges from lighter Antimony Yellow (fawn yellow) to Buckthorn Brown and these colours, which provide the tipping of hairs of both abdomen and back, are less extensive in these regions and where they occur create a 'lighter' overall colour to pelage.

Baculum

Shape of baculum of *C. brachyotis* variable but less so than in *C. sphinx* and *C. nusatenggara.* Its basic shape triangular with apex distal, sides of this triangle notched sometimes close to apex but usually halfway down sides (Figure 14). Some of these shapes are similar to those found in other *Cynopterus* spp. considered.

The maximum lengths and breadths (in mm), respectively of *C. brachyotis* bacula from several regions are as follows:

	Length (N = 5)	Breadth (N = 5)
Java	2.02 ± 0.23	1.66 ± 0.11
Borneo	2.30 ± 0.14	1.95 ± 0.07
Peninsular Malaysia/Singapore	2.16 ± 0.33	1.84 ± 0.15

Distribution

The localities of South East Asian *C. brachyotis* specimens examined by us are shown in Figure 19. They are from Peninsular Malaysia, Penang I., Singapore I., Sumatra, Borneo, Pulau Laut I., Bunyu I., Java., Pulau Dua I., Madura I., Kangean I. and Bali I. as well as from Sri Lanka. We have not examined specimens of *C. brachyotis altitudinis* (Malayan highlands); *C. b. concolor* (Enggano I.); *C. b. brachysoma* (Andaman Is) or *C. b. brachyotis* from Burma to Vietnam and from many small islands such as Bawean. However, based on descriptions available of these forms they are considered to be *C. brachyotis.*

Cynopterus minutus Miller, 1906

(Table 1; Figures 3-11, 14, 20, 21)

Cynopterus minutus Miller, 1906, Proc. Biol. Soc. Wash. 19: 63.

Holotype

U.S. National Museum Reg. No. 141240, adult male, skin and skull.

Type Locality

Nias I., Indonesia.

Diagnoses

Cynopterus minutus differs from *C. nusatenggara* in averaging smaller in all measurements except ZB, BW and C^1-C^1 in females, and ZB in males (Table 1): e.g., ♀♀-GSL 26.6 (25.4-27.6) *v.* 28.1 (26.0-29.9), C_1-M_2 9.6 (9.0-10.2) *v.* 9.9 (9.3-10.6), RAD

57.5 (54.2-61.9) *v.* 59.9 (55.1-64.8) and ♂♂-GSL 27.2 (26.2-28.3) *v.* 28.3 (27.2-29.7), C_1-M_2 9.8 (9.4-10.2) *v.* 10.1 (9.3-10.6), RAD 57.3 (52.9-60.9) *v.* 59.3 (54.7-61.9); ONL generally shorter relative to ZB and M^1W (Figures 6 and 9, respectively); P4 posterolabial corner generally much less square. White or light coloured edge to margin of ear present; pelage on head not markedly darker than that of back and surface of metacarpals; and phalanges markedly lighter and contrasting with colour of wing membrane.

It differs from *C. sphinx* in averaging smaller in all measurements (Table 1). It is absolutely smaller in the following: ♀♀-CDL 24.5 (23.0-25.6) *v.* 28.0 (25.7-30.5); ♂♂-GSL 27.2 (26.2-28.3) *v.* 30.4 (28.7-33.7), CDL 24.9 (23.3-26.1) *v.* 28.2 (26.1-31.1), PL 13.7 (13.0-14.2) *v.* 15.7 (14.9-18.2), P^3L 1.8 (1.6-1.9) *v.* 2.1 (2.0-2.4). RAD 57.3 (52.9-60.9) *v.* 65.1 (59.2-75.0) RAD ♀♀ 57.5 (54.2-61.9) *v.* 65.7 (58.1-75.8), BW smaller relative to M^1W (Figure 4); canines much smaller. Pelage on dorsum a lighter Wood Brown (brown fawn) to Buffy Brown compared to Chaetura Drab (olive black).

It differs from *C. brachyotis* in averaging smaller in all measurements (except P^3W in females) (Table 1): e.g. ♀♀-GSL 26.6 (25.4-27.6) *v.* 28.6 (27.0-29.7), C_1-M_2 *9.6 (9.0-10.2)* *v.* 10.2 (9.4-10.8), RAD 57.5 (54.2-61.9) *v.* 61.7 (54.7-66.2) and ♂♂-GSL 27.2 (26.2-28.3) *v.* 29.0 (26.9-30.7), C_1-M_2 9.8 (9.4-10.2) *v.* 10.5 (9.8-11.4), RAD 57.3 (52.9-60.9) *v.* 61.8 (55.9-66.7); ONL generally shorter relative to ZB and M^1W (Figures 6 and 9, respectively); and C_1-M_2 generally shorter relative to ZB (Figure 3).

It differs from *C. luzoniensis* in averaging smaller in all measurements except ZW, BW and C^1-C^1 in females and ZW in males (Table 1): e.g., ♀♀-GSL 26.6 (25.4-27.6) *v.* 28.1 (26.0-29.9), C_1-M_2 9.6 (9.0-10.2) *v.* 9.9 (9.3-10.6), RAD 57.5 (54.2-61.9) *v.* 59.9 (55.1-64.8) and ♂♂-GSL 27.2 (26.2-28.3) *v.* 28.3 (27.2-29.7), C_1-M_2 9.8 (9.4-10.2) *v.* 10.1 (9.3-10.6), RAD 57.3 (52.9-60.9) *v.* 59.3 (54.7-61.9); ONL shorter relative to ZB and M^1W (Figures 6 and 9 respectively); and P4 posterolabial corner generally much less square.

Description

The description is generally as for *C. nusatenggara* except for the following:

Skull, dentary and dentition (Figure 20)

Cynopterus minutus averages smaller than *C. nusatenggara* for most measurements (see diagnoses and Table 1).

It differs from *C. nusatenggara* in that cranium dorsal view generally slightly more inflated and globose, rostrum lateral profile slopes more sharply from frontals to nasal distal tip, rostrum noticeably shorter with rostrum length: greatest skull length averaging 0.22 *v.* 0.24 such that front of rostrum in lateral view squarer, zygomatic arch averages wider relative to greatest skull length (0.67 *v.* 0.63), median frontal sulcus tends to be more concave, and postsquamosal ridge immediately dorsal to bulla frequently reaches lambdoidal crest. Postorbital lateral process tends to face more posteriorly in specimens from Nias I. (e.g. MZB 13445-6); dentary coronoid process with blunt rounded apex or with slight posterior hook, posterior margin gently concave or almost straight; P^3 lingual cusp connected to base of taller labial cusp by a commissure that angles slightly posterior of the right angle to axis of molar row; P^4 with low commissure linking lingual cusp to base of labial cusp (obscure in worn teeth). P3 and P4 occlusal surfaces generally less square, particularly posterolabial corners of P4.

Externals and palatal ridges

Smallest of the *Cynopterus* spp. considered. Its external measurements presented in Table 1. Overall shape of externals and palatal ridges as described for *C. nusatenggara.*

Pelage and skin colour

Pelage colour of adult males and females differ principally in collar of fur in neck region and adjacent parts: both sexes have a collar of lighter coloured hair around throat and extending to chin, top of chest, flanks of venter, side of neck to behind ears (and in females, usually around teats) — occasionally this collar faintly connects behind neck.

In adult females, this collar Buff to Chamois (yellow tan); overall colour of pelage on top of head, back and rump Buffy Brown; venter Light Yellowish Olive to Light Brownish Olive; ventral aspect of plagiopatagium adjacent to body and forearm with scattered Deep Olive-Buff hairs; uropatagium ventral and dorsal surfaces lightly furred with Buffy Brown, more dense at margins particularly nearer tail; radius proximal half furred dorsally with same colour as dorsum; base of ear same colour as neck collar, remainder naked. Skin of ear, lips, feet and patagia Clove Brown; inner and outer margins of ear a contrasting Cartridge Buff (pale tan). Surfaces of metacarpals and phalanges a light Cartridge Buff contrasting with colour of patagia.

Adult males coloured as for females but with dorsal surfaces generally a darker Light Brownish Olive to Brownish Olive; neck collar a more strongly coloured Olive Ochre to Clay Color (olive tan) particularly in Sumatran specimens.

Baculum

Shape of *C. minutus* variable but less so than *C. nusatenggara* and *C. sphinx.* Shape basically triangular or arrow shaped with the apex distal (Figure 14). Maximum length and maximum breadth (in mm) of bacula are:

	Length (N = 3)	Breadth (N = 3)
Borneo	2.10 ± 0.12	1.46 ± 0.21
Sumatra	2.21 ± 0.34	1.60 ± 0.19

Distribution

The localities of *C. minutus* specimens examined are shown in Figure 21.

They are from the type locality of Nias I., Sumatra, Java, Borneo and Sulawesi.

Remarks

Andersen (1912) presents measurements from 5 paratypes of *C. minutus* from Nias I. Our measurements of 45 specimens from a much wider geographic area largely conform to those of Andersen. For example, our maximum skull measurements exceed those of Andersen's only for: mesopterygoid fossa (4.2 *v.* 4.0), zygomatic width (19.0 *v.* 18.0) and braincase width (12.7 *v.* 12.2).

External measurements for our specimens average similar to those of Andersen but maximum values tend to exceed his maxima: e.g., radius length (61.9 *v.* 59), DIG 2 (29.0 *v.* 25.5), DIG 3 (42.8 *v.* 37.5), DIG 4 (39.4 *v.* 35), DIG 5 (41.7 *v.* 36.0). This may reflect that the body size of some animals examined by us exceed the size of the Nias I. population, or it may relate to different measuring techniques (external measurements are more dependent on nature of fixation of specimens and the recorder, than are skull measurements).

Cynopterus luzoniensis (Peters, 1861)

(Table 1; Figures 3-11, 14, 22, 23)

Pachysoma luzoniense Peters, 1861, Mber. K. Preuss Akad. Wiss. p. 708.

Cynopterus marginatus var. *philippensis* Grey, 1870, Cat. Monkeys and Fruit-eating Bats in the Collections of the British Museum p. 123.

Cynopterus marginatus var. *cumingii* Grey, 1870, Cat. Monkeys and Fruit-eating Bats in the Collections of the British Museum p. 123.

Types

Syntypes: two adult females, 'alcoholic', both with skull *in situ,* Berlin Museum, nos. 2425 and 2426 (Andersen 1912: 620).

Type Locality

Volkan Yriga, S. Camarines, Luzon, Philippines.

Diagnoses

Cynopterus luzoniensis differs from *C. nusatenggara* in having all wing measurements, averaging slightly longer (Table 1): DIG 1 longer relative to DIG 3 (Figure 10); DIG 1 generally longer relative to ZB (Figure 7); DIG 3 generally longer relative to BW (Figure 8). White or light coloured edge to margin of ear present; pelage on head not markedly darker than that of back; dorsum Light Drab (cinnamon fawn) to Hair Brown (grey brown) rather than darker Olive Brown; surface of metacarpals and phalanges markedly lighter and contrasting with colour of wing membrane; P^4 lingual and labial cusp commissure slopes slightly posteriorly and P^4 lingual and labial cusps connected by low ridge or distinct commissure.

It differs from *C. sphinx* in averaging smaller in most measurements (except P^3L, P^3W, M^1L and DIG1 in females and LIW in males (Table 1): e.g., ♀♀-28.6 (27.3-30.5) *v.* 30.3 (28.1-32.9), C_1-M_2 10.2 (9.4-11.2) *v.* 11.0 (9.9-13.1), RAD 61.4 (57.2-68.9) *v.* 65.7 (58.1-75.8); ♂♂-GSL 28.6 (27.2-30.0) *v.* 30.4 (28.7-33.7); C_1-M_2 10.4 (9.7-11.1) *v.* 11.1 (10.1-12.8), RAD 60.9 (56.0-65.9) *v.* 65.1 (59.2-75.0); ZB generally narrower relative to ONL (Figure 6); BW narrower relative to M^1W (Figure 4); GSL generally shorter relative to DIG 1 (Figure 5). P4 posterolabial corner generally much more square.

It differs from *C. brachyotis* in that it has on average longer metacarpals I to IV (Table 1): e.g. ♀♀-DIG 3 42.0 (38.8-45.3) *v.* 41.0 (37.1-45.0); ♂♂-DIG 3 42.2 (40.5-44.0) *v.* 40.7 (39.2-42.6); DIG 1 longer relative to both DIG 1 and BW (Figures

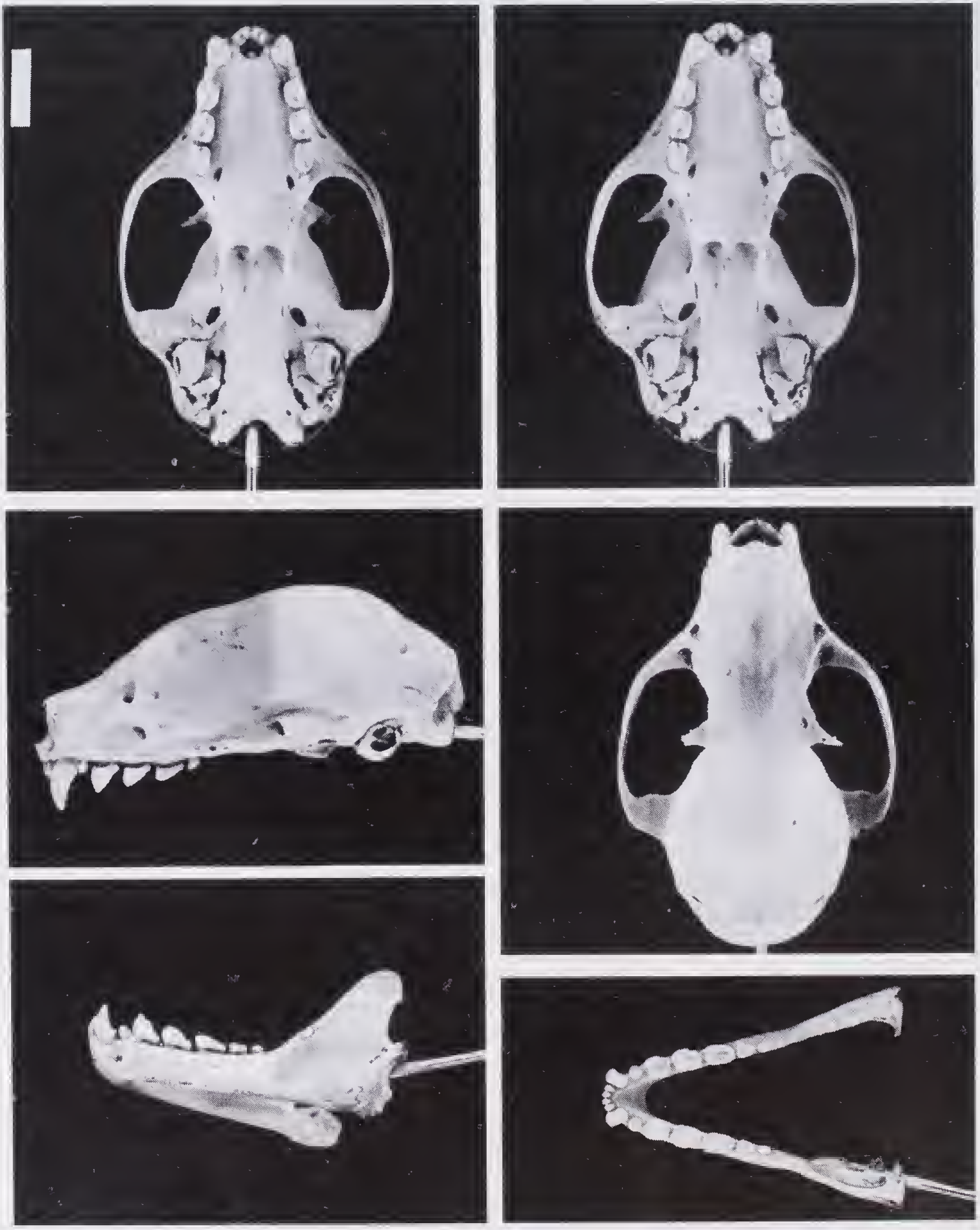


Figure 22 Skull, dentary and dentition of *Cynopterus luzoniensis*, WAM M25475 from N. Sulawesi. Ventral view as stereopairs. Scale line 5 mm.

Figure 23 Localities of *Cynopterus luzoniensis* examined in this study.

10 and 11, respectively); P4 posterolabial corner generally much more square; pelage on dorsum Drab (cinnamon fawn) to Hair Brown (grey brown).

It differs from *C. minutus* in averaging larger in all measurements except ZB, BW and C^1-C^1 in females and ZB in males (Table 1): e.g. ♀♀-GSL 28.1 (26.0-29.9) *v.* 26.6 (25.4-27.6), C_1-M_2 9.9 (9.3-10.6) *v.* 9.6 (9.0-10.2), RAD 59.9 (55.1-64.8) *v.* 57.5 (54.2-61.9) and ♂♂-GSL 28.3 (27.2-29.7) *v.* 27.2 (26.2-28.3), C_1-M_2 10.1 (9.3-10.6) *v.* 9.8 (9.4-10.2), RAD 59.3 (54.7-61.9) *v.* 57.3 (52.9-60.9); ONL longer relative to ZB and M^1W (Figures 6 and 9, respectively); P4 posterolabial corner generally much more square.

Description

The description is generally as for *C. nusatenggara* except for the following:

Skull, dentary and dentition (Figure 22)

Median frontal sulcus of skull tends to be more deeply concave in adults compared to adults of *C. nusatenggara* with similar tooth wear; external auditory meatus tends to be more oval in lateral view and lambdoidal ridge immediately posterior to bulla generally with a more pronounced curve than in *C. nusatenggara;* P^3 basal area more variable, ranges from slightly less, or subequal rather than slightly larger than that of C^1; P^3 labial and lingual cusps connected by low commissure that slopes noticeably backward particularly in Sulawesi specimens, rather than at right angles to long-axis of tooth row as in *C. nusatenggara*; occasionally M^2 present (e.g. WAM M25475 in right dentary) which is subequal in occlusal area to P^1; P^4 with obvious low commissure joining labial and lingual cusps in specimens from Sulawesi; commissure present in Philippine specimens but generally less prominent (sometimes obscure in worn teeth).

Externals and palatal ridges

Moderate sized *Cynopterus.* External measurements presented in Table 1. Overall shape of external and palatal ridges as described for *C. nusatenggara.*

Pelage and skin colour

Generally overall pelage a greyish olive colour with less contrasting pelage colours than in the other *Cynopterus* spp. considered.

Adult males have a collar of lighter coloured Warm Buff (cream yellow) to Yellow Ochre (orange yellow) fur around throat and extending to chin, chest and side of neck, barely perceptible at nape of neck, ventrally usually colours chest and extends along sides of abdomen flanking the Grayish Olive venter. Head and back Light Grayish Olive to Grayish Olive frequently tipped with Drab; rump and legs Drab (cinnamon fawn). Plagiopatagium ventral surface adjacent to body and forearms thinly furred with Chamois (yellow tan) to Grayish Olive; uropatagium ventral and dorsal surface generally lightly furred with Drab but thicker at middle margins; radius proximal one-third lightly furred on dorsal surface with same colour as on rump; ear naked apart from base. Skin of ears, lips, feet and patagia Benzo Brown (deep lilac-brown); ear margin Pale Olive Buff contrasting with darker remainder of ear — in Sulawesi specimens both internal and external margins of ear lightly coloured, whereas in the Philippines specimens lighter margins usually on internal side of ear. Surfaces of metacarpals and phalanges lighter, generally Olive Buff contrasting with colour of patagia.

Adult females generally lighter coloured than adult males, although the pattern of colour similar. Neck collar much less distinct and paler, ranges from Deep Olive Buff to Chamois — its colour generally restricted ventrally to chin, throat and top of chest, infrequently as a contrasting flanking colour to grey of abdomen but generally its colour tips abdominal fur. Other colours as for adult males.

Baculum

Shape of baculum variable (Figure 14). Maximum length and maximum breadth (in mm) of baculum is:

	Length (N = 3)	Breadth (N = 3)
Sulawesi	1.64 ± 0.47	1.58 ± 0.43
Philippines	1.63 ± 0.52	1.38 ± 0.46

Distribution

The locality of specimens examined are shown in Figure 23. They are from Sulawesi and Negros I., Philippines. *C. luzoniensis* is also from Luzon Island (type locality) and Taylor (1934) lists it (as *C. b. brachyotis*) from Mindanao, Polillo and Palawan Is. Heideman and Heaney (1989) also report it from Leyte I. and Heaney (pers. comm.) from Dinagat, Biliran and Maripipi Is (as *C. brachyotis*).

Results and Discussion

Sexual Dimorphism

The two factor MANOVA resulted in significant ($P < 0.05$) sexual dimorphism, with males generally larger than females, for 14 of the 19 skull characters, with most significant at $P < .01$; those not significant were MFL, POW, BW, CPL and M^1W.

Only one of the 8 external characters (DIG 3P, $P = 0.031$) was sexually dimorphic.

There was a significant interaction between sex and species in only one character (M^1L, $P = 0.01$).

Because of the broad extent of sexual dimorphism in the skull and dental characters, the sexes are treated separately in the following analyses.

Discriminant function analysis

Females

The cumulative variation explained by the first three canonical variate functions is 98.3%, with functions 1, 2 and 3 explaining 52.4, 26.3 and 19.6% respectively.

The overall percentage of cases correctly classified to their species group was 93.0%. All *C. nusatenggara* were correctly classified as were 94% of *C. minutus*, 93% of *C. luzoniensis*, 90% of *C. brachyotis* and 90% of *C. sphinx*. Species groups into which individuals were misclassified can be gainsayed from Figures 24 and 25.

For females, CVI best separates *C. minutus* from *C. sphinx*, and both these species from the other species considered (Figures 24 and 25). Characters most influencing this function (GSL, PL, RAD, DIG 1, DIG 3, DIG 5) relate to overall length of skull and of radius and metacarpals and relate to the relatively overall smaller size of *C. minutus* and larger size of *C. sphinx* (Table 1).

Of the remaining three species, *C. brachyotis* separated from both *C. luzoniensis* and *C. nusatenggara* on both CV2 and CV3 (Figures 24 and 25). Characters most influencing these functions (BW, ONL, P^4-P^4, C_1-M_2, M^1-M^1, RAD, DIG 1 and DIG 3) relate to braincase width, shape of rostrum, distances between and along toothrows and shape of

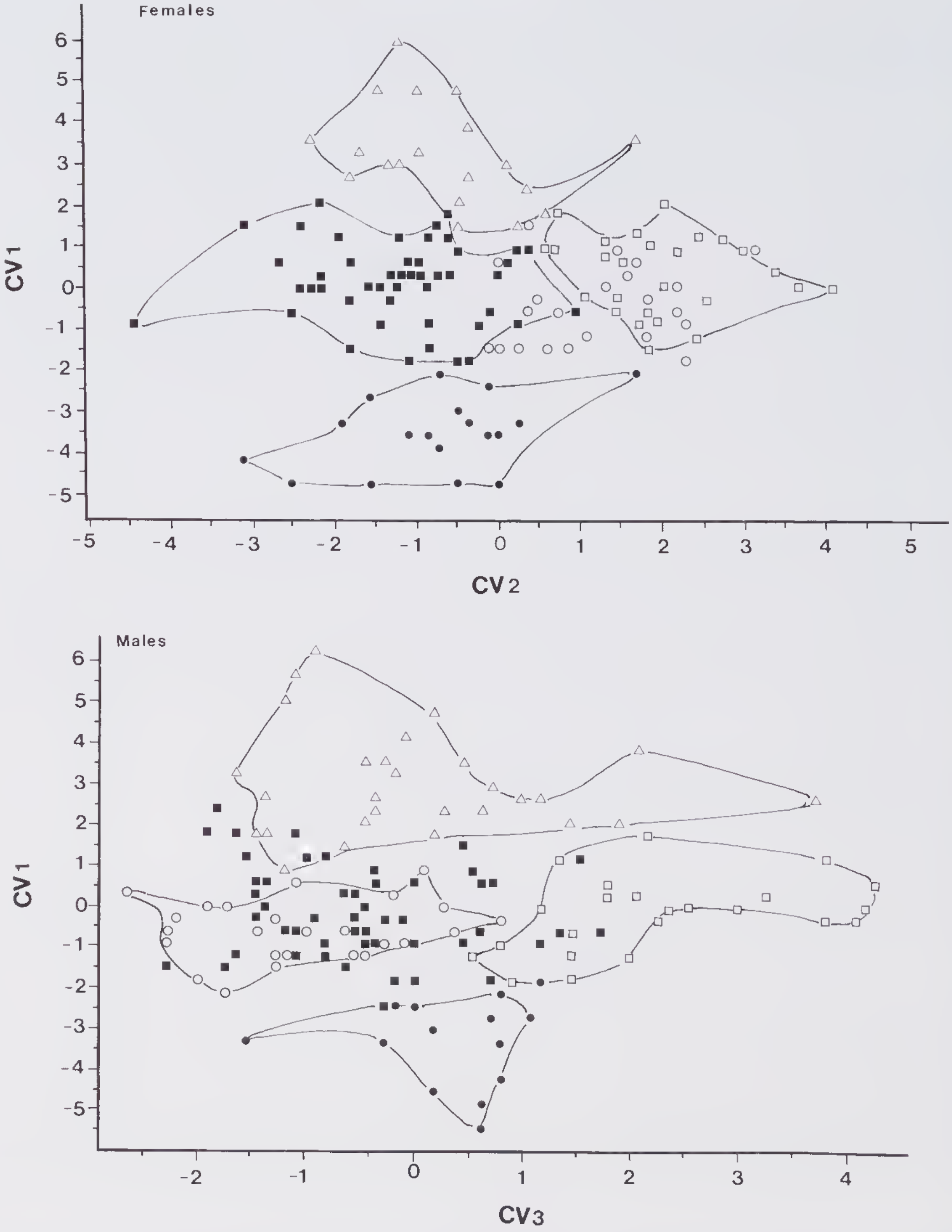


Figure 24 Plot of CV1 and CV2 for males and females of five species of *Cynopterus*; performed on all skull and external characters considered. O, *C. nusatenggara;* △, *C. sphinx;* ■, *C. brachyotis;* ●, *C. minutus* and □, *C. luzoniensis.*

wing. *C. luzoniensis* and *C. nusatenggara* are separated on CV3. Characters most influencing this function (ONL, P^4-P^4, M^1-M^1, C^1-M^2, DIG 1 and DIG 3) emphasise shape of rostrum, distances between and along toothrows and length of terminal wing digits.

Males

The cumulative variation explained by the first three canonical variate functions is 96.1%, with functions 1, 2, and 3 explaining 47.7, 30.3 and 18.2%, respectively.

The overall percentage of cases correctly classified to their species group was slightly less (89.4%) than for the females. All *C. nusatenggara* and *C. minutus* were correctly classified, as were 93.0% of *C. sphinx,* 87.5% of *C. luzoniensis* and 80.3% of *C. brachyotis.* Species groups into which individuals were misclassified can be gainsayed from Figures 24 and 25.

As was the situation with females, males of *C. minutus* and *C. sphinx* are best separated by CV1. Characters most influencing this function (GSL and CDL) again relate to overall length of skull but unlike the situation with females, external characters did not contribute heavily to this factor (Table 2). Of the remaining three species, *C. brachyotis* is separated from both *C. nusatenggara* and *C. luzoniensis* on CV2. Characters most influencing this factor are the length of the rostrum (ONL) and M^1 length. *C. nusatenggara* and *C. luzoniensis* are separated most on CV3. Characters most influencing this factor (GSL, PL, C^1-M^2, M^1-M^1, M^1W, DIG 3 and TIB) relate to overall length of skull, length of toothrow, breadth between outside surfaces of M^1, length of digit 3 metacarpal and tibia length.

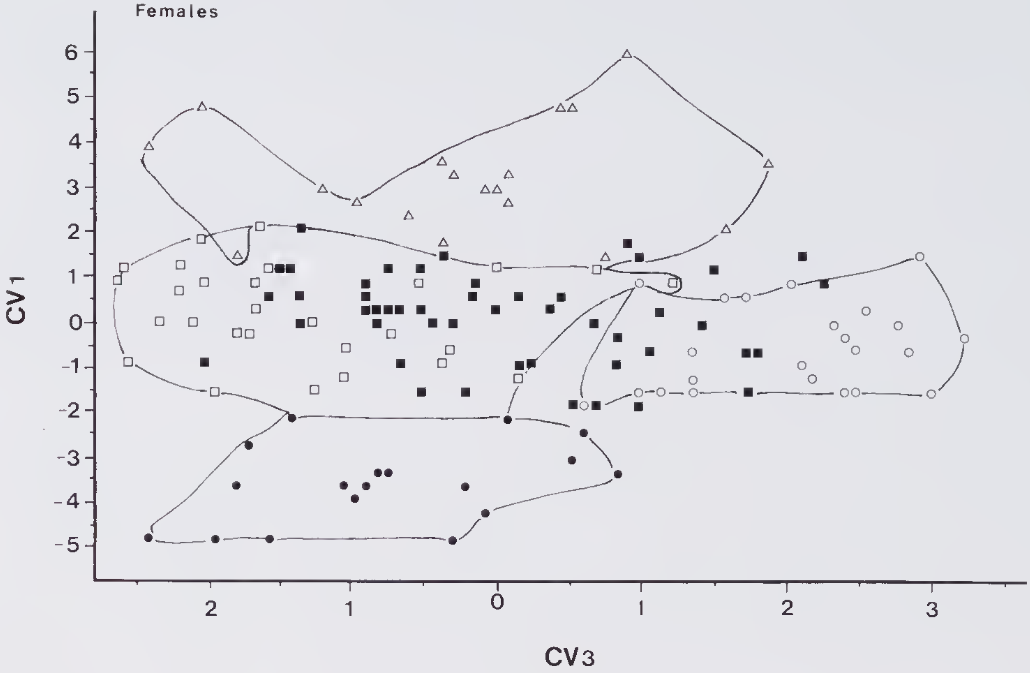
Slightly different characters are important in females and males in discriminating between these species of *Cynopterus.*

Bivariate plots

All characters in the stepwise discriminant function analysis were significant at $P < 0.001$. The first ten of these characters (all with a Wilks Lambda for entry >0.08) were as follows: GSL, DIG 1, ZB, BW, M^1W, C^1-M^2, ONL, M^1L, POW, and M^1-M^1. These characters were all important discriminants in the canonical variate analysis and weighed heavily in one or more functions (Table 2). Additionally DIG 3, P^4-P^4 and M^1-M^1 also had high (>0.5) standardised discriminant functions (Table 2). Combinations of bivariate plots were examined among all the 13 characters mentioned above for their ability to discriminate between the five recognised *Cynopterus* spp.

Taxonomy

We have not attempted in this study to examine intraspecific variation in the five species of *Cynopterus* considered, but it is apparent that regional variation does occur within the species. For example, while there is considerable overlap in the canonical plots of *C. luzoniensis* from the Philippines and Sulawesi regions, specimens from these two regions cluster somewhat separately. A similar situation occurs within *C. brachyotis,* where specimens from Java, Sumatra, Bali and associated islands cluster somewhat separately from those of Borneo and Singapore. In *C. sphinx* the specimen from Pagai I. is removed from its species cluster — although it is associated with that cluster; the



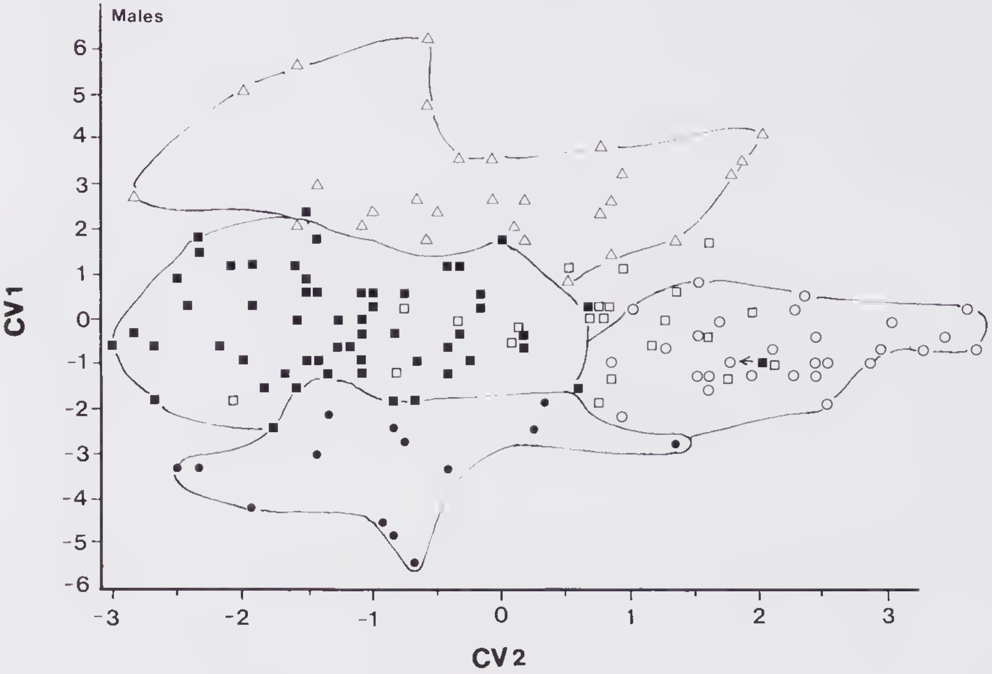


Figure 25 Plot of CV1 and CV3 for males and females of five species of *Cynopterus*; performed on all skull and external characters considered. Species code as for Figure 24.

Table 2 Standardised and unstandaradised (in brackets) canonical variates based on skull measurements of adult *Cynopterus nusatenggara, C. sphinx, C. brachyotis, C. minutus* and *C. luzoniensis.* Canonical scores are calculated as the summation of the products of the unstandardised canonical variates and the respective length measurements plus the constant. For explanation of character codes see Figure 1 caption (a) females, (b) males.

Table 2a

	FUNCTION 1	FUNCTION 2	FUNCTION 3
GSL	0.5164 (0.6031)	0.2154 (0.2516)	0.2252 (0.2630)
PL	0.4962 (0.9529)	—0.1151 (—0.2210)	—0.2219 (—0.4261)
MFW	0.1300 (0.5563)	0.1435 (0.6141)	—0.1442 (—0.6171)
ONL	—0.3384 (—0.8674)	0.1270 (0.3254)	0.8908 (2.2831)
LIW	0.0606 (0.1823)	0.2498 (0.7513)	—0.0661 (—0.1989)
POW	0.3043 (0.6575)	0.1143 (0.2470)	—0.1924 (—0.4158)
ZB	—0.3633 (—0.5060)	—0.1880 (—0.2618)	—0.3731 (—0.5197)
BW	—0.0730 (—0.1965)	—0.5183 (—1.3951)	0.1324 (0.3565)
CPL	0.3605 (0.3377)	—0.0427 (—0.0400)	0.0396 (0.0371)
C^1C^1	—0.2295 (—0.8258)	—0.1043 (—0.3751)	—0.3141 (—1.1295)
P^4P^4	—0.0355 (—0.0988)	0.5340 (1.4867)	—0.5365 (—1.4938)
M^1M^1	—0.1273 (—0.3422)	—0.3899 (—1.0484)	1.0936 (2.9410)
C_1M_2	0.3159 (0.8466)	—0.4545 (—1.2180)	—0.7701 (—2.0636)
P^3L	0.1194 (0.8855)	—0.2207 (—1.6371)	0.1067 (0.7917)
M^1L	0.1221 (1.0386)	0.1861 (1.5831)	0.3141 (2.6721)
M^1W	0.1679 (1.6203)	0.3583 (3.4587)	0.0795 (0.7673)
RAD	0.4285 (0.1469)	—0.5939 (—0.2036)	0.1576 (0.0540)
DIG 1	0.4137 (0.3583)	0.8331 (0.7216)	—0.5058 (—0.4380)
DIG 2	0.1844 (0.1129)	—0.2622 (—0.1606)	0.3739 (0.2289)
DIG 3	—0.6408 (—0.3177)	0.3318 (0.1645)	—0.7156 (0.3548)
DIG 3P	0.0949 (0.0696)	0.1434 (0.1052)	—0.4033 (—0.2960)
DIG 5	—0.5347 (—0.2568)	0.2611 (0.1254)	0.3876 (0.1862)
TIB	0.3011 (0.2136)	—0.1024 (—0.0726)	0.4449 (0.3157)
Constant	-36.7194	4.8222	8.5493
% Variation explained	52.38	26.27	19.61

specimens from central India also group at the edge of their species cluster. In all these situations, except *C. sphinx* from India, the canonical variate separation is on CV2, perhaps suggesting shape differences and not size are involved in these intraspecific variations. With Indian *C. sphinx*, the separation is on CV1, suggesting that they vary in being larger rather than in having a different shape.

Baculum size and shape is variable within the *Cynopterus* spp. considered without clear diagnostic differences apparent between species. In most species baculum shapes may be found which are not too dissimilar to those in other species — although generally *C. nusatenggara*, for example, has bacula with less serrated outlines than does *C. sphinx.*

This study was principally to diagnose *C. nusatenggara* against species of *Cynopterus* with which it could be confused. It has highlighted to us the need for different taxonomic characters and tools to be applied to resolve the complex taxonomy of South East Asian

Table 2b

	FUNCTION 1	FUNCTION 2	FUNCTION 3
GSL	−0.5582 (−0.7175)	0.0387 (0.0498)	−0.8885 (−1.1420)
CDL	0.8144 (1.1567)	−0.2751 (−0.3908)	0.2659 (0.3776)
PL	0.2188 (0.4113)	−0.0041 (−0.0078)	0.6101 (1.1472)
MFW	−0.1827 (−0.8238)	0.2387 (1.0764)	0.1024 (0.4617)
ONL	0.2816 (0.7543)	0.6562 (1.7580)	−0.3167 (−0.8487)
LIW	−0.0658 (−0.1741)	0.2269 (0.6006)	0.3990 (1.0563)
ZB	−0.2814 (−0.4690)	−0.4501 (−0.7503)	−0.0629 (−0.1049)
BW	0.4234 (1.1886)	−0.1203 (−0.3376)	−0.1040 (−0.2920)
CPL	0.0438 (0.0418)	−0.0850 (−0.0812)	−0.4017 (−0.3839)
C^1C^1	0.0688 (0.1978)	0.2201 (0.6323)	0.3809 (1.0944)
M^1M^1	0.1479 (0.5019)	0.0055 (0.0187)	−0.5494 (−1.8651)
C^1M^1	−0.1099 (−0.3304)	−0.4763 (−1.4321)	−0.3740 (−1.1246)
C_1M_2	0.0274 (0.0700)	−0.3515 (−0.8962)	0.7139 (1.8201)
P^3L	0.1960 (1.7133)	−0.1992 (−1.7414)	−0.0962 (−0.8407)
P^3W	0.1253 (1.4291)	0.3292 (3.7554)	−0.0942 (−1.0747)
M^1L	0.0801 (0.6320)	0.7407 (5.8415)	−0.3537 (−2.7892)
M^1W	0.0816 (0.9837)	−0.0460 (−0.5551)	0.5379 (6.4883)
DIG 1	0.2758 (0.2352)	0.3121 (0.2662)	0.4672 (0.3984)
DIG 2	−0.3189 (−0.2251)	−0.0097 (−0.0069)	−0.1504 (−0.1062)
DIG 3	0.1235 (0.0752)	−0.1582 (−0.0964)	0.7042 (0.4290)
DIG 3P	−0.1049 (−0.0715)	−0.0834 (−0.0568)	−0.0337 (−0.0230)
DIG 5	0.1860 (0.1165)	−0.0953 (−0.0597)	0.1632 (0.1022)
TIB	0.1057 (0.0759)	0.2083 (0.1495)	−0.6933 (−0.4975)
Constant	−41.0646	14.3015	3.8983
% variation explained	47.67	30.26	18.21

Cynopterus spp. In particular, further clarification of some problems exposed in this paper may have to wait upon comprehensive genetic studies, because the basic morphology of the *Cynopterus* skull and externals is not very variable. Dr Lincoln Schmitt, University of Western Australia, has begun an electrophoretic study of some species examined in this study. These results indicate that genetic variation between island populations of *C. nusatenggara* is not very variable. However *C. nusatenggara* differs from *C. brachyotis* from West Java, in having 3 genes distinct out of the 35 enzyme systems examined (L. Schmitt pers. comm.).

There is a natural tendency among taxonomists who examine morphological variation among closely related forms in island archipelagos, to name as species only those forms that exist together on the same island in reasonably close sympatry. Other variations may be considered subspecific. Although the form which is the basis of this paper (*nusatenggara*) is not sympatric with morphologically close forms of *Cynopterus* found elsewhere in the Malay Archipelago (e.g. *brachyotis, luzoniensis, minutus*) we consider it a species for several reasons. Firstly, it is the most easily recognisable of these taxa, both in its pelage and dental morphology. It is for example, more distinct than are *C. brachyotis* and *C. sphinx* or *C. brachyotis* and *C. minutus*. Secondly, *C. nusatenggara* is found throughout many of the islands of Nusa Tenggara, but does not appear to cross the strait of Lombok and occur on Bali (where *C. brachyotis* is found). Other similar water gaps between islands in Nusa Tenggara do not appear to have been substantial barriers to the distribution of *C. nusatenggara* or to other species of bats in this region (Kitchener *et al.* 1989). There is, for example, little genetic differentiation between *C. titthaecheilus* from W. Java and Lombok islands and between *C. horsfieldi* from Lombok and Sumbawa islands (L. Schmitt pers. comm.). These data tend to indicate that water gaps such as those found between Lombok and Bali islands do not pose significant barriers to gene flow in other closely related *Cynopterus* spp. It may be assumed, then, that potential gene flow occurs between *C. brachyotis* on Bali I. and *C. nusatenggara* on Lombok I. Despite this, both forms appear morphologically distinct on these two islands.

Acknowledgements

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Mrs N. Cooper, Western Australian Museum, carried out all the statistical analyses as well as photographing the skulls; we are indebted to her for this work.

Additionally we thank the Directors of our respective Museums, Mr J. Bannister (WAM) and Drs M. Amir, and Dr S. Kadarsan (MZB) for their support of the field programme.

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Postscript

After acceptance of this paper, Dr Lincoln Schmitt, University of Western Australia, completed his electrophoretic appraisal of *Cynopterus* species, including *C. brachyotis* (W. Java, Borneo); *C. nusatenggara* (including Lombok, Sumbawa, Moyo); *C. luzoniensis* (S.W. Sulawesi); *C. titthaecheilus* (Lombok, W. Java); *C. terminus* (S.W. Timor); *C. horsfieldi* (Lombok, Sumbawa). While this information will be published separately, an analysis of genetic similarity of these species, based on an investigation of some 35 enzyme systems, concluded, among other things, that the genetic distance between *C. nusatenggara,* and both *C. brachyotis* and *C. luzoniensis* are of a similar order to genetic distances of the other recognised species of *Cynopterus* he studied. The species that is closest genetically to *C. nusatenggara* appears to be both the Javan and Lombok populations of *C. titthaecheilus.*

Appendix I: Specimens examined

Cynopterus nusatenggara sp. nov. (all paratypes)

(i) *Adults, complete data set*

Area 82: Komodo I., 3♀, 5♂ MZB 9385-8, MZB 14716, MZB 9379-80, MZB 9382; Area 85: Pelangan, Lombok, 1♀, 2♂ WAM (M33631, M33633-4); Area 86: Desa Kuta, Lombok, 2♀, 1♂ WAM (M33630, M33635-6); Area 87: Suranadi, Lombok, 2♀, 1♂ WAM (M3073-4, M33637); Area 89: Desa Belo, Jereweh, Sumbawa, 1♀, 2♂ WAM (M31326, M31328, M31330); Area 90: Merenti, Sumbawa, 3♀, 1♂ WAM (M31157, M31159, M31170, M31217); Area 91: Batu Dulang, Sumbawa, 5♀, 5♂ WAM (M31744, M31746-9, M31759-60, M31763-4, M31766); Area 92 Moyo I. (Sebatok and Brang Kua), 3♀, 5♂ WAM (M31899, M31908, M31916-7, M31920, M31925, M31928, M31934); Area 93: Dahu, C. Sumbawa, 2♀, 4♂ WAM (M31692, M31695, M31700, M31716, M31719, M31721); Area 94: Waworada, E. Sumbawa, 3♂ WAM (M31644, M31646, M31654); Area 95: Sangeang I., Sumbawa, 1♀ WAM M31593; Area 96: Batu Tering, Sumbawa, 1♀, 2♂ WAM (M31469-70, M31478); Area 97: Teluk Santong, Sumbawa, 1♀, 2♂ WAM (M31329, M31385, M31408).

(ii) *Subadults (SA); juveniles (J); damaged adults, incomplete data sets (D)*

Area 82: Komodo, 1♀, 1♂ MZB 938 (D), MZB 9284 (D); Area 85: Pelangan, Lombok, 1♀ WAM M33582 (J); Area 86: Desa Kuta, Lombok, 1♀, 3♂ WAM M33583 (D), WAM M33632 (D), WAM M33537 (J), WAM M31079 (J); Area 87: Suranadi, Lombok, 1♀ WAM M30705 (D); Area 88: Batu Koq, Lombok, ♀ WAM M33580 (J); Area 91: Batu Dulang, Sumbawa, 1♂ WAM M31825 (J); Area 92: Moyo I., (Sebatok & Brang Kua) nr Sumbawa, 1♀, 2♂ WAM M3187-8 (D), WAM M31923 (SA); Area 93: Dahu, C. Sumbawa, 1♂ WAM M31696 (D); Area 94: Waworada, E. Sumbawa, 1♂ WAM M31667 (D); Area 95: Sangeang I., nr Sumbawa, 1♀ WAM M31583 (D); Area 96: Batu Tering, Sumbawa, 1♀ WAM M31517 (SA); Area 97: Teluk Santong, Sumbawa, 2♀ WAM M31415 (D), WAM M31407 (SA).

Cynopterus sphinx

(i) *Adults, complete data set*

Area (?) Aceh region, Sumatra, 2♀ MZB (13490, 13575); Area 19: Curup, Bengkulu, Sumatra, 1♀, 2♂ MZB (13266, 13273, 13299); Area 20: Lebang Selatan, Bengkulu, Sumatra, 1♂ MZB 13292; Area 26: Pasir Putih, Lampung, Sumatra, 1♂ MZB 9042; Area 46; Solie, Soppeng, S. Sulawesi, 1♂ MZB 13616; Area 49: Gunung Tangkoko, Pare, N. Sulawesi, 1♂ MZB 12670; Area 58: Jampen (?), Salayar, S. Sulawesi, 2♂ MZB (14091, 14093); Area 68: Bogor, W. Jawa, 1♀ MZB 8859; Area 71: Pelabuhan Ratu, W. Jawa, 2♀ MZB (10706, 10715); Area 80: W. Bali (Panjar, Kuta, Klampok), 1♀ MZB 11361; Area 81: Central Bali, 1♀, 1♂ WAM (M16164, M16165); Area 95: Sangeang I., nr E. Sumbawa, 1♀, 7♂ WAM (M31580, M31582, M31584-5, M31587, M31589, M31592 M31594); Area 103: Kinibalu, Sabah, 1♂ WAM M23771; Area 114: Baluran, E. Jawa, 1♀, 1♂ MZB 11131, MZB 11130; Area 118: Krakatau (Sertung, Anak and Rakata Is), 3♀, 4♂ WAM (M26356, M26358, M26360, M26365, M26368, M26377, M26555); Area 119: Nagpur, India, 1♀, 1♂ WAM M29363-4; Area 121: Pagai I., nr W. Sumatra, 1♂ AMNH 103314; Area 123: Bangkok, Thailand; 4♀, 4♂ WAM (M23780-1, M23783-4, M23786, M23791, M23793, M23795).

(ii) *Subadults (SA); Juveniles (J); damaged adults, incomplete data sets (D)*

Area 4: Asahan, N. Sumatra, 1 MZB 13623 (SA); Area 5: Bohorok, N. Sumatra, 1♂ MZB 13035 (SA); Area 8: Kayutanam, W. Sumatra, 1♂; MZB 13180; Area 20: Lebang Selatan, Bengkulu, Sumatra, 1♀ MZB 13269 (D); Area 23: Blimbing, Lampung, Sumatra, 1 ♀ MZB 13597 (D); Area 24: Pulau Panggung, Lampung, Sumatra, 1♀ MZB 11262 (SA); Area 25: Wai Kambas, Lampung, Sumatra, 1♀ MZB 8976 (SA); Area 26: Pasir Putih, Lampung, Sumatra, 1♀ MZB 8978 (SA); Area 27: Pringsewu, Lampung, Sumatra, 1♀, 1♂ MZB 10986 (D), MZB 10999 (D); Area 33: Kotim, C. Kalimantan, 1♂ MZB 13941 (D); Area 46: Solie, Soppeng, S. Sulawesi, 1♀, 1♂ MZB [13650 (SA), 13652 (J)]; Area 69: Banten, W. Jawa, 1♂ MZB 9141 (D); Area 80: W. Bali (Panjar, Kuta, Klampok) 1♀, 2♂ MZB [9173 (D), 11362-3 (J, J); Area 95: Sangeang I., nr Sumbawa 1♀ WAM M31586 (D); Area 98: Sipora I., nr W. Sumatra, 1♀ ZRC 45901 (D); Area 100: Siberut

I., nr W. Sumatra, 1♀ ZRC 45900 (J); Area 114: Baluran, E. Jawa, 3♂ MZB [9844 (D), 1129 (D), 13922 (D)]; Area 118: Krakatau (Sertung, Anak, Rakata) 2♀, 2♂ WAM M23313 (SA), WAM M26350 (D), WAM M26376 (SA), WAM M26386 (SA); Area 119: India, 1♀ WAM M29362 (D); Area 121: Pagai I., W. Sumatra 2♀, 1♂ AMNH (?) (103213-4 (D), 103211 (D); Area 123: Bangkok, Thailand, 1♂ WAM M23787 (D).

Cynopterus brachyotis

(i) *Adults, complete data set*

Area 1: Aceh (Mt Leuser, Ketambe and Kutacane), 2 ♂ MZB (12983, 13135); Area 4: Asahan, N. Sumatra, 1 ♂ MZB 13624; Area 7: Bukit Tinggi, W. Sumatra, 1 ♀, 2 ♂ MZB (9149, 9757-8); Area 11: Kuto Tuo, Riau, Sumatra, 2 ♀, 2 ♂ MZB (11845-6, 11848, 11853); Area 12: Kampai, Riau, Sumatra, 1 ♂ MZB 11885; Area 13: Siak, Riau, Sumatra, 2 ♂ MZB (11838, 13843); Area 15: Palembang, S. Sumatra, 1 ♂ MZB 12763; Area 16: Kayu Agung, S. Sumatra, 2 ♂ MZB (12762, 12765); Area 18: Sitiung, W. Sumatra 3 ♀, 3 ♂ MZB (11756, 11767-8, 11778, 11785, 11795); Area 19: Bengkulu, Sumatra (Muara Aman and Curup), 2 ♀, 1 ♂ MZB (13272, 13274, 13289); Area 20: Lebang Selatan, Bengkulu, Sumatra, 1 ♀, 2 ♂ MZB (13267, 13276-7); Area 21: (Palas, Wai Sekampung, Sukadana) C. Lampung, Sumatra, 5 ♀, 2 ♂ MZB (10756, 10806, 10810, 10813-14, 10851, 10860); Area 23: Blimbing, Lampung, Sumatra, 1 ♂ MZB 13596; Area 27: (Pringsewu and Natar) Lampung, Sumatra, 1 ♂ MZB 11001; Area 29: Pulau Laut (Kota Baru and Stagen), 1 ♀ MZB 14006; Area 31: Telang, S. Kalimantan, 1 ♀, MZB 11674; Area (?): Hantakan, S. Kalimantan, 1 ♀, 3 ♂ MZB (11665, 11669, 11673, 11679); Area 33: Kotim, C. Kalimantan, 2 ♀, 2 ♂ MZB (13951, 13954-5, 13968); Area 34: Kuala Kapuas, C. Kalimantan, 1 ♀, 1 ♂ MZB (12753-4); Area 37: Longnawan, E. Kalimantan, 2 ♀, 1 ♂ MZB (13634, 13636-7); Area 38: Long Iram, E. Kalimantan, 1 ♀, 1 ♂ MZB (13531-2); Area ?: Punyit, E. Kalimantan, 2 ♂ MZB (13836, 13839); Area 59: Kudus, C. Jawa, 1 ♂ MZB 9066; Area 60: Yogya, C. Jawa 1 ♀ MZB 9175; Area 61: Batu Raden, C. Jawa, 1 ♀ MZB 9114; Area 63: Sumenep, Madura I., nr E. Jawa, 1 ♀ MZB 9189; Area 64: Kangean I., 1 ♀, MZB 13120; Area 66: Ciomas, W. Jawa, 1 ♂ MZB 9120; Area 67: Ujung Kulon, W. Jawa, 1 ♂ MZB 9159; Area 69: Banten, W. Jawa, 3 ♀ MZB (9187, 12777, 11413); Area 70: Sukabumi, W. Jawa, 1 ♀, 1 ♂ MZB (9889, 10532); Area 71: Pelabuhan Ratu, W. Jawa, 3 ♂ MZB (10725-6, 10735); Area 73: Garut, W. Jawa, 2 ♀, 2 ♂ MZB (11299, 12131-3); Area 74: Pandeglang, W. Jawa, 1 ♀ MZB 13098; Area 75: Gunung Salak, W. Jawa, 1 ♀, 1 ♂ MZB (14023-4); Area 80: W. Bali (Denpasar, Kuta and Klampok), 1 ♀ MZB 11364; Area 81: C. Bali 2 ♂ WAM (M16160, M16162); Area 84: Krawang, W. Jawa, 1 ♂ MZB 12972; Area 99: Kuala Lumpur, Malaysia, 1 ♀, 1 ♂ ZRC (45828-9); Area 103: Kinibalu, Sabah, 4 ♀, 1 ♂ WAM (M23772-4, M23776, M23779); Area 104: Teluk Bahang, Penang I., 1 ♀, 2 ♂ ZRC (45835-7); Area 105: Kedah Peak, Kedah, 2 ♀, 1 ♂ ZRC (45843, 45845, 45848); Area 106: Singapore I., 1 ♂ ZRC 45862; Area 110: Pulau Dua, Banten, W. Jawa, 1 ♂ MZB 9160; Area 111: Jepara, C. Jawa, 2 ♀ MZB (13981, 14072); Area 112: Bunyu I., E. Kalimantan, 2 ♀, 1 ♂ MZB (9391, 9396, 9399); Area 114: Baluran, E. Jawa, 1 ♀, 1 ♂ MZB (9047, 11121); Area 115: Barito Hulu, C. Kalimantan, 2 ♀, 2 ♂ MZB (9361, 9365, 9367, 9373); Area 120: Santubong, Sarawak, 1 ♀, 4 ♂ WAM (M23760, M23763, M23766-8).

(ii) *Subadults (SA); Juveniles (J); damaged adults, incomplete data sets (D)*

Area 1: Aceh (Mt Leuser, Ketambe and Kutacane) 2 ♀, 1 ♂ MZB [12997-8 (D, D), 12989 (SA)]; Area 6: Langkat, N. Sumatra, 1 ♀ MZB 13025 (D); Area 7: Bukit Tinggi, W. Sumatra, 1 ♀, 1 ♂ MZB [9755 (D), 9759 (D)]; Area 11: Kuto Tuo, Riau, Sumatra, 1 ♂ MZB 11854 (SA); Area 14: S.M. Barbak, Jambi, Sumatra 3 ♀, 3 ♂ MZB [12731 (SA) 12733 (SA) 12734-5 (D, D), 12738 (SA), 12739 (D)]; Area 17: Lahat, S. Sumatra, 1 ♂ MZB 12767 (D); Area 19: Bengkulu, Sumatra (Muara Aman and Curup), 1 ♀ MZB 13281 (D); Area 21: (Palas, Wai Sekampung, Sukadana) C. Lampung, Sumatra, 1 ♀, 1 ♂ MZB [10754 (SA), 10861 (J)]; Area 24: Kec. Panjang, Lampung, 1 ♂ MZB 11259 (SA); Area 25: Wai Kambas, Lampung, 1 ♂ MZB 9048 (D); Area 27: (Pringsewu and Natar) Lampung, Sumatra, 1 ♀ MZB 10974 (SA); Area 29: Pulau Laut (Kota Baru and Stagen), 3 ♂ MZB [14005 (D), 14008 (D), 14195 (D)]; Area 35: Kotim, C. Kalimantan, 1 ♀ MZB 9162 (D); Area 37: Longnawan, E. Kalimantan, 1 ♀ MZB 13926 (D); Area 60: Yogya, C. Jawa, 1 ♀ MZB 9168 (J); Area 64: Kangean I., nr E. Jawa, 1 ♀ BMNH 104613 (D); Area 65: Kalibaru, E. Jawa, 1 ♀ MZB 13915 (D); Area 67: Ujung Kulon, W. Jawa, 1 ♀ 1 ♂ MZB [9102 (D), 10938 (SA)]; Area 68: Bogor, W. Jawa, 2 ♀, 1 ♂;

MZB [9107 (D), 9128 (D), 9150 (D)]; Area 69: Banten, W. Jawa, 1 ♀, 1♂ MZB [11415 (SA), 12776 (D)]; Area 70: Sukabumi, W. Jawa, 2 ♀ MZB [9890 (D), 9893 (SA)]; Area 71: Pelabuhan Ratu, W. Jawa, 1 ♀, 1 ♂ MZB [10723 (J), 10724 (SA)]; Area 84: Krawang, W. Jawa, 1 ♀ MZB 12974 (SA); Area 102: Batu, Selangor, Malaysia, 1 ♀, 1 ♂ ZRC (45822-3); Area 105: Kedah Peak, Kedah, 1 ♀ ZRC 45847; Area 106: Singapore I., 1 ♀ ZRC 45869; Area 110: Pulau Dua, nr Banten, W. Jawa, 1 ♂ MZB [9065 (D)]; Area 112: Bunyu I., nr E. Kalimantan, 1 ♀ MZB 9400 (J); Area 113: Sri Lanka, 1 ♀ BMNH 665495 (D); Area 114: Baluran, E. Jawa, 1 ♀ MZB 13921 (SA); Area 115: Barito Hulu, C. Kalimantan, 1 ♀ MZB 9372 (D); Area 120: Santubong, Sarawak, 1 ♀ WAM M23761 (J); Area ?: Peunyit, E. Kalimantan, 1 ♂ MZB 13837 (SA); Area ?: Hantakan, S. Kalimantan, 1 ♀ MZB 11668.

Cynopterus minutus

(i) *Adults, complete data set*

Area 1: Kutacane, Aceh, Sumatra, 1 ♀, 1 ♂ MZB (13142, 12985); Area 9: Tapanuli Selatan, N. Sumatra, 1 ♀, 1 ♂ MZB (13802, 13804); Area 19: Muara Aman, Bengkulu, Sumatra, 1 ♀ MZB 13268; Area 20: Lebang Selatan, Bengkulu, Sumatra, 1 ♂ MZB 13270; Area 21: Sukadana, Lampung, Sumatra, 1 ♂ MZB 10857; Area 28: Ketapang, W. Kalimantan, 1 ♂ MZB 13808; Area 29: Kota Baru, Pulau Laut, 1 ♀ MZB 14194; Area 31: Telang, S. Kalimantan, 1 ♀, MZB 11700; Area 36: Kutai, Samarinda, E. Kalimantan, 1♀, 1 ♂ MZB 13689-90; Area 37: Long Nawam, E. Kalimantan, 1 ♀ MZB 13925; Area 38: Long Iram, E. Kalimantan, 1 ♀, 2 ♂ MZB (13539, 13541, 13549); Area 40: Kendari, C. Sulawesi, 2 ♀ MZB (12610, 12612); Area 42: Poso, C. Sulawesi, 1 ♂ MZB 14402; Area (?): Lamedai, S. Sulawesi, 1 ♀, 1 ♂ MZB (14151, 14155); Area 55: Malili, S. Sulawesi, 1 ♂, MZB 11605; Area 69: Banten, W. Jawa, 1 ♀ MZB 9138; Area 83: Nias I., nr N. Sumatra, 2 ♀, 1 ♂ MZB (13445-6, 13443); Area 115: Barito Hulu, C. Kalimantan, 4 ♀, 2 ♂ MZB (9363-4, 9366, 9369-70, 9375).

(ii) *Subadults (SA); Juveniles (J); damaged adults, incomplete data sets (D)*

Area 1: Kutacane, Aceh, Sumatra, 1 ♂ MZB 13140 (D); Area 2: Simpang Kanan, Aceh, Sumatra, 1 ♀ MZB 13801 (D); Area 9: Tapanuli Selatan, N. Sumatra, 1 ♀ MZB 13803 (D); Area 36: Kutai, Samarinda, E. Kalimantan, 1 ♂ MZB 13691 (D); Area 40: Kendari, C. Sulawesi, 1 ♂ MZB 14166 (D); Area 41: Kolaka, SE Sulawesi, 1 ♀ MZB 14164 (D); Area 42: Poso, C. Sulawesi, 1 ♀, 1 ♂ MZB (13695 (D); 13698 (D)); Area 52: Luwuk, C. Sulawesi, 1 ♀ MZB 13978 (J).

Cynopterus luzoniensis

(i) *Adults, complete data set*

Area 40: Kendari, C. Sulawesi, 2 ♀, 1 ♂ MZB (12599-600, 12611); Area 42: Poso. C. Sulawesi, 1 ♀, 3 ♂ MZB (13663, 13701, 13709, 13717); Area 46: Solie, Soppeng, S. Sulawesi, 1 ♀, 1 ♂ MZB (13618, 13649); Area 48: Tondano, N. Sulawesi, 1 ♂ MZB 12863; Area 49: (Bitung and Mt Tangkoko), N. Sulawesi, 2 ♂ MZB (12862, 12869); Area 50: Bolaang Mongandow, N. Sulawesi, 1 ♂ MZB 13743; Area 51: Maros, S. Sulawesi, 1 ♀, 1 ♂ MZB (13196, 14446); Area 52: Luwuk, C. Sulawesi, 3 ♀, 2 ♂ MZB (11884-5, 13972, 13987, 14447); Area 53: Timampu, S. Sulawesi, 1 ♀, 1 ♂ MZB (11609, 11611); Area 54: Buton, S. Sulawesi, 1 ♀ MZB (12601); Area 55: Malili, S. Sulawesi, 1 ♀, 1 ♂ MZB (11604, 11606); Area 56: Mamuju, S. Sulawesi, 2 ♀, 1 ♂ MZB (14098-100); Area 57: Mangkutana, Kolonedale, C. Sulawesi, 1 ♀, 1 ♂ MZB (14390, 14444); Area (?): Lamedai, S. Sulawesi, 3 ♀ MZB (14116, 14152, 14156); Area (?): Katamanta, C. Sulawesi, 1 ♀, 2 ♂ MZB (14383, 14401, 14404); Area (?): Bukit Palapi, C. Sulawesi, 2 ♂ MZB (13986, 13989); Area 101: Negros I. (Dumaquete), Philippines, 8 ♀, 4 ♂ WAM (M25845-8, M28931-8); Area 117: Gunung Dua Saudara, N. Sulawesi, 2 ♀ MZB (12665, 12667); Area 124: Kotamobagu, N. Sulawesi, 1 ♂, WAM M25475.

(ii) *Subadults (SA); Juveniles (J); damaged adults, incomplete data sets (D)*

Area 40: Kendari, C. Sulawesi, 1 ♂ MZB 12593 (D); Area 42: Poso, C. Sulawesi, 2 ♂ MZB [13776 (D), 13778 (D)]; Area 44: Toli-toli, C. Sulawesi, 1 ♂ MZB 14040 (D); Area 45: Kolonedale, C. Sulawesi 1 ♂ MZB 14394 (D); Area 52: Luwuk, C. Sulawesi, 2 ♀ MZB [13975 (SA), 13977 (J)]; Area 56: Mamuju, S. Sulawesi, 1 ♂ MZB 14101 (D); Area 58: Jampea, Salayar, S. Sulawesi, 1 ♂ MZB 14092 (D); Area (?): Lamedai, S. Sulawesi, 1 ♂ MZB 14160 (D); Area 122: Palawan I., 1 ♀ WAM M28693

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Revision of *Lerista aericeps* (Lacertilia: Scincidae) of central Australia

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Abstract

Lerista aericeps, L. xanthura and *L. taeniata* are redescribed.

Introduction

In 1986 I described *Lerista aericeps aericeps* and *L. aericeps taeniata,* the first from the eastern interior of the Northern Territory and south-west Queensland, the second from the western interior of the Northern Territory. Recently Greer (1990) concluded that *L. taeniata* was a full species and that *L. a. aericeps* was the same as *L. xanthura* of the far eastern interior of Western Australia. In order to check these conclusions and to redescribe *L. taeniata* (which has recently been found in Western Australia) I examined specimens in the South Australian Museum (catalogue numbers prefixed by SAM), Australian Museum (AM), Queensland Museum (QM), Northern Territory Museum (NTM) and Western Australian Museum (WAM).

Even if the apparent sympatry between *L. taeniata* and *L. aericeps* in South Australia were not confirmed, I would agree that these taxa differ in too many ways (including two additional characters discovered by Greer) to be conspecific. However I am not yet convinced that *L. aericeps* is the same as *L. xanthura.* More specimens are required of the latter; and the critical area that separates them (the far south of the Tanami Desert) needs exploring.

One of Greer's reasons for merging *L. aericeps* in *L. xanthura* was the breakdown of a character I used in separating them, i.e. number of preoculars. As Greer pointed out, the condition is variable in *L. aericeps.* At one extreme the upper preocular is as large as the lower and completely above it; at the other it is much smaller and located more caudal, wholly or partly within the orbital depression, and thus scarcely to be construed as a preocular at all. I have avoided the difficulty of defining preoculars by reverting to my earlier practice of only counting the scales behind the loreals and immediately above the labials, and calling the lower preocular a presubocular.

Systematics

Lerista aericeps Storr

Lerista aericeps aericeps Storr (1986: 145).

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Diagnosis

A small slender *Lerista* with 4 fingers, 4 toes and immovable eyelid (a spectacle), distinguishable from *L. xanthura* by its darker coloration, stronger pattern (including dark loreo-temporal stripe and narrow bands on tail) and shorter appendages, and from *L. taeniata* by absence of dark upper lateral stripe and fewer midbody scale rows (mostly 18, *v.* mostly 20).

Description

Snout-vent length (mm): 24-52 (N 75, mean 42.3). Length of appendages etc. (% SVL): foreleg 8-14 (N 73, mean 10.2), hindleg 19-30 (N 72, mean 23.6), tail 104-133 (N 20, mean 122.4), snout to foreleg 24-34 (N 72, mean 28.3).

Nasals narrowly to very narrowly separated (N 22), just touching (22) or in very short to medium contact (20). Prefrontals widely separated. Frontoparietals in short to long contact (N 47), just touching (1) or very narrowly separated (4); a little larger or little smaller than interparietal. Nuchals 0-5 on each side (N 63, mean 2.8). Supraoculars 3, first two in contact with frontal. Supraciliaries 5, second and fifth smallest (N 56) or 4 (1). Loreals 2, second much the smaller (except in two of 53 specimens, where fused to first presubocular). Presuboculars 2, second much to very much the smaller. Upper labials 6. Midbody scale rows 18 (N 56) or 20 (3). Lamellae under longest toe 11-17 (N 57, mean 13.9), each with a fine keel.

Head and back pale to moderately dark reddish brown (dorsals edged with golden brown), tinged with olive or grey and marked with dark brown or blackish brown: stipples on head, 4 rows of dots on back (central pair extending to proximal quarter of tail) and two rows of upper lateral spots on body which coalesce on side of head to form a diffuse or ragged stripe. Upper and lateral surfaces of tail pale reddish brown, stippled with greyish brown, markings distally becoming larger and more transverse so that distal half or two-thirds of tail is narrowly cross-banded. Upper surface of limbs pale reddish brown, stippled with greyish brown. Lower lateral and ventral surfaces whitish.

Distribution

Arid eastern interior of Australia: east of Northern Territory north nearly to the Barkly Tableland and west to Mt Doreen and Mt Conner; far western Queensland north to the Tropic; north-eastern South Australia west to Billa Kalina and south nearly to the Murray River; and far western New South Wales south to the Menindee district. See map, Figure 1.

Remarks

The palest specimens come from the vicinity of the Simpson Desert. Much the darkest specimen is the westernmost (Mt Doreen), and it alone has 4 supraciliaries. For colour photograph of a specimen from Kinchega see Wilson and Knowles (1988, pl. 521).

Material

Northern Territory: 71 km W Barry Caves (WAM 55381-2); Tennant Creek (SAM 3376A-B); Kurundi (NTM A/S1140); Barrow Creek (SAM 3378; AM 52048, 95770); Mt Doreen (AM 49547); Dulcie Range (NTM 14496-8); Ewaninga (NTM A/S1573;

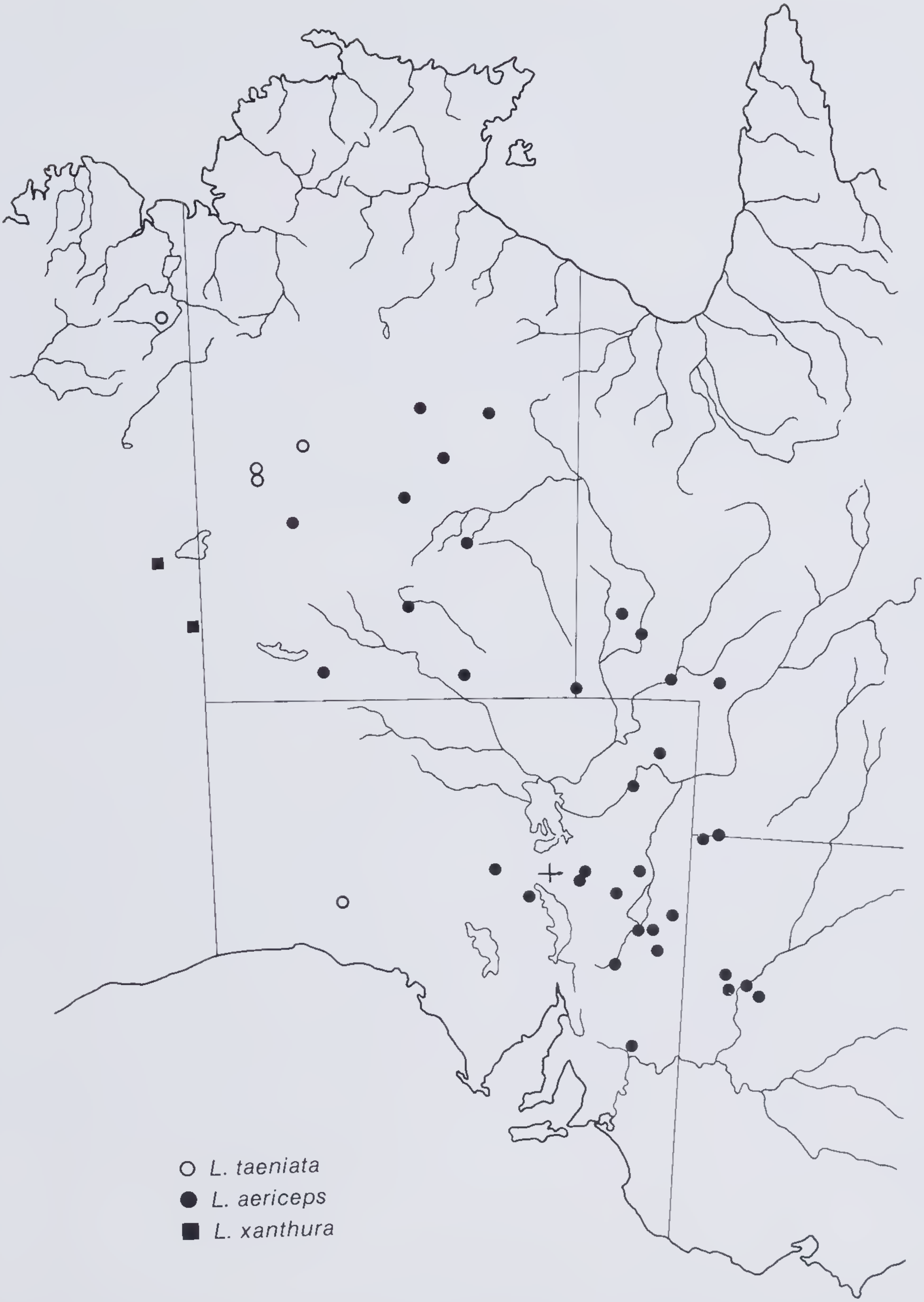

Figure 1 Map of central parts of Australia showing location of specimens of *Lerista taeniata, L. aericeps* and *L. xanthura*. A cross indicates where both an *L. taeniata* and an *L. aericeps* were collected.

WAM 95833); near Old Andado (AM 26536, 26553-4); 24 km SSE Curtin Springs (SAM 29943).

Queensland: 10 km N Sandringham (AM 93700); 20 km N Ethabuka (AM 113222); Cluny (QM 34137); Durrie (QM 39572); Cuddapan (QM 26502); 25 km N Poeppel Corner (QM 44235; AM 113223-5).

South Australia (all in SAM): Coongie Lake (32452, 32454); Cooper Creek in 27°54′S, 139°21′E (24549); 7 km S Prescott Point, Lake Eyre (31012-3); Billa Kalina (17282); Wilpoorinna (18049); Farina (15952); Old Moolawatana (11954, 15952); 3 km SW Mulgaria (19074); Roxby Downs (20941, 20962-3); Gammon Ranges National Park (24904); Glenmanyie Bore (14884); Frome Downs (12426A-B) and 15 km E (19075); Strathern (16819A-G, 17333-5); Baratta (3377); Bungunnia (15041).

New South Wales (all in AM): Binerah Downs (105992); Fort Grey (61386); Menindee district, including Kinchega National Park (32606, 68366-9, 68371-81, 73739-40, 87671).

Lerista xanthura Storr

Lerista xanthura Storr (1976: 247).

Diagnosis

A small, slender, almost patternless *Lerista* with 4 fingers, 4 toes and immovable eyelid (a spectacle), distinguishable from *L. aericeps* by its paler coloration, longer appendages (especially foreleg and tail) and absence of loreo-temporal stripe and of narrow bands on tail.

Description

Snout-vent length (mm): 32-36.5 (N 2). Length of appendages etc. (% SVL): foreleg 14-16, hindleg 28-30, tail 142-145, snout to foreleg 31-32.

Nasals in moderately long contact or narrowly separated. Prefrontals widely separated. Frontoparietals in moderately long to long contact, about as large as interparietal. Nuchals 1-3 on each side. Supraoculars 3, first two in contact with frontal. Supraciliaries 5, second and fifth smallest. Loreals 2, second much the smaller. Presuboculars 2, second much the smaller. Upper labials 6. Midbody scale rows 18. Lamellae under longest toe 14-16, each with a fine keel.

Upper surfaces pale pinkish brown (palest on head and tail), each scale edged with brown. In the Lake Hopkins specimen (but not the holotype) body and tail faintly flecked with reddish brown, and an upper lateral series of small faint reddish brown spots that disappear on snout and posterior part of body. Lower surfaces whitish.

Distribution

Arid far eastern interior of Western Australia. See Map, Figure 1.

Remarks

In colour and pattern the Lake Hopkins specimen of *L. xanthura* approaches the palest specimens of *L. aericeps*. It is, however, very different from the geographically nearest specimen of *L. aericeps*, viz. AM 49547 from Mt Doreen, which is dark and has short limbs (foreleg 9% and hindleg 22% of SVL).

Material

Western Australia: 7 km SW Pollock Hills (holotype WAM 40174); near Lake Hopkins (AM 26388).

Lerista taeniata Storr

Lerista aericeps taeniata Storr (1986: 148).

Diagnosis

A small slender *Lerista* with 4 fingers, 4 toes and immovable eyelid (a spectacle), distinguishable from *L. xanthura* and *L. aericeps* by its dark upper lateral stripe and more numerous midbody scale rows (usually 20, *v.* usually 18).

Description

Snout-vent length (mm): 21-44 (N 21, mean 35.6). Length of appendages etc. (% SVL): foreleg 10-16 (N 13, mean 13.9), hindleg 23-31 (N 13, mean 26.8), tail 116-142 (N 6, mean 121.8), snout to foreleg 27-33 (N 13, mean 30.3).

Nasals in short to moderately long contact (N 16), just touching (1) or very narrowly separated (1). Prefrontals widely separated. Frontoparietals in medium to long contact (N 18), a little larger or little smaller than interparietal. Nuchals 1-4 on each side (N 18, mean 2.4). Supraoculars 3, first two in contact with frontal. Supraciliaries normally 5 (second and fifth smallest); 4 on side of at least two specimens due to fusion of first and second. Loreals 2, second much the smaller. Presuboculars 2, second very much the smaller. Upper labials 6. Midbody scale rows 18 (N 3), 19 (1) or 20 (14). Lamellae under longest toe 14-18 (N 16, mean 15.7), each with a fine keel.

Upper surfaces brownish white, very pale brown or pale, slightly reddish brown, palest on head and along narrow dorsolateral strip on body; all scales edged with brown and mid-dorsals flecked with brown; occasionally a paravertebral series of dark brown dots. Narrow diffuse or wide sharp-edged dark brown or blackish brown upper lateral stripe, becoming broken on base of tail and extending forward to nasal and sometimes narrowing, curving down and meeting opposite number of rostral (as in *Lerista orientalis*). Dorsal and upper lateral surfaces of tail and upper surface of limbs stippled with dark brown or blackish brown. Lateral scales of body and tail edged with brown. Remaining surfaces whitish.

Distribution

Disjunct in arid and semiarid interior: east Kimberley of Western Australia, Tanami Desert of Northern Territory, and north-western South Australia. See map, Figure 1.

Remarks

Only the two South Australian specimens have the foreleg less than 13.5% of SVL. For colour photograph of holotype see Wilson and Knowles (1988, pl. 522).

Material

Western Australia: Bungle Bungle National Park (WAM 103012, 103055).

Northern Territory: Tanami Desert in 20°15′S, 131°45′E (NTM A/S1043), in 20°34′S, 130°38′E (NTM A/S1565-7, 1569-72, 1574-6; WAM 95834-7) and in 20°53′S, 130°24′E (NTM 14472, A/S1314).

South Australia: 3 km SW New Mulgaria (SAM 19060); 5.5 km S Immarna (SAM 32057).

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Australites from three localities in south-western Australia

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Abstract

The morphology, weights and specific gravities of australites from three localities in south-western Australia are described and compared. Samples from Earaheedy Station at the northern margin of occurrence of the "normal australite" chemical type are like those of the Eastern Goldfields of Western Australia, except insofar as the quality of the sample has been affected by the circumstances of collection. Sampling from around Corrigin in the south-west of the "normal australite" area has been influenced by the natural abundance of very heavy australites up to weight 437g, the obscuring effect of vegetation, shallow burial in surface sand, and minor factors. Australites from near Hughes on the Nullarbor Plain include numerous flakes but no large specimens because of destructive use by Aborigines. The average weights of australites in the Corrigin, Eastern Goldfields and Nullarbor Plain samples are 30.03g, 1.86g and 0.55g respectively, suggesting that the average dimensions of australites in those samples are in the ratio 2.5:1:0.67.

The natural and human factors which influence the nature of australite locality samples are briefly discussed.

Introduction

Australites which fell in the southern half of Western Australia and adjoining part of South Australia belong to the "normal australite" chemical type of Chapman (1971). Seven locality samples of australites found in the Eastern Goldfields of Western Australia have been previously examined (Cleverly 1986, 1988, 1990, in Press). This paper concerns samples from three localities distant from the Eastern Goldfields. The localities, as stated relative to Kalgoorlie-Boulder (the business centre of the Eastern Goldfields), are Earaheedy Station (550 km north), the vicinity of Corrigin (390 km west-south-west) and a small part of the Nullarbor Plain near Hughes, South Australia (740 km east) (Figure 1).

General features and source of australite samples

1. **Earaheedy Station, W.A.** Earaheedy homestead is located 25°36′S, 121°35′E in marginal pastoral country with mean rainfall 234 mm/a. Drainage is internal to salt lakes, as in the Eastern Goldfields. Earaheedy and the adjoining Granite Peak Stations constitute the northernmost part of Western Australia where australites have been found in abundance (Cleverly 1976). Documented australites, including australite artifacts, found further north than Earaheedy Station (Cleverly and Dortch 1975; Cleverly 1976; Horwitz and Hudson 1977; Dortch 1979; Mason 1986), together with three solitary specimens reported to the Western Australian Museum, total fewer than 50. This figure contrasts with more than 2700 from Earaheedy Station in collections.

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The following australite collections from Earaheedy Station were examined: 1. Western Australian Museum (WAM) 57; 2. T. Wilks private collection 314; 3. Western Australian School of Mines (WASM) 1578; 4. Quartermaine family private collection 259. There are also at least 535 in other collections including WASM registered No. 11 597 of 175 specimens. The last mentioned was excluded from consideration because it is the rejected part of a collection made for sale, and 66% of the specimens are artifacts (Akerman 1975).

Item 1 above was collected from a single claypan and item 2 from two small lakes (Figure 2). These two items have been combined as the sample "Earaheedy A" representing the "lake country", a complex of small basins and dunes occupying much of the eastern half of Earaheedy Station.

Items 3 and 4 are partly from places visited in connection with station activities, such as mills and fence lines. Another major component is the result of searching the vicinity of Mesquite Swamp, Pope's Claypan and Hamilton's Claypan (Figure 2), which are natural water sources. Of 1138 australite specimens recovered from those localities, 285 (25%) are flakes or flaked cores. Worked flakes of chert and similar materials are also present in those areas, suggesting that the water sources were Aboriginal occupation sites and that the flaked australites are artifacts. Thus the sample "Earaheedy B", comprising items 3 and 4 from the station as a whole, has considerable bias.

A frequency diagram of specific gravity for Earaheedy australites has been presented by Chapman (1971, Figure 5(b)). The single mode in the 2.45-2.46 interval and lack of values >2.47 are typical features of the "normal australite" diagram (Chapman *op. cit.*, Figure 4(d)). Specific gravity values and analyses presented by Mason (1979) confirm that Earaheedy australites belong to the "normal australite" type.

2. **Vicinity of Corrigin, W.A.** Corrigin is located 32°20′S, 117°52′E in what was previously light woodland. Mean rainfall in 379 mm/a, with strong mid-year (winter) maximum. The author assembled the bulk of the australite sample by farmhouse visits within an arbitrary 50 km radius of the town. The sample comprised 244 privately owned specimens and 39 from various public collections, in all 283 australites from 41 sources. This meagre number from an area of c.8000 km^2 is nevertheless greater than the number known from the balance of the country south-west of a line from Geraldton to Esperance (Figure 1), an area of nearly 200,000 km^2 (Cleverly 1976).

The sites to find are known for a little more than half the sample. The collection of F. Davis (59 specimens) was found on his farm. The collection of N. Ioannisci (72 specimens) and several smaller collections were obtained by watching the unloading and spreading of "gravel" (pisolitic laterite) during road construction. The sources of the australites were the various borrow pits, which are specifically known for some specimens.

3. **Vicinity of Hughes, S.A.** The sample area is on the Nullarbor Plain c. 30 km north-west of Hughes at approximately 30°30′S, 129°15′E (Figure 1). The sample area is midway between Forrest, W.A. (mean rainfall 186 mm/a) and Cook, S.A. (174 mm/a). The australite sample of 344 specimens is the Australian Museum share of the 1437

collected by a joint Australian and American party (Mason 1968; Chalmers *et al.* 1976). It is not known how well the Australian Museum holdings are representative of the whole collection.

Specific gravities and analyses presented by Mason (1979) indicate that australites from the Hughes area belong to the "normal australite" type of Chapman (1971).

Morphology, mean weights and specific gravity

Each sample was classified morphologically and extracts of salient features including mean weights were made (Table 1) according to the system of Cleverly (1986).

Adequate specific gravity studies of australites from Earaheedy and Hughes have been noted above. The specific gravities of 239 australites from the Corrigin area were determined, and a frequency diagram is presented in Figure 3.

Table 1. Features of australite samples. 1.* Earaheedy A; 2. Earaheedy B; 3. Vicinity of Corrigin; 4. 30 km north-west of Hughes; 5. Eastern Goldfields (average of seven samples).

	1	2	3	4	5
1 Complete forms of essentially so %	38.0	38.8	84.4	17.7	37.3
2 Incomplete but classifiable %	11.3	11.8	6.4	8.7	12.9
3 Unclassifiable, largely abraded or fragments %	47.7	27.0	9.2	59.2	48.6
4 Flakes and flaked cores %	3.0	22.4	—	14.4	1.2
5 Round forms %	70.8	63.2	72.3	51.3	68.2
6 Broad oval forms %	7.9	15.2	17.2	9.1	8.4
7 Narrow oval forms %	8.4	8.8	4.7	2.3	7.7
8 Boat forms %	5.6	4.4	0.4	3.4	5.1
9 Dumbbell forms %	3.9	5.1	4.7	12.5	7.3
10 Teardrop forms %	3.4	3.3	0.4	11.4	3.3
11 Flanged forms, discs & plates, bowls, canoes %	1.1	2.0	—	4.5	2.3
12 Indicators I %	—	1.2	—	1.1	1.8
13 Lens-forms %	34.3	42.1	9.0	88.7	61.6
14 Indicators II %	2.2	3.3	3.9	—	1.1
15 Cores %	62.4	51.4	87.1	5.7	33.2
16 Number of essentially complete australites	141	713	239	59	
17 Mean weight of above (g)	2.92	3.73	32.94	0.80	2.74
18 Total number in sample	371	1837	283	334	
19 Mean weight of all specimens (g)	2.36	2.34	30.03	0.55	1.86
20 Cores/lens-forms	1.82	1.22	9.65	0.06	0.54

*1-4. This work. 5. From Cleverly (1986, 1988, 1990, in press).

Discussion

Earaheedy A: This sample (Table 1, col. 1) is generally similar to those from the Eastern Goldfields. The un-weighted average figures for seven samples from the Eastern Goldfields (Cleverly 1986, 1988, 1990, in Press) are shown for comparison in Table 1, col. 5. Thus the total classifiable specimens in Earaheedy A (Table 1, items 1 and 2) is 49.3%,

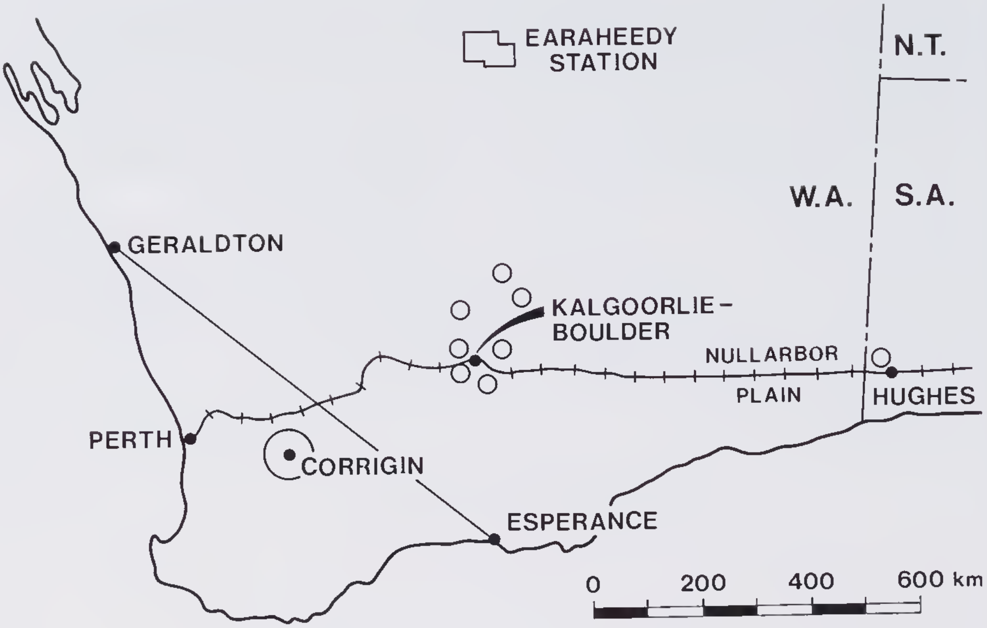

Figure 1. Map of south-western Australia showing find sites of the Earaheedy Station, Corrigin and Hughes australite samples. Sites of Eastern Goldfields samples previously examined are shown by small open circles around Kalgoorlie-Boulder.

and for the Eastern Goldfields 50.2%: round plus broad oval forms (items 5 and 6) total 78.7% of identifiable forms in Earaheedy A and 76.6% for the Eastern Goldfields. The major differences are in the abundances of cores and lens-forms (items 15 and 13), and hence in the cores/lens-forms ratio of 1.82 (Eastern Goldfields 0.54). If the Earaheedy sample is representative, the ratio reflects the higher mean weight of the Earaheedy australites (items 17 and 19).

Earaheedy B: This sample (Table 1, col. 2) has a higher mean weight (3.73 g) for complete specimens than Earaheedy A (item 17), which could be attributable to casual and unsystematic collecting and the high 22.4% of flakes (item 4) resulting from search around water sources. In other respects, it is of the Eastern Goldfields type. The mean weight of 2.34 g for all specimens (item 19) is distinctly higher than the 1.86 g for the Eastern Goldfields samples, despite the presence of 411 flakes averaging less than 1 g each. Classifiable specimens which have not yet been reduced to cores or lens-forms (items 11, 12 and 14) total 6.5%, nearly twice the 3.3% surviving in the harsher conditions of the "lake country" (col. 1).

Corrigin sample (Table 1, col. 3). The outstanding features of the Corrigin sample are the irregular, sometimes almost faceted, posterior surfaces of certain cores, and the abundance of heavy specimens, which include the heaviest known australite.

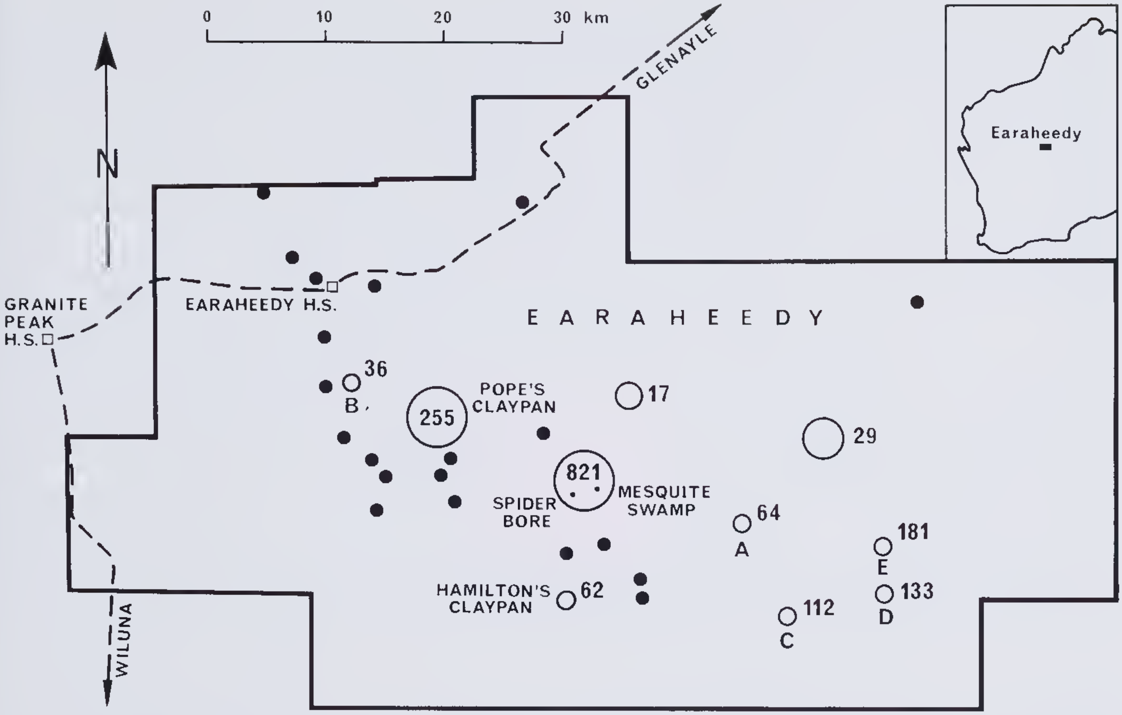

Figure 2. Map of Earaheedy Station, Western Australia showing areas of recovery of australites circled with numbers of specimens. A is the approximate find site of australites in the Western Australian Museum collection, B and C the Smithsonian Institution collection, D and E the T. Wilks private collection. Balance is in other collections. Small solid circles represent 5-10 australites.

Chapman (1964) estimated that about two thirds of the primary cores of round or nearly round shape found within 200 km of Kulin have irregularly contoured, often somewhat faceted "bases" (posterior surfaces). The Corrigin sample was collected within the 200 km circle around Kulin, and therefore provides an opportunity to check Chapman's estimate.

"Primary" is taken to mean those larger cores from which the stress shell spalled spontaneously, as distinct from the generally smaller cores formed as the result of piecemeal losses during weathering (Cleverly 1986, Figure 3). Chapman (1964) has figured a "primary" core from Woyerling (within the sample area) weighing only 18.0 grams. An arbitrary minimum weight of 18 g for primary cores was adopted for the purposes of this investigation. "Round or nearly round" was also given an arbitrary limit of elongation (length/width) of 1.1. Such cores have formed from non-rotating or slowly rotating masses. Irregular posterior surfaces have not been observed on the more elongated oval, boat, or dumbbell-shaped australites, presumably because centrifugal force, which also enters the equation of shape, assisted surface tension in producing a smoothly curved, equilibrated surface.

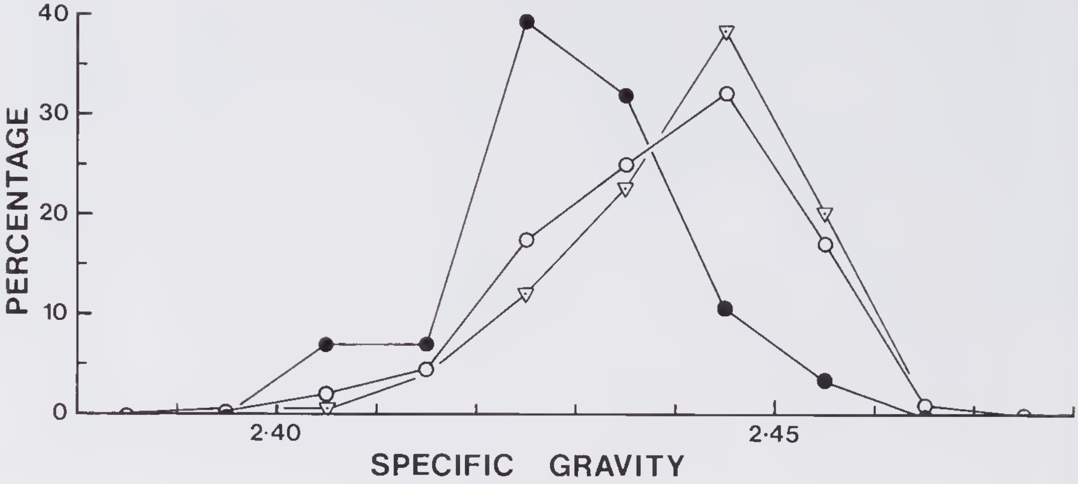

Figure 3. Specific gravity frequency diagrams for australites from the vicinity of Corrigin. Open circles: sample of 239 australites. Filled circles: 56 australites in the sample weighing ≥ 40 g each. Triangles: balance of 183 australites in the sample weighing ≤ 40 g each.

Chapman (1964, Figure 11) has included with cores having irregular "bases" a specimen from Bullaring with abundantly vesicular areas on the posterior surface. Irregular depressions on such cores may have resulted from the weathering out of the weakened, cellular areas. However, the persistence rather than collapse of the vesicles, is a likely result of the lower temperature and resultant higher viscosity envisaged by Chapman, and the inclusion of such cores may therefore be justified.

Sixty two percent of the "primary" cores of weight ≥ 18 g and of elongation ≤ 1.1 in the Corrigin sample have irregular posterior surfaces, a result in close agreement with Chapman's estimate of two thirds.

Australites from south-western Australia may thus show peculiarities of the posterior surface, such as irregular curvature, peaked or almost faceted shape, and unusual abundance of vesicles. Less commonly, they may show peculiarities of the secondarily produced surfaces also, such as spalling of the stress shell extending to the posterior surface (Cleverly 1981), a double rim (Cleverly 1987) and a groove around the anterior surface, as on a core in the collection of N. Ioanissci. The generally large size of the Corrigin specimens is suggested by the high mean weights of 32.94 g for whole specimens and 30.03 g for all specimens (Table 1, items 17 and 19). The sample area lies entirely within the western of two sectors of occurrence of large australites (Cleverly and Scrymgour 1978). The sample of only 283 specimens, a fraction of 1% of those in collections, nevertheless contains 10 of the 22 heaviest known australites (Table 2, upper 10). At the other end of the size range, only 16% of the essentially complete specimens weigh less than 5 g each, compared with 87% of those in an Eastern Goldfields sample (Cleverly 1986, Figure 3).

The mean weight of 30.03 g for the Corrigin specimens contrasts with 1.86 g for Eastern Goldfields collections (Table 1, item 19). The Corrigin specimens thus average 16.15 times as heavy, and have average dimensions more than 2.5 times as great (third root of 16.15) as those in the Eastern Goldfields sample. Deductions of that kind are valid because mean specific gravities of australite samples from within the "normal australite" region vary so little. Some mean specific gravities for samples of 50 specimens are: Farm of F. Davis, Corrigin area 2.436; "Lake country" NW of Kalgoorlie 2.452; Leonora district, 210 km N of Kalgoorlie 2.446; Mulga (north) meteorite strewnfield, Nullarbor Plain 2.442. The above values differ mutually by less than 1%. Mean weights of representative samples are therefore a reliable guide to mean size.

High mean weights arising from an abundance of large australites unequalled elsewhere in Australia, have been further exaggerated by several factors. The large average size and small number of australite recoveries could be partly accountable to the difficulty of detection in well vegetated country, which constrast with the bare ground and dry lake basins of the Eastern Goldfields (Cleverly 1976). The burial of australites in the drifting surface sands of the region (the leached soil horizon over laterite) has not been adequately recognised, though examples have long been known. Public collections contain examples of australites recovered from a post-hole, pipeline cutting, drain, sand pit, diggings for poison weed, and excavations of soaks and earthwork dams. At numerous roadside borrow pits, the surface sand has been stripped to reveal the underlying pisolitic laterite, which is quarried for road building. Australites have been recovered from several such quarries, and also by watching the distribution of the laterite during road building. Some australites were found later on "gravelled" roads. No australites are known to have been taken out of the laterite in the quarry faces i.e. there is no suggestion that they are pre-lateritisation in age. More likely, carelessly or incompletely stripped surface sand containing australites has fallen into the quarries or been incorporated in loads of laterite. Most australites in the Corrigin sample were either ploughed up or otherwise exhumed from shallow burial. These circumstances do not favour detection of small specimens.

Another factor which may have influenced the nature of the australite sample is that the occurrence of very large australites has conditioned some people to expect only large ones. A typical attitude was an apology for the "small" size of four medium to large specimens (weighing 27.3-62.4 g) offered for examination by a farmer who knew that an australite weighing 197.4 g (Cleverly 1981) had been found on his farm by previous owners.

The occurrence of large australites is also dependent upon their survival. Destructive use by aborigines, as discussed for the Hughes sample below, is not known to have occurred in the Corrigin area, though there are numerous aboriginal occupation sites (L. Lewis, pers. comm.).

Various items in Table 1, col. 3 contribute to, or are influenced by, the high mean weights. Thus the round plus broad oval forms (items 5 and 6) constitute an unusually high 89.8% of identifiable forms. Lists of large australites (e.g. Cleverly 1974, Table 2)

Table 2. Heavy australites found in Corrigin area.

Weight g	R.W.[1] g	Core shape	Locality	Ref.[2]
437.5		Broad oval	c. 3 km W of Notting	1
233.9		Broad oval	c. 14 km W of Kondinin	1
225.1		Teardrop	Near Shackleton	2
218.0		Round	Lake Yealering	1
200.5		Round	c. 7 km S of W of Gorge Rock	3
197.4		Round	c. 10 km SE of Babakin	3
194.4		Round	c. 7 km E of Gorge Rock	1
171.4		Round	8 km WNW of Wogerlin Hill	
168.0		Round	c. 5 km SE of Corrigin	1
167.0	176	Broad oval	15 km SW of Billericay	
147.0		Round	Near Corrigin	1
117.7		Round	7 km NE of Wogerlin Hill	
116.9		Broad oval	c. 22 km N or E of Wickepin	1
113.1	117	Broad oval	Babakin	1
99.9		Round	2 km N of E of Bilbarin	
97.7		Broad oval	23 km E of Corrigin	
95.1		Round	Kulin	
93.9		Round	c. 20 km S of Corrigin	
86.8	100	Broad oval	Jubuk	1
85.7		Round	Near Corrigin	
84.1		Round	7.5 km NNW of Kulin	
81.0		Round	Shackleton	
80.1	>100	(?) Round	6 km SW of Gorge Rock	3

[1] Estimated restored weights for artifically damaged specimens.

[2] References to descriptions. 1. Cleverly (1974); 2. Scrymgour (1978); 3. Cleverly (1981).

show the dominance of such shapes amongst large australites. The low percentage of the smaller, lens-type specimens and high percentage of the generally larger cores (items 13 and 15) yield an exceptionally high cores/lens-forms ratio of 9.65 (item 20).

The frequency diagram of specific gravity for 239 specimens from the Corrigin area (Figure 3) has the general features of the "normal australite" type (Chapman 1971), but the mode in the 2.44-2.45 interval contains only 32% of the sample, and the diagram is convex upward on the lower value side of the mode. The 33 known australites from the south-west region having weight >100 g (Cleverly 1974, 1981, This Paper; Scrymgour 1978) have the distinctly lower mean specific gravity and standard deviation 2.425±0.012. This observation prompted consideration of the heavier specimens in the Corrigin sample. The diagram for the 56 specimens in the Corrigin sample, each weighing >40g, has its mode in the same low interval (2.42-2.43) as the convexity. If those 56 specimens are excluded from the general sample, the frequency diagram has an increased mode and no convexity (Figure 3). The abundance of heavy specimens is therefore at least partly responsible for the unusual features of the original diagram.

Hughes sample (Table 1, col. 4). The mean weight of 0.55 g (item 19) is at the other end of the scale from the Corrigin sample, and in close agreement with the mean of 0.57 g for 1933 specimens in 17 widespread Nullarbor Plain samples (calculated from data of Chalmers *et al.* 1976). The mean weight of the Hughes sample is only 0.296 of the 1.86 g mean for Eastern Goldfields specimens. The average dimensions are therefore only two thirds those of Goldfields specimens.

The low percentage (26.4%) of classifiable specimens (items 4 and 5) is partly accountable to the high percentage (14.4%) of flaked material (item 4). In collecting this sample, search was not knowingly directed towards water sources, as was the case for the sample Earaheedy B. A sample of 102 australites from the strewnfield of the Mulga (north) meteorite, on the Nullarbor Plain 270 km WNW of Hughes (Cleverly 1972) has comparable abundance (15.7%) of australite flakes. The percentage may be much higher around aboriginal occupation sites, even 100% (Edwards 1966; Cleverly 1976).

The terrestrial changes of australite shapes (Cleverly 1986, Figure 3), accelerated by semi-arid climatic conditions, are shown in the abundance (94.4%) of lens-forms and cores (items 13 plus 15), the identifiable end products of the smaller and larger primary bodies respectively. However, cores comprise only 5.7% and lens-forms 88.7% of classifiable specimens, quite the inverse of the Corrigin sample. The resulting cores/lens-forms ratio is only 0.06 (item 20). The abundance of the smaller lens-forms, paucity of cores, and resultant low mean weights can be explained by the joint circumstances of ready visibility of small australites and the destruction of larger australites by Aborigines. The heaviest specimen in the Hughes sample is a fragment weighing 3.4 grams. The heaviest specimen known to the writer from anywhere on the Nullarbor Plain is an artifically detached fragment weighing 27.1 g found east of Rawlinna (A. Levy private coll.). The report of a 98 g core from the Nullarbor Plain (Fenner 1955) is erroneous. The specimen (SAM T510) was found in the vicinity of Kalgoorlie and has the etch pattern developed in highly saline environments (Cleverly 1986), but unknown on cores from the Nullarbor Plain.

Conclusions

The nature of an australite sample depends upon both natural and human factors. Patches of unusual australite abundance which cannot be attributed to terrestrial transporting agents (e.g. Cleverly 1986: 82) are common and indicate that the shower varied in density. There was probably also a variation in the sizes of the primary bodies from place to place. The sizes and size distribution influenced the numbers of cores formed by spontaneous spalling of the stress shell and number of lens-forms resulting from loss of flange in flight during aerodynamic (secondary) modification of the primary form, thus establishing the initial cores/lens-forms ratio. Differences in the intensity and nature of erosion and weathering processes during subsequent terrestrial residence caused losses of flanges and stress shells, which vary in percentage completion from place to place. Some australites, especially frail and smaller ones, have been reduced beyond cores and lens-forms to unidentifiable shapes. Australites may become enclosed in surficial sand or sediments and re-exposed by natural agencies such as stream erosion.

They may therefore be affected by chemical corrosion in moist soils and by erosion at different stages of their terrestrial history, each modifying, or even erasing the earlier effects. Ideally, the preceding and allied natural factors would be responsible for the nature of an australite locality sample, but human factors may also have an influence.

Where vegetation obscures the ground, only the most painstaking search can yield a representative sample with a full quota of smaller specimens. This difficulty is less in semi-arid places such as the Eastern Goldfields, and almost non-existent in desert regions. However, casual or careless collection, even in places of ready visibility, can result in an undue number of the larger, core-type specimens in the sample. Shallowly buried australites may be re-exposed by a variety of human activities, such as clearing of vegetation, ploughing, engineering excavation and mining. The expectation of finding only large australites may have influenced the nature of the sample in some areas. The widespread occurrence of artifacts made on australites in places such as the Nullarbor Plain, where alternative materials are limited in quality or variety, may result in samples containing unusually high numbers of flaked specimens and few large ones. Samples from near natural water sources are likely to contain exaggerated percentages of artifacts. On the other hand, the survival of larger australites may be dependent upon a lack of Aboriginal interest in them as raw materials. Non-destructive use of australites by Aborigines as charms, medicine stones, or death-pointers (Baker 1957) may have resulted in their movement along Aboriginal trade routes and their eventual recovery in places where australites did not fall (Cleverly 1976).

There may yet be clues to australite origins in their distribution pattern. While current theories of tektite origins agree only to differ, it is desirable that collecting be very thorough to ensure that the sample is truly representative, and that the natural and human factors responsible for the nature of the sample be assessed as carefully as possible.

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The subterranean aquatic fauna of the North West Cape peninsula, Western Australia.

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Abstract

The current status of the subterranean aquatic fauna on the semi-arid tropical North West Cape peninsula of Western Australia is discussed and placed in the context of the rich troglobitic fauna of Cape Range. The range of all four subterranean species has been considerably extended and an amphipod added to the known fauna. The fauna includes the only vertebrate troglobites known from Australia.

The Blind Cave Eel, *Ophisternon candidum*, has been seen for the first time in more than a decade and from the east coast of the peninsula where it was previously unkown. Allozyme electrophoretic data show that the Blind Gudgeon, *Milyeringa veritas*, is not panmictic within its known range. The overt geological discontinuities along the coast of the North West Cape peninsula do not constitute genetic barriers between the gudgeon populations.

Allozyme electrophoretic data confirm that two species of atyid shrimps occur but the species were found on opposite sides of the peninsula. Analysis suggests that the species composition on the east coast is different from that on the west coast.

The relationship between genetic and metric distance between the populations suggests that the coastal fauna is essentially linear along the coast and does not spread beneath Cape Range.

Within Cape Range all four wells with water contain an undescribed amphipod. Allozyme electrophoretic data suggest the presence of a single species showing genetic discontinuities through its range.

There is a cline in the water chemistry, with most parameters increasing from the mid-east coast, round the north coast and south along the west coast of the peninsula. All coastal species seem to occupy the full range of water chemistries sampled. There is a lack of effective monitoring of the quantity and quality of the water. Examination of diverse evidence from a number of sources suggests that the water table is declining and becoming more saline. Potential disruption of the habitat is discussed and a model presented which indicates that the critical areas for conservation may be close to the scarp where, owing to the absence of wells, the fauna has not been sampled.

Introduction

The troglobitic fauna of the North West Cape peninsula of Western Australia was first mentioned in the context of the subterranean freshwater fauna of the coastal plain (Whitley 1945) and later by Cawthorn (1953). This fauna was the focus of a paper by Mees (1962) who described the composition and known range of the fauna. Since then the known range of the fauna has expanded considerably but the species composition has remained unchanged. In addition, a rich troglobite fauna has been found within

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Cape Range, which forms the spine of the peninsula (Vine, Knott & Humphreys 1988; Humphreys 1989, 1990; Humphreys, Adams & Vine 1989).

Nearly three decades after Mees's (1962) publication it is pertinent to review what is known of the four troglobitic species of the coastal plain and relate it to the troglobitic fauna of the peninsula as a whole (Figure 1). Since that time the peninsula has started to be developed rapidly as an international tourist region and two major national parks have been established (Cape Range National Park and the contiguous Ningaloo Marine Park). This trend represents both quantitative and qualitative changes to the human impact on the region. For this unique troglobite fauna to survive the development must be sensitive to its needs.

More than 300 caves and wells are known from Cape Range, many containing a rich troglobitic fauna of terrestrial arthropods, while an undescribed amphipod inhabits the four caves containing water (Vine, Knott & Humphreys 1988; Humphreys 1989, 1990; Humphreys, Adams & Vine 1989). This fauna is distinct from that inhabiting the subterranean waters on the *ca.* 2 km wide coastal plain fringing Cape Range which contains a unique subterranean fauna, comprising two species of fish and two species of atyid shrimps. Although these taxa were described between 1945 and 1962, almost nothing is known of their biology. Some coastal caves, which were major water sources for aboriginal people (Carter 1902), and recent bores, have been heavily utilized for water by pasturalists, Exmouth Town and military facilities.

This paper reviews the status of the subterranean aquatic fauna of the North West Cape peninsula and shows the lack of information on the biology and dynamics of species involved.

The fauna

Four species are known to occur in the subterranean freshwater on the coastal plain. The Blind or Cave Gudgeon, *Milyeringa veritas* Whitley 1945 (Perciformes: Eleotridae) (Whitley 1960) was described from Milyering Well (cave number C-24). It is classified as rare and total protection has been recommended (Michaelis 1985). The Blind Cave Eel, *Ophisternon candidum* (Mees 1962) (Synbranchiformes: Synbranchidae) was described from Tantabiddi Well (C-26). It is classified as vulnerable (Michaelis 1985). These two species of fish comprise the entire troglobitic vertebrate fauna of Australia. The atydid shrimps *Stygiocaris lancifera* Holthuis 1960 and of *S. stylifera* Holthuis 1960 (Decapoda: Natantia) were both described from Kudumurra Well (C-25). The Indo-West Pacific area seems to be deficient in troglobitic Decapoda compared with e.g. the Mediterranean and the West Indies (Holthuis 1960). The four species known from the coastal limestone are endemic to the peninsula and co-occur in the same water bodies (Mees 1962, Hamilton-Smith 1967).

Within Cape Range itself amphipods occur in each of the four caves known to contain standing water *viz.* C-18, C-64, C-103 and C-163 (Humphreys 1989, 1990; Humphreys, Adams & Vine 1989). The amphipoda are of marine origin and part of the *Victoriapisa* complex (Gammaridae; B. Knott; pers. comm. 1988).

Methods

Numbers with a C- prefix refer to caves or karst features described in the karst Index of Cape Range (M. East and B. Vine; pers. comm.). They will eventually be included in the Australian Speleological Federation's catalogue of karst features.

Table 1. Location and distribution of samples collected for genetic analysis in 1989. The gudgeons are *Milyeringa veritas,* while the shrimps are *Stygiocaris lancifera* except for those from Mowbowra Well and Kubura Well which are *S. stylifera.*

Cave	Name	Location		Numbers	
			Shrimps	Gudgeons	Amphipods
C-18	Dry Swallett	22°05′S; 114°00′E	—	—	4
C-24	Milyering Well	22°01′S; 113°56′E	4	—	—
C-25	Kudamurra Well	21°53′S; 114°01′E	4	5	—
C-27	Kubura Well	21°56′S; 114°08′E	8	3	—
C-64	Shot Hole Tunnel	22°03′S; 114°01′E	—	—	9
C-103	Trionomo	22°07′S; 113°59′E	—	—	4
C-149	Tulki Well	22°06′S; 113°54′E	4	5	—
C-163	Wanderer's Delight	22°09′S; 114°00′E.	—	—	9
C-273	5 Mile Well	21°51′S; 114°04′E	4	7	—
C-274	Pilgramunna Well	22°12′S; 113°52′E	—	5	—
C-361	Mowbowra Well	22°00′S; 114°07′E	3	3	—
C-362	Javis Well	22°36′S; 113°41′E	—	2	—

Distribution

Distributions of the taxa have been ascertained incidentally from a series of expeditions examining the troglobitic fauna of Cape Range, by records in the literature and from discussion with people who have examined the caves over a long period. Collections of shrimps and fish were made in September 1989 as detailed in Table 1.

A total of 24 sites, including all known locations for the subterranean coastal fauna were visited with the aim of collecting a minimum of six specimens each of shrimps and gudgeons to be divided between alcohol-preserved material and liquid nitrogen material for genetic analysis. The small number of specimens and few sites of collection (Table 1) attest to the sparsity of the fauna. The following sites were visited: 4-mile Well, 5-mile Well (C-273), Bundera Rockhole (C-28), C-215, Cape Well, Dozer Cave (C-23), Javis Well (C-362), Kuburu Well (C-27), Kudumurra Cave, Kudumurra Well (C-25), Milyering Cave (C-172), Milyering Well (C-24), Mowbowra Well (C-361), Nabalgee Well, Ned's Well, Pilgramunna Well (C-274), South Yardie Well (C-275), Tantabiddy Well, Trealla Well, Tulki Well (C-149), unnamed small rockhole near south ranger's camp, unnamed small rockhole south of Bundera Rockhole, unnamed well (old water supply for NorWest Seafoods) and Woolcott Well.

Water analysis was conducted using standard methods (American Public Health Association 1965) except for pH which was determined at the time of collection using narrow range pH papers (Merck).

Electrophoresis

Cellulose acetate gel electrophoresis was conducted using standard methods (Richardson, Baverstock & Adams 1986). Homogenates were made from whole individuals of four taxa (*Milyeringa veritas*, *Stygiocaris lancifera*, *S. stylifera* and the amphipods) and used to examine the allozyme variation between the populations around the peninsula. Samples were available from between four and seven natural or artificial wells or caves depending on the taxon under study. For systematic purposes, the null hypothesis under test was that all populations were sampled from the gene pool of a single species. A large number of enzymes and non-enzymic proteins were examined (Table 4), of which 37 displayed electrophoretic patterns suitable for reliable genetic interpretation in at least one of the four taxa. The enzymes used are as follows: aconitate hydratase (ACON, E.C. 4.2.1.3), aminoacylase (ACYC, E.C. 3.5.1.14), adenosine deaminase (ADA, E.C. 3.5.4.4), alcohol dehydrogenase (ADH, E.C. 1.1.1.1), adenylate kinase (AK, E.C. 2.7.4.3), aldolase (ALD, E.C. 4.1.2.13), alkaline phosphatase (AP, E.C. 3.1.3.1), arginine kinase (ARGK, E.C. 2.7.3.3), carbonate dehydratase (CA, E.C. 4.2.1.1), creatine kinase (CK, E.C. 2.7.3.2), diaphorase (DIA, E.C. 1.6.99.?), enolase (ENOL, E.C. 4.2.1.11), esterase (EST, E.C. 3.1.1.1), fructose-1, 6-diphosphatase (FDP, E.C. 3.1.3.11), fumarate hydratase (FUM, E.C. 4.2.1.2), glyceraldehyde-phosphate dehydrogenase (GAPD, E.C. 1.2.1.12), guanine deaminase (GDA, E.C. 3.5.4.3), lactoyl-glutathione lyase (GLO, E.C. 4.4.1.5), aspartate aminotransferase (GOT, E.C. 2.6.1.1),

Table 2. The current status of the subterranean fauna on the North West Cape peninsula. Mees refers to Mees (1962). ✓=reported to occur. —= not found and never reported.

Cave #	Name	Shrimp	Gudgeon	Eel	Salinity (‰)		pH
					1983	1988	1988
—	Unnamed	✓	—	—	—	—	—
—	Woolcott Well	—	—	—	—	—	7.0
—	Nabalgee Well	—	—	—	—	—	7.3
—	4-Mile Well	none	none	—	—	—	7.6
C-23	Dozer Cave	none	few	—	—	—	—
C-24	Milyering Well	Mees[1]	1989	Mees	5	4	7.4
C-25	Kudamurra Well	1989	Mees[1]	Mees	—	2	7.3
C-26	Tantabiddy	none	none	Mees	—	3	—
C-27	Kubura Well	1989	1989	1973	—	—	6.8
C-28	Bundera Sinkhole	—	1988	—	—	16	—
C-105	The Gnamma Hole	none	none	1988	1	—	—
C-149	Tulki Well	1989	1989	—	5	5	7.5
C-215	Unnamed	none	1989	—	—	—	7.3
C-273	5 Mile Well	1989	1989	—	—	—	—
C-274	Pilgramunna Well	1989	1989	—	—	—	7.5
C-332	—	1977	—	—	—	—	—
C-361	Mowbowra Well	1989	1989	1989	—	—	7.3
C-362	Javis Well	1989	1989	—	—	—	7.3

[1] Also collected in 1989.

general protein (GP), glucose-phosphate isomerase (GPI, E.C. 5.3.1.9), alanine aminotransferase (GPT, E.C. 2.6.1.2), glutathione reductase (GSR, E.C. 1.6.4.2), hexosaminidase (HEX, E.C. 3.2.1.30), hexokinase (HK, E.C. 2.7.1.1), isocitrate dehydrogenase (IDH, E.C. 1.1.1.42), leucine 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), malic enzyme (ME, E.C. 1.1.1.40), mannose-phosphate isomerase (MPI, E.C.5.3.1.8), peptidases (PEP, E.C. 3.4.11.? or 3.4.13.?), phosphoglycerate mutase (PGAM, E.C. 5.4.2.1), 6-phosphogluconate dehydrogenase (6PGD, E.C. 1.1.1.44), phosphoglycerate kinase (PGK, E.C. 2.7.2.3), phosphoglucomutase (PGM, E.C. 5.4.2.2), pyruvate kinase (PK, E.C. 2.7.1.40), L-iditol dehydrogenase (SORDH, E.C. 1.1.1.14) and triose-phosphate isomerase (TPI, E.C. 5.3.1.1). The nomenclature and conventions for referring to alleles and loci follow Richardson, Baverstock & Adams (1986).

All species met the criteria for adequate genetic work at the within-species level (Richardson, Baverstock & Adams 1986) in that they had at least six polymorphic loci; the samples could be drawn from the smallest and homogeneous population units (wells or caves) and they were sampled over some geographical distance including the extremities and intermediate locations.

Results and Discussion

Distribution of the fauna

The distribution of the subterranean aquatic fauna of the North West Cape peninsula is outlined in Figure 1 and Table 2, together with salinity and pH readings from 1983 and 1988. The distributional range of each species has been considerably extended by this study over that detailed by Mees (1962). There are clearly inadequate data on the time course of the water chemistry as will be discussed more fully below.

The gudgeon, *Milyeringa veritas*, was known in 1962 from only two locations on the north-west coast of the peninsula, namely Milyering Well (C-24) and Kudamurra Well (C-25). It is now fairly widely known from south of Yardie Creek at Javis Well (C-362), round North West Cape and down the east coast as far as Mowbowra Well (C-361: Figure 1). The latter locality is south of the proposed Exmouth marina. The range extension since 1962 is ca 740%. The gut contents of four specimens contained detrital matter and the remains of diptera; it is not known whether the latter are taken live.

The eel, *O. candidum*, was known also in Mees's time (1962) only from Milyering and Kudamurra Wells on the north-west coast of the peninsula. In 1973 it was seen in Kubura Well (C-27) on the north east coast in Exmouth town site (Figure 1). The only known sightings in more than a decade have been south of the proposed Exmouth marina:in the Gnamma Hole (C-105: 29 May 1988 - M. East; pers. comm.) and in Mowbowra Well (C-361: 10 September 1989 - B. Vine; pers. comm.). In 1977 one was seen for several days in a recently excavated 4 m deep well south of Yardie Creek (Allen 1982). The range extension since 1962 is *ca.* 340%.

The shrimps, *Stygiocaris lancifera* and *S. stylifera* are here treated together as field observers have not been able to distinguish the two species; this point will be discussed further below. Holthuis (1960) described the species sympatrically from both Milyering and Kudamurra Wells and unspecified water holes near Milyering. They are now known to occur from Tulki Well on the west coast, round North West Cape and down the east coast as far as Mowbowra Well (Figure 1). The latter locality is south of the proposed Exmouth marina. The range extension since 1962 is *ca.* 530% for *Stygiocaris lancifera* and 340% for *S. stylifera.* All range extensions were calculated assuming the fauna occupies only the coastal plain (see below).

The Cape Range amphipods (*Victoriapisa* complex) were not known in Mees' time and occur in a band about 12 km long in the central part of the range (Figure 1). Alcohol preserved material from each cave is held at the Western Australian Museum; Cape Range 1989 -3212, -3225, -3236, -3241; and WAM 954/88 to 98/8).

There are reports of 'shrimps' pumped from a bore further south on the east coast (M. East; pers. comm.), the west coast and from the bore field supplying Exmouth, but no specimens are known. Their identity cannot be assumed because the Exmouth bore field enters Tulki Limestone from which only the Cape Range amphipods have been confirmed.

Only 1.1 km from Milyering Well is a cave (C-215) within the same Tulki Limestone formation that contains the typical Cape Range troglobitic fauna (Humphreys 1989 and unpublished). The coastal water table is reached at a depth of 23.8 m (*ca.* +1.2 m MSL; cf +0.42 to +0.98 m MSL in Exmouth bores 1 to 6; Bestow 1966). This is the only locality known from the North West Cape peninsula where elements of both the Cape Range and the coastal fauna co-occur, namely the gudgeon and a troglobitic millipede (an undescribed genus of the Paradoxosomatidae [Craspedosomida]; W. A. Shear, pers. comm. 1989). Clearly the potential exists for the subterranean fauna to extend from close to the coast into the foothills of Cape Range proper (see below).

Numbers

No estimates of the continuity or abundance of this subterranean fauna has been made and so assessment of its status relative to the time of its discovery is impossible; detailed biological work is required to set this base line. The impression of those who have examined the wells over many years is that numbers are considerably lower than they once were. We present below the little information about numbers that can be deduced.

Mees (1962: 29) describes removing the *ca.* six visible specimens of the gudgeon from Milyering Well several times during one day as they were replaced by individuals from the subterranean channels. Several days later only one or two individuals were found on subsequent visits. The next year about six were seen again.

The collections made from which Holthuis (1960) described the shrimps are well documented as to the number of specimens; Snell's samples were collected mainly in May 1959 (a few in April 1957), and Mees and Douglas' samples were collected in August that year (Table 3). The proportion of the two species of shrimps, *Stygiocaris lancifera* and *S. stylifera,* did not differ between collectors (Table 3: $\chi^2_1 = 2.635$, P=0.105) or the two major collections (Table 3: $\chi^2_1 = 3.166$, P=0.075). Note the large number of

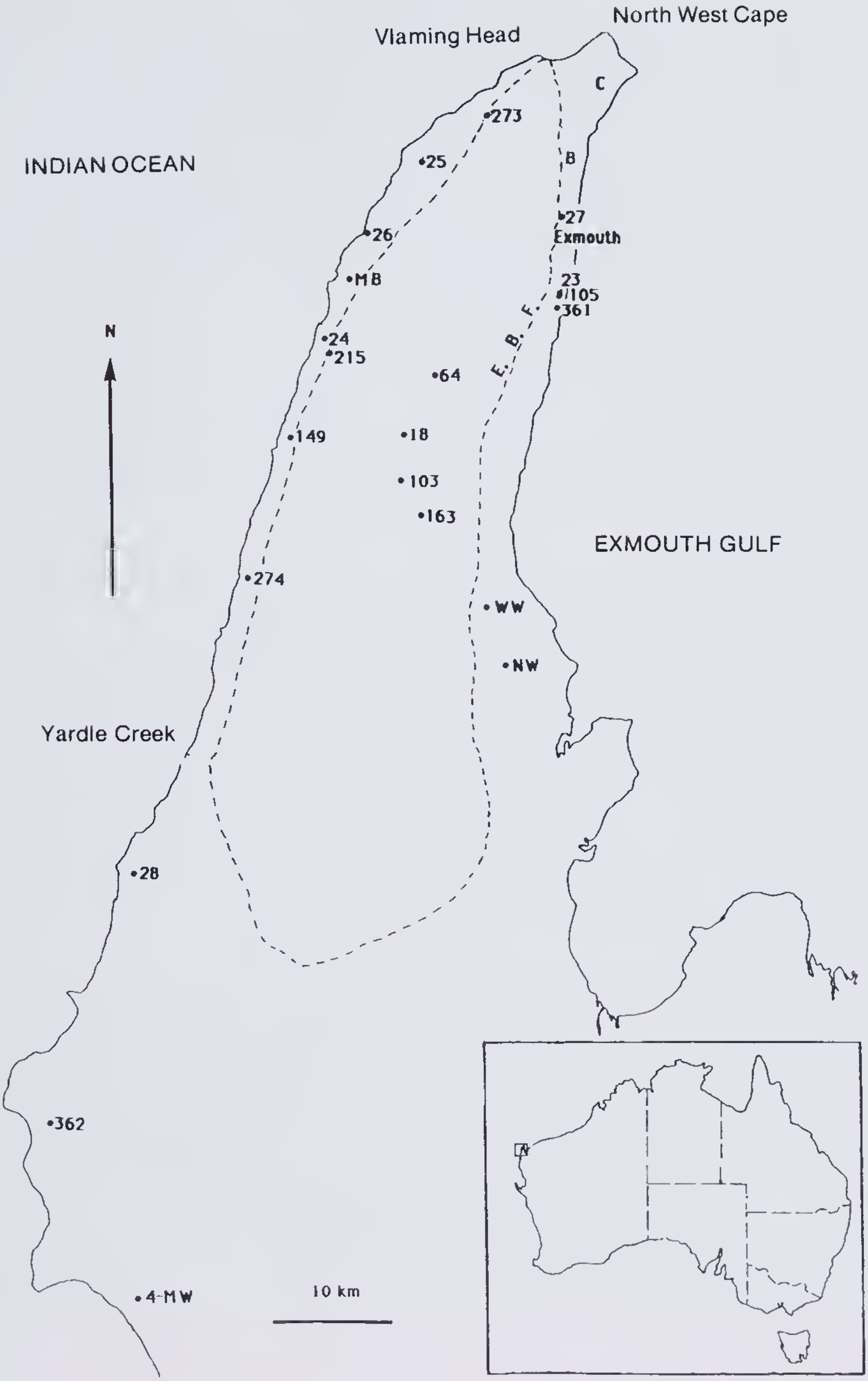

Figure 1. Map showing the North West Cape peninsula of Western Australia and the localities of wells, caves and other geographical features mentioned in the text. E.B.F. denotes the Exmouth bore field from which the town draws its water supply. The military facilities (B and C) have a separate water supply drawn from area B. The stippled line denotes the position of Cape Range. NW, Nabalgee Well; WW, Woolcott Well; 4-MW, 4-Mile Well. C-172 is adjacent to C-24. C-275 is 1 km ESE of C-28.

specimens collected in the wells at that time where it is now difficult to find several specimens.

In the samples collected for genetic analysis (below) all specimens from the west coast were of one genetic species while all those from the east coast were of another genetic species. Some specimens collected at the same time as the samples used for genetic analysis were fixed in formalin and preserved in alcohol. Comparison of these specimens with paratypes held at the Western Australian Museum shows all specimens from the west coast to be *Stygiocaris lancifera* Holthuis, while all those from the east coast were *S. stylifera* Holthuis (Table 3). The proportion of the two species of shrimps collected on the west coast in the 1950's (Mees 1962) and in 1989 did not differ (Table 3: $\chi^2_1 = 0.980$, P = 0.322), despite the total absence of *S. stylifera* in 1989. Hence, it is unclear whether there has been a change in the composition of the shrimp populations on the west coast as we may be considering a sampling artifact. However, there is a significant difference in the proportion of the two species collected on the east coast in 1989 and the earlier samples (Table 3: $\chi^2_1 = 106.05$, $P<0.001$); hence, it seems that a real difference may exist between the shrimp communities on the east and west coasts.

Table 3. The numbers of shrimps (*Stygiocaris* spp.) collected by various people and their locations. Data for Mees & Douglas and Snell are from Holthuis (1960).

Well	Collector	*S. lancifera*	*S. stylifera*
Kuddamurra	Snell	75	12
Kuddamurra	Mees & Douglas	56	2
Milyering	Snell	7	0
near Milyering	Snell	9	1
		147	15
West coast	Humphreys	20	0
East coast	Humphreys	0	24
		20	24
		167	39

Genetics of the subterranean fauna.

On the coastal plain of the North West Cape peninsula, within the known range of the subterranean aquatic fauna, there are two geological discontinuities which potentially could isolate water bodies. The first is at Vlaming Head (Figure 1), where a band of Vlaming Sandstone and the Pilgramunna Formation abut the coast. The second is the bisection of the coastal plain by Yardie Creek which exposes to the coast the Tulki Limestone in which the caves of Cape Range are formed (see surface geology maps in Condon, Johnstone & Perry 1955). The genetic analyses were conducted to test the null hypothesis that species are panmictic throughout their range, and secondly, that the potential geological barriers do not constitute a barrier to gene flow around the coastline. A summary of the genetic analyses is given in Table 4 and the data are in Appendices 1-4.

Table 4. Summary of the genetic information.

Attribute	*Milyeringa veritas*	*Stygiocaris lancifera*	*Stygiocaris stylifera*	Amphipoda
*caves/wells sampled	7	4	2	4
*individuals	24	16	11	25
*loci scored	43	28	28	28
*loci invariate (%)	12 (28)	21 (75)	22 (79)	13 (46)
*polymorphic loci (%)	31 (72)	7 (25)	7 (21)	15 (54)
More than one species?[1]	No	No	No	No
Panmictic population[2]	No	—	Yes	No
Geographic explanation	Yes	No	No	Yes
Troglobite	Yes	Yes	Yes	Yes

[1] Null hypothesis of all populations from the gene pool of a single species.

[2] Null hypothesis of panmixia not refuted using genetic data.

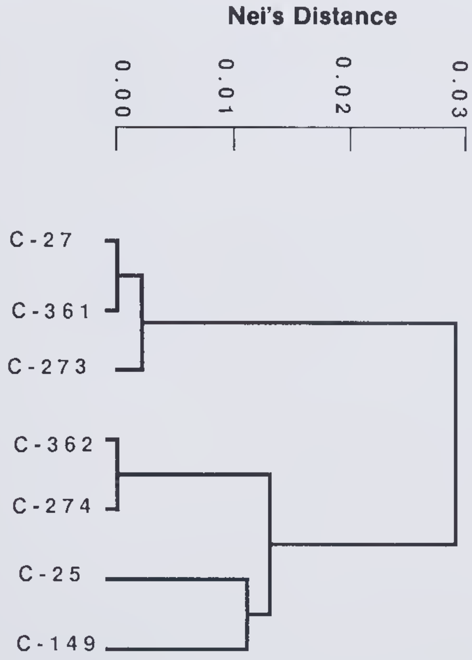

Figure 2. Dendrogram of the relationships between the populations of the The Blind Gudgeon, *Milyeringa veritas* from six localities on the North West Cape peninsula, based on Nei's Distance (corrected: see Appendix 1).

Gudgeon

Forty-three loci were scored of which 12 were found to be polymorphic. Examination of the genetic distances (Figure 2 and Appendix 1) shows that there are four populations separated by a Nei's Distance of >0.01: the north and east coast, on either side of Yardie Creek, and two partly isolated populations on the mid-west coast. The populations on either side (C-362 and C-274) of Yardie Creek, 35 km apart, are very similar genetically (Figure 2, Appendix 1). Similarly, the geological discontinuity at Vlaming Head straddles populations 10 km apart (C-27 and C-273) which are also of close genetic similarity. Clearly, the two geological discontinuities do not constitute genetic barriers to the gudgeons.

Nevertheless, the gudgeon populations are not sampled from one panmictic gene pool. This was tested by pooling the data within the four groups identified in Figure 2. Four loci show significant departure from the distribution of allele frequencies expected in sample sets taken from a panmictic population, namely Gpi-1 ($\chi^2_1 = 8.89$, $P= 0.012$), Enol-2 ($\chi^2_1 = 17.55$, $P<0.001$), Mdh-3 ($\chi^2_1 = 15.86$, $P<0.001$) and Idh-2 ($\chi^2_1 = 17.12$, $P= 0.002$).

Shrimps

Twenty-eight loci were scored of which 9 were found to be invariant (Appendix 2). The electrophoretic data clearly demonstrate the presence of two species as the two genetic groups identified have 50% fixed differences, differing at 14/28 loci (Appendix 2), and they conform with the taxonomy of Holthuis (1960).

Examination of the genetic distances (Figure 3 and Appendix 2) shows two groups in the data for the west coast (*S. lancifera*), one from the extreme north-west of the peninsula and the other from the mid-west coast. The distribution of the species and the lack of common species between the east and the west coasts prevent testing the geological discontinuity hypothesis using the shrimp genetical data.

However, the data suggest that the populations on the west coast (*S. lancifera*) are not panmictic. This was tested by pooling the data within the two groups identified in Figure 3. The locus Got-1 showed significant departure from the distribution expected in a panmictic population ($\chi^2_1 = 18.31$, $P<0.001$), while the locus Got-2 was significant if Yates correction is not applied ($\chi^2_1 = 4.57$, $P= 0.033$, or $\chi^2_1 = 2.93$, $P=0.087$ with Yates correction), a matter of statistical debate. No significant departure from panmixia was detected for *S. stylifera* on the east coast.

Given the small size of the shrimps compared with the gudgeons, the genetic continuity of the latter between the east and west coasts suggests that there are no obvious barriers to the continuity of distribution in the shrimps. The data presented here do not demonstrate this. It is clear that suitable habitat for the gudgeons does not imply that the area is also suitable for the shrimps. In C-215, where the Cape Range troglobites and the coastal subterranean fauna co-occur, the gudgeons were common but shrimps were absent, despite once being present in Milyering Well, only 1.1 km away.

Amphipods

Twenty-eight loci were scored of which 13 were found to be invariant (Appendix 3). In

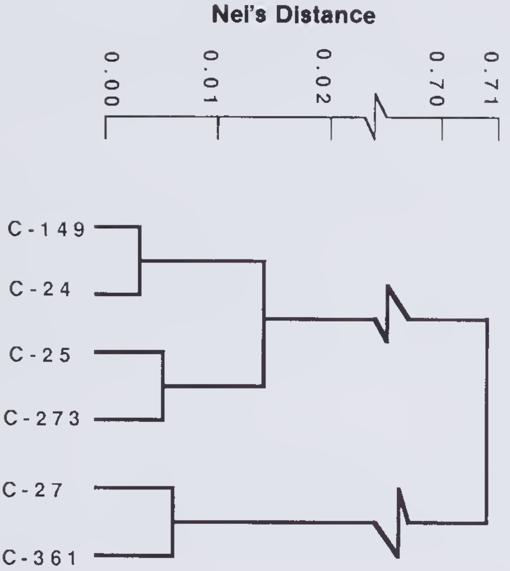

Figure 3. Dendrogram of the relationships between the populations of the atydid shrimps *Stygiocaris spp.* from six localities on the North West Cape peninsula, based on Nei's Distance (corrected: see Appendix 2). The four localities on the left represent *Stygiocaris lancifera,* while the two to the right represent *S. stylifera.* Note the break in the scale.

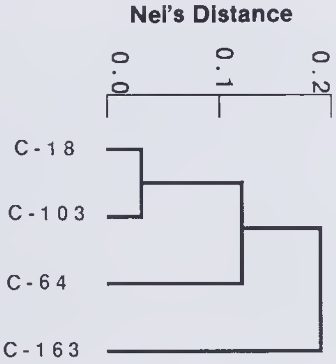

Figure 4. Dendrogram of the relationships between the populations of the amphipods from the four caves in Cape Range known to contain standing water. It is based on Nei's Distance (corrected: see Appendix 3).

contrast to the other taxa, there is evidence of considerable genetic divergence between the four cave populations (Appendix 3, Figure 4). Populations C-18 and C-103, in the centre of the distribution, are genetically similar, displaying minor differences in allele frequency (not significant because of small sample sizes) at several loci. Population C-64 at the northern edge of distribution shows more divergence, although only one locus, Tpi, reveals the presence of a fixed difference involving a unique allele. The most divergent population is C-163, located at the southern end of the distribution. This population displays a number of fixed differences when compared with the other three populations (range 14-23%), although only three loci (Gpi, Pgm-1, and Tpi) involve alleles unique to C-163.

Clearly the null hypothesis of panmixia is refuted on the evidence of the allozyme data. The levels of genetic divergence are quite high, and by themselves might indicate the presence of more than one species. However, the data are not able to resolve this situation because of the allopatric nature of the distribution of the genetic types. The high levels of polymorphism, coupled with the fact that only a small component of the genetic distance estimates is due to the fixation of unique alleles, suggests that the concept of a single, highly variable species, consisting of discrete sub-populations is the more appropriate model.

The caves in Cape Range are formed in Tulki Limestone which is highly dissected by gorges, some of which cut into the Mandu Calcarenite below. C-18 and C-103 are 4 km apart and are not separated by deep gorges cutting into the Mandu Calcarenite. C-18 and C-64 are 5.5 km apart and are separated by deep gorges cutting into the Mandu Calcarenite and exhibit 4% fixed differences. C-103 and C-163 are only 3.4 km apart but the latter is separated from the other caves by a major gorge which, however, does not appear to cut into the Mandu Calcarenite as far as can be ascertained from surface geology maps. These major gorges are associated also with genetic discontinuities in terrestrial troglobites, but not in cave dwelling but non-troglobitic species (Humphreys 1990).

Continuity of the fauna

The possibility exists that the coastal aquatic fauna is continuous beneath Cape Range, where it cannot be sampled. The four caves in Cape Range which contain amphipods have all been surveyed. The water in the caves is at an altitude of from 110 m (C-64) to 240 m (C-103), whereas the freshwater lens beneath Cape Range has an expected elevation of <5 m (Hocking, Moors & van de Graaff 1987), perhaps as low as 0.7 m (calculated from the hydraulic gradient of 6 cm km^{-1}; Bestow 1966). No cave known from Cape Range approaches a depth where a continuation of the coastal fauna beneath Cape Range would have been sampled. If the coastal fauna extends beneath the range then the genetic distances between the populations would be expected to be correlated with the direct metric distance between the populations. If the populations are restricted to the coastal limestone then the genetic distances between the populations, would be expected to be correlated with their metric distance apart along the coastal plain, namely around the northern end of the peninsula. This analysis is appropriate as panmixia has already been rejected, hence this relationship will not be a straight line with a slope of zero (see Richardson, Baverstock & Adams 1986: 287). The two measures of genetic distance for the gudgeons were regressed on both these measures of metric distance (Appendix 4; this cannot be done for the shrimps because the samples for each species are restricted to either the east or the west coast).

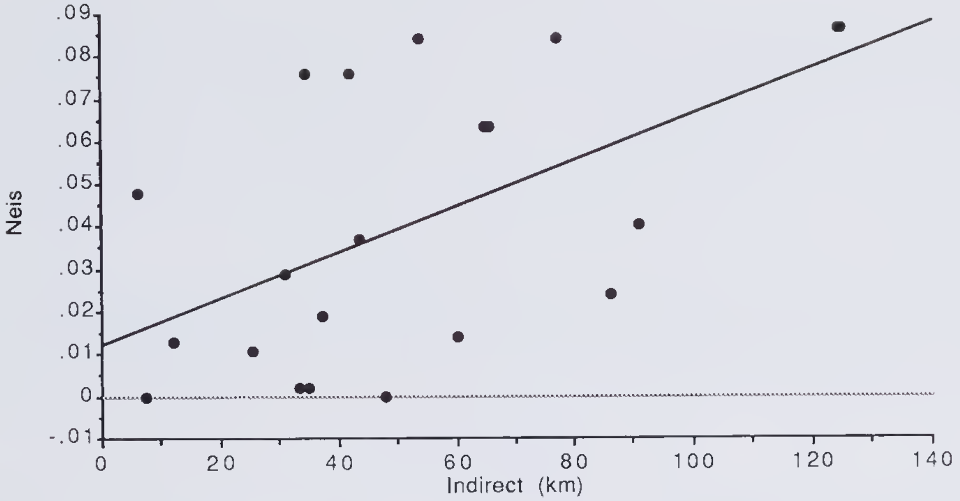

Figure 5. The relationship between Nei's Distance for the gudgeons and the indirect metric distance (km) which assumes the populations inhabit only the coastal plain.

No significant relationship was found between genetic separation of the gudgeon populations and the direct metric distance between the wells (Table 5). However, both measures of genetic distance were significantly regressed on indirect metric distance (assuming contact only along the coastal plain; Table 5, Figure 5). In addition there is a close relationship between metric and genetic distance for the shrimps, *S. lancifera* (Table 5, Figure 6). Together these analyses suggest that the coastal fauna on the North West Cape peninsula inhabits a linear system (corridor), and does not occupy the available water lens beneath Cape Range.

The form of these relationships does not fit that expected of the panmixia model (panmixia has already been rejected), nor the isolation by distance model in which the

Table 5. Summary of the statistics relating genetic distance between the gudgeon populations to two measures of metric distance between the sampling locations (see text), and the direct measure between shrimp (*S. lancifera*) populations.

Genetic Distance	Metric Distance	D.f.	Fs	P	r^2adj.	Intercept	Slope
			Gudgeon				
Nei's	Direct	1,5*	1.062	>0.25	—	—	—
Nei's	Indirect	1,5	8.497	<0.05	0.273	0.012	0.00014
Fixed	Direct	1,5	0.313	>0.10	—	—	—
Fixed	Indirect	1,5	7.651	<0.05	0.250	-0.158	0.012
			Shrimp				
Nei's	Direct	1,2	72.241	<0.03	0.934	-0.008	0.00036

*In Figs 5 and 6 each point represents a comparison between two of n populations and there are n(n-1)/2 points. As these are not statistically independent the degrees of freedom in the above analyses are based on n rather than n(n-1)/2 comparisons.

curve should be steep initially and gradually flatten out with increasing distance (see Richardson, Baverstock & Adams 1986: 287). This suggests that the discrete sub-population model may be appropriate but more detailed sampling would be required to verify this hypothesis as the sample sizes used here are too low for detailed analysis of population sub-structuring. Morton's Kinship Coefficient (not shown) is zero at a distance apart of 44 km; individuals at this distance can be considered independent of one another.

The consequences of non-panmictic cave populations have been discussed extensively elsewhere (Humphreys 1989). It is suffice to say that uncertainty about the extent of the interconnection of the fauna in the coastal system(s) complicates considerably potential management of the region. A more detailed analysis of the interconnections is required.

Groundwater

Nature of the water bodies

Water occurs in four of the caves in Cape Range for which the only evidence of continuity are the contained amphipods; one (C-64) is an outflow cave and always contains water, two caves contain accessible pools (C-18 and C-103; the former can silt up; Humphreys 1989) , while the fourth (C-163) contains long water filled passages (R. Wood; pers. comm. 1988). The estimated height of the water in the caves is >100 m above the freshwater lens beneath Cape Range (see above). The latter is recharged after exceptional rain, and the coastal areas are recharged by run off from the range (Hocking, Moors & van de Graaff 1987). The coastal fauna probably occurs at the periphery of this freshwater lens barely above sea level (up to *ca.* 1.2 m; see above).

From the mouths of the gorges in Cape Range alluvial gravel deposits fan across the coastal plain (Sofoulis 1951a). In the foothills and on the coastal plain a wedge of freshwater overlies sea water so the water is more saline closer to the coast. Dissolved solids in the water increase from 430 mg L^{-1} near the scarp to more than 2850 mg L^{-1} near the coast. The successful bores are on these drainage lines, while between them water is absent or saline (Sofoulis 1951b). This could result in interfluvial salinity barriers to the dispersal of the coastal fauna, indeed all the known faunal sites are on these drainage lines.

The lateral hydraulic conductivity in the Exmouth bore field varies by three orders of magnitude (10 to 1000 m d^{-1}; Forth 1973) and is indicative of the varied cavernous nature of the Mandu, Tulki and Trealla Limestones where the bores occur; cavernous flow can be seen at some coastal locations (*ibid.*). In such cavernous karst areas the sea water/freshwater interface is rarely found as a line of demarcation, as in a uniformly porous and permeable medium, but will occur as a broad irregular zone of diffusion which is broadest at the coast due to tidal influence and is reduced away from the sea (Forth 1973).

The influence of marine tides on the water level is not known in detail. There are daily tidal movements of 15 cm in Kudamurra, Tantabiddy and Milyering Wells on the west coast (Mees 1962). Bundera Sinkhole, a cenote, to the south of Yardie Creek clearly is

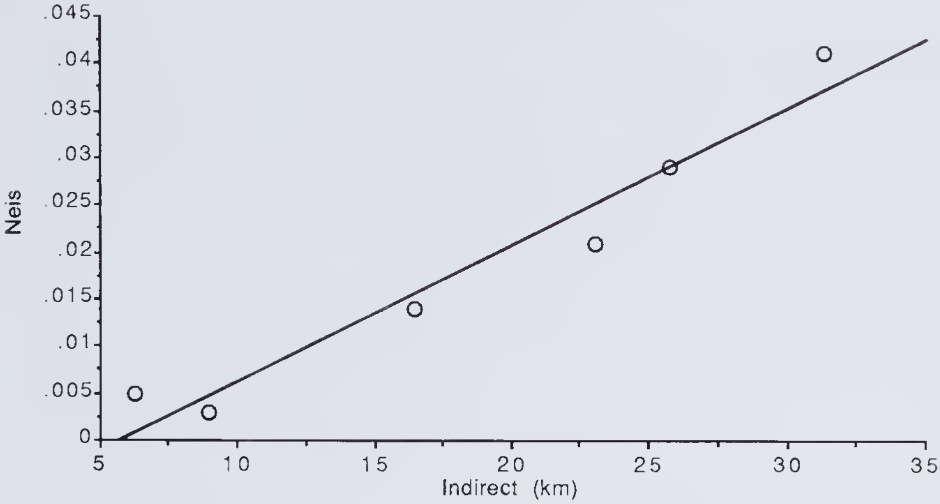

Figure 6. The relationship between Nei's Distance for the shrimp (*S. lancifera*) populations and the direct metric distance (km). No indirect measure of distance is available because all samples were from the west coast.

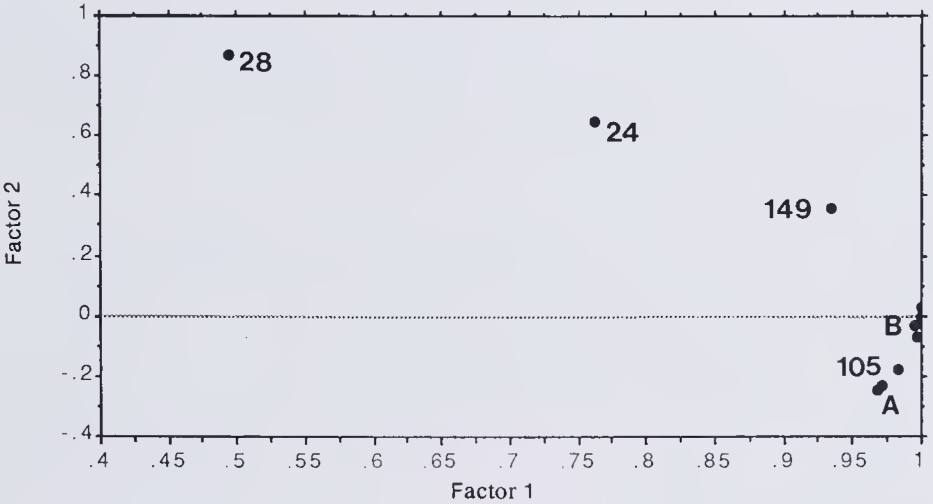

Figure 7. Unrotated orthagonal plot from a factor analysis on the parameters in Table 4 arranged by well number or name. Note that there is a trend in the data from the east coast, round the north coast and south down the west coast. Cluster A includes C-23, C-64, C-103 and C-163. Cluster B includes C-25, C-26, C-273 , C-275 and Mangrove Bore.

also tidal. On the east coast, south of Exmouth, tidal effects on the groundwater level are evident up to *ca.* 3.5 km inland (Forth 1973) and this probably affects the draw capacity of the bores.

A model for population interaction

From the foregoing discussion it is evident that there is a band of decreasing salinity away from the coast. This is superimposed on fan-shaped channels of freshwater drainage broadening towards the coast and on the gradient in the thickness of the zone of mixing of fresh and saltwater. This information permits the development of a general model, with direction but not magnitude, of the likely form of the isohalines along the coast near the drainage lines from Cape Range. It can be seen (Figure 7) that any connections between populations along the coast, and hence gene flow, will likely be close to or in the foothills of Cape Range. These areas, away from productive wells and from known subterranean fauna, are likely to be the critical areas for conservation. While this model is contraindicated by the distributional data, it needs to be explored or else any management may be both misdirected and sidetracked. The gudgeons do indeed occur in at least one area of Tulki Limestone, well into the foothills of Cape Range (C-215; see above).

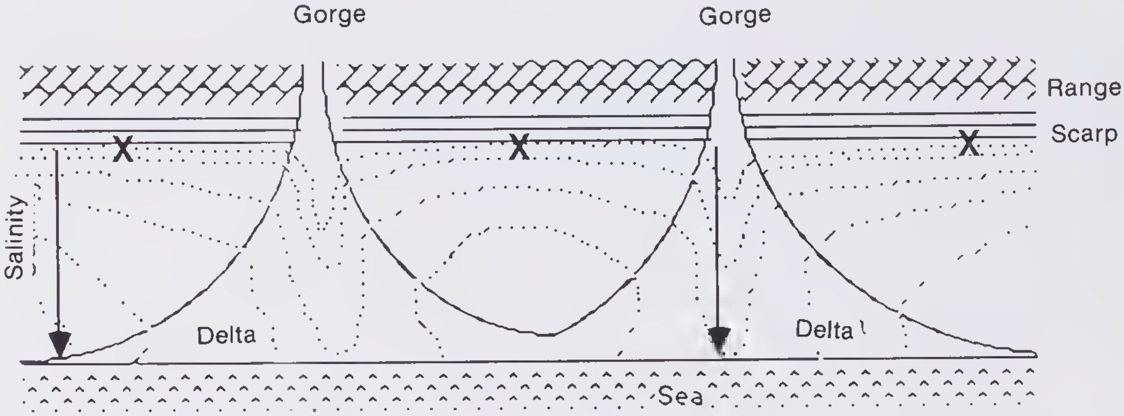

Figure 8. Schematic diagram of the scarp and coastal plain of the peninsula. The general form of the isohalines (.........) was determined from the evidence discussed in the text. The wells, hence the coastal fauna, are known mainly from the fan shaped drainage areas below the mouths of gorges in Cape Range. X marks the narrow corridor of lower salinity hypothesised to be close to or in the foothills of Cape Range and through which the populations may connect.

Water quality

The fauna inhabits water from which samples vary in salinity from 0 (C-23) to 16‰ (Bundera Sinkhole; Tables 2 and 6). Excluding the latter the salinity range is from 0 to 5‰ and a more detailed analysis of Bundera Sinkhole should be made to confirm this anomalous reading. Such coastal freshwater usually floats on a saltwater wedge but no salinity profiles have been conducted in these wells. The pH range of 6.8-7.6 (mean 7.3 [S.D. 0.29, N=11]) is characteristic of limestone areas with fast flowing water (Culver 1982).

The results of water chemistry analysis from some of the wells on the coastal plain and from caves in Cape Range are presented in Table 6. A factor analysis by sample location shows that there is a cline in the quality of the water, with a gradual increase in ionic content anti-clockwise around the coast, from the caves in Cape Range, down onto the east coastal plain, around the north coast and on down the west coast to the south of Yardie Creek (Figure 8). Linear regression analysis (Table 7) shows that most of the parameters exhibit a significant cline in this direction. If the anomalous data from Bundera Sinkhole (C-28) are excluded, salinity (log) is still significantly regressed on distance (log) ($F_{s\,1,\,10}$= 5.367, P=0.043: r^2adj. = 0.284).

Groundwater salinities in the Carnarvon Basin, of which the peninsula is a part, show a systematic increase in the direction of the groundwater flow (Hocking, Moors & van de Graaff 1987: 239), with the exception of areas of very saline groundwater such as occur on the coastal plain to the east of Exmouth Gulf (*ibid.*). This appears to be the case around Cape Range. Groundwater flow should radiate from the range but the only long reach is south of the range; it is in this downstream area that the ionic content of the groundwater is greatest. Elsewhere on the peninsula the sampling resolution is too low to detect this.

Examination of the known range of the parameters reveals that the coastal fauna inhabits a wide range of water chemistries (Table 8). The amphipods from the caves in Cape Range inhabit a narrower range of these parameters but, as a wider range of parameters does not occur within Cape Range, the data are not informative as to the tolerance of the amphipod species involved. The most notable feature is the high level of total nitrogen in the caves in Cape Range compared with the water bodies on the coastal plain.

Table 6. The results of water analysis from caves within Cape Range and from wells and bores on the coastal plain. The locations are shown in Figure 1.

Cave Number	Cave name	Salinity ‰	Na^+ mM/L	K^+ mM/L	Ca^{++} mM/L	Mg^+ mM/L	Cl^- mM/L	Total P µg/L	Total N µg/L
C-23	Dozer Cave	0.0	3.60	0.04	0.21	0.19	2.04	9	193
C-24	Milyering Well	4.0	55.80	1.12	2.90	4.80	58.70	9	68
C-25	Kudamurra Well	2.0	21.20	0.45	1.67	2.87	23.20	4	114
C-26	Tantabiddy Well	5.0	41.10	0.81	2.47	4.54	39.60	32	207
C-28	Bundera Sinkhole	16.0	248.70	5.44	5.72	23.40	253.70	21	167
C-64	Shot Hole Tunnel*	0.0	1.59	0.03	0.74	0.46	2.10	4	187
C-103	Trionomo*	0.0	0.88	0.01	1.18	0.09	1.48	14	286
C-105	The Gnamma Hole	1.0	7.34	0.15	0.75	1.10	7.73	3	134
C-149	Tulki Well	3.0	66.70	1.36	3.31	7.00	70.50	7	141
C-163	Wanderer's Delight*	0.5	1.59	0.02	1.33	0.19	2.35	4	174
C-273	5 Mile Well	4.0	57.80	1.18	3.03	5.94	59.50	23	259
—	Mangrove Bore	1.5	13.90	0.31	1.53	2.30	15.54	3	101

*Denotes caves in Cape Range rather than wells on the coastal plain; the two areas have no fauna at the level of Order in common.

Together, Tables 4 and 8 suggest that within the known range of the coastal subterranean fauna all sampled sites have a water chemistry suitable for habitation. Hence, the absence of fauna from any water body within this range is likely to be explained by the isolation of that water body from adjacent inhabited water. Such absence may result from lack of continuity of adequately sized cavities within the coastal limestone, or from a temporary drop in the water table which would prevent recolonisation following local extinction due to the stochastic processes operating on small populations.

Table 7. Results of regression analysis of various water chemistry parameters (log [Y+1]) on distance around the coast (log [X+1]) of the North West Cape peninsula. The distance is measured from the most southerly cave on the east coast, around the north coast and down the west coast, hence it is assumed that the water body is coastal and does not continue beneath Cape Range. It illustrates the significant cline in most water chemistry parameters.

Parameter	Fs	P
Salinity (‰)	7.80	0.018
Na^+ (mM/L)	10.30	0.008
K^+ (mM/L)	9.94	0.009
Ca^{++} (mM/L)	13.72	0.004
Mg^+ (mM/L)	12.91	0.004
Cl^- (mM/L)	10.61	0.008
Total P (μg/L)	2.44	0.147
Total N (μg/L)	2.26	0.161

Status of the water table

The Water Authority of Western Australia consider that the water being drawn from the Exmouth bore field is connate water, namely recharge not 'fossil water (pers. comm. 1989), and that there is plenty of space left to expand the bore fields (pers. comm. 1988). While this water is heavily drawn upon there appears to have been no consistent monitoring of the level, depth of the saline layer or the quality of the water in the areas known to be inhabited by the subterranean fauna; monitoring bores have recently been added to the Exmouth bore field. There is consistent evidence, of diverse types and sources, that the water table and water quality are falling, but it is not known whether this has resulted from fluctuations in the rainfall or from the extraction of the water for human use. That the latter is the cause, at least within the Exmouth bore field, is indicated by the rising salinity of this water supply (Water Authority of Western Australia; pers. comm. 3 February 1988).

The North West Cape peninsula of Western Australia lies just within the tropics. This semi-arid region is in that part of Australia with the least predictable rainfall, with both the constancy and contingency (*sensu* Colwell 1974) being low (Humphreys, Adams & Vine 1989). In consequence there is low probability of rainfalls sufficient to flood deeply the caves within the range (see full discussion in Humphreys, Adams & Vine 1989), and the recharge pattern of the coastal groundwater will be similarly influenced.

Table 8. The known range of various of water chemistry parameters within which the various taxa of subterranean species have been found.

Parameter	Shrimps[1]	Eel[1]	Gudgeon[1]	Amphipods[2]
pH 1988	6.8-7.5	6.8-7.3	6.8-7.5	6.8
Salinity (‰)	2-5	1-5	0-161	0-0.5
Na^+ (mM/L)	21.2-66.7	7.34-55.80	3.60-248.70	0.88-1.59
K^+ (mM/L)	0.45-1.36	0.45-1.12	0.04-5.44	0.01-0.03
Ca^{++} (mM/L)	1.67-3.31	0.75-2.90	0.21-5.72	0.74-1.33
Mg^+ (mM/L)	2.87-7.00	1.10-4.80	0.19-23.4	0.09-0.46
Cl^- (mM/L)	23.2-70.5	7.73-58.70	2.04-253.7	1.48-2.35
Total P (μg/L)	4-9	3-32	4-21	4-14
Total N (μg/L)	68-141	68-207	68-193	174-286

[1] These species occur exclusively as subterranean fauna of the coastal plain; the Blind Cave Eel, (*O. candidum*), being too rare, is the only member of the fauna not represented in the analysis. [2] Amphipods occur exclusively in caves in Cape Range, where they are the only aquatic fauna.

The evidence

Several bores have dried up or gone saline in the Joint Naval Communications Facility, to the north of the Exmouth bore field (L. Banfield; pers. comm. and *Exmouth Expression,* February 1989: 6). Town Well has become more saline and a number of other wells have dried up (Cape Well, Trealla Well and South Yardie Well), or the water level has been substantially lowered (Neds Well, C-119, Milyering Cave, Tantabiddy Well; B. Vine, pers. comm. 1989). The presence of recent bores alongside many of the wells is an indication of lowering water table. In addition a number of natural seepages from the scarp slopes have dried up e.g. Maduradura gorge (flow greatly diminished; 'used to be able to swim but can now hardly get wet feet'), a spring in Shot Hole Canyon (dried up mid to late 1970's; 'used to flow continuously but is now not even damp') and Padjari Manu (formerly Bunbury cave) in which there used to be a permanent soak into a gour pool but since the mid 1970's has been dry except after heavy rain (B. Vine, pers. comm. 1989); this was a traditional site for aboriginal people (Site Reference P0267).

The trend in water use in Exmouth was described as 'alarming' (Water Authority of Western Australia; pers. comm. 3 February 1988), even before the major development of the area was mooted. The salinity of the water extracted from the Exmouth bore field is constantly rising (*ibid.*) but it is not known whether this results from saltwater coning below the bore or from a general rise in the level of the saltwater. Clearly this is not a sustainable usage and if it continues lasting damage may be done to both the water supply and the habitat of the subterranean fauna. Extension of the bore field, the current method of management (*ibid.*), will extend the area over which this damage occurs. Considerable accuracy (±5 mm) is required to monitor changes in water level and salinity because changes need to be distinguished from the tidal influence reported in these bores and because a mere 75 mm lowering of the water table would reduce freshwater storage by 20% (Forth 1973)

Age

The age of isolation of troglobitic species remains controversial. Some authors claim a general trend/pattern for cave fauna. In general aquatic cave species are considered to have been isolated in caves for longer periods than terrestrial species, up to 2000 k yr BP (Hobbs and Barr 1972) or even earlier (Holsinger 1978). Of the species examined from North West Cape peninsula the aquatic amphipods show the most genetic divergence between caves (Humphreys 1990), while within the coastal fauna speciation has occurred in the shrimps. However, some other aquatic groups are considered to have been isolated more recently; <10 k yr BP in the Mexican characin *Astyanax mexicanus* (Mitchell, Russell & Elliott 1977) and between 20 and 0.09 k yr BP for the diverse Hawaiian larva tube fauna, but the latter may be complicated by the ability of the species to move between caves (Howarth 1972). Peck (1981a, 1981b) has suggested pulses in the rate of isolation of putative troglobites in caves of the Grand Canyon during Pleistocene interglacials, namely >350, 320-275, 235-185, 150-90 and <15 k yr BP.

The coastal plain limestones on the North West Cape peninsula originate from fringing coral reefs during periods of higher sea level. There are three higher terraces along the west coast scarp of Cape Range, to a height of *ca.* 57 m above the present sea level, which are thought to represent stadia in the Quaternary sea levels changes (Graaff, Denman & Hocking 1976). The high degree of troglobitic adaptation in the species suggests that the coastal subterranean fauna is of an age such that it did not evolve *in situ* in the current limestones (Mees 1962). They could not have occupied the current coastal limestone during the high sea levels, at which time Cape Range (together with Rough Range) would have been an island, separated from Giralia Range, and large areas of the hinterland of Cape Range would have been inundated by the sea.

With the changing sea levels following the uplift of the Miocene limestones into the Cape Range anticline, there has been ample opportunity for the present coastal fauna to have colonised water within Cape Range itself or to have evolved there and subsequently moved down to their present location. However, the lack of common fauna (no common Orders) between Cape Range and the coastal plain (Humphreys 1989), despite the suitability of the water and probable opportunity for its invasion (superficial speleothem material from C-163 has been dated by Th/Ur method at 123014 y BP [+50886, -34814]; D. Smith, pers. comm. 1990) suggests neither to be the case.

Alternatively the coastal fauna may have arrived in the area by migration along the coast in similar limestones with connecting water channels. Current conditions (not considering sea level changes) preclude migration along the coast owing to the highly saline groundwater to the east (along the shore of Exmouth Gulf) and to the south (salinity is high [Hocking, Moors & van de Graaff 1987] and traditional water sources were lacking [Carter 1902]). Indeed, there is currently a barrier of high salinity (>6000 mg L^{-1} total dissolved solids) in the unconfined groundwater across the neck of the peninsula (Hocking, Moors & van de Graaff 1987: 240).

Milyeringa's closest affinity is possibly with the eleotridid genus *Butis*. *Butis* is a mangrove dwelling genus of brackish and fresh waters of the Indo-Australian

Archipelago (i.e. ,Malay Peninsula to northern Australia including Indonesia, Philippines and most of Melanesia) (G.R. Allen; pers. comm. 1990). At the height of the Pleistocene glaciation, when sea level was 150 m lower than the present level (Chappell & Thom 1977), the western shore would have been no more than 12 km from the current shoreline (Morse 1988). Such slow lateral migration of the shoreline, over what are presumably coastal limestone deposits, offer an alternative route for immigration onto the North West Cape peninsula along a broad coastal plain.

Hence, it may be worth searching wider afield for this fauna or for related faunae. However, the cline in salinity, increasing to the south-west, suggests that isolation may have resulted from increasing salinity in the groundwater as the climate dried. Adjacent to Cape Range the groundwater is recharged from water captured in the limestone of the range. The water supply here is probably more consistent and less saline than in adjacent coastal areas without an elevated hinterland, thus permitting the fauna to survive.

Concluding remarks

The karst area on North West Cape contains a very rich troglobitic fauna (Humphreys 1989, 1990; Humphreys, Adams & Vine 1989). Some of the caves and wells lie within Cape Range National Park where legislation provides for the 'protection of indiginous . . . . fauna and . . . . any feature of scientific interest' and management objectives aim to 'protect and conserve indiginous . . . . animals and their habitats', to 'maintain scientific reference areas' and to 'conserve and protect groundwater resources' (CALM 1987). However, informed management of the coastal subterranean aquatic fauna is hampered by its main distribution being outside Cape Range National Park and by the lack of information on the biology of the fauna and the characteristics of the subterranean water. Recent sightings of the eel lie in the area of greatest development and the other species occur as isolated populations on the north-west and east coasts are outside the area of protection, as are two of the four amphipod localities, all lying in a temporary limestone reserve (TR5980H), under the authority of the Minister for Mines.

The fauna is presumably dependent upon allochthonous energy sources washed into the system during heavy rain (Humphreys, Adams & Vine 1989), although in C-215 it may receive substantial energy inputs from the dense root mats, and their exudates (Culver 1982) which penetrate the cave system; the extent of these is unknown as the coastal subterranean caverns are rarely accessible to people, but a characteristic fauna associated with such root mats seems absent. The total nitrogen levels in the coastal waters is much lower than found in Cape Range.

Alteration to the quantity or quality of the water in the caves and wells of the North West Cape peninsula will affect the populations of aquatic troglobites, as changes affecting the Tulki Limestone will influence the humid adapted terrestrial troglobites of Cape Range (Humphreys 1989; Humphreys, Adams & Vine 1989; Humphreys & Collis 1990).

At this stage little is known of the water bodies within Cape Range other than, as there is no common fauna, they are isolated from those of the coastal plains. The genetical evidence from the amphipods within Cape Range suggests that the major gorges separate not only the populations, but also the water bodies they inhabit (Humphreys, Adams & Vine 1989). In addition the genetical evidence from the coastal plain suggests that there may be partially separate water bodies also along the coastal plain. A faunal survey would have the advantage of determining the extent of the Cape Range fauna and the continuity of the water bodies.

Cave faunae generally, even terrestrial components, are vulnerable to change in the water table. *Schizomus wessoni* (Chamberlin) was eliminated from its type locality due to long term drying of the Santa Cruz River due to agricultural activities, and oases were rendered unsuitable for *S. joshuensis* by draining (Rowland & Reddell 1981). *Schizomus vinei* inhabits many caves within Cape Range, and with its associated fauna is highly dependent on the status of hydration of the caves, being derived from a tropical wet forest community (Humphreys 1989; Humphreys, Adams & Vine 1989).

Dewatering during the construction of the proposed Exmouth marina could be expected to affect the area within a 1000 m radius (Morgan and Associates 1990: 16). This will cause the saltwater wedge to move further inland and potentially bisect the known distribution of all species of the subterranean aquatic fauna. While this paper shows that knowledge of the distribution of this coastal fauna is sparse and fragmentary, the information available has led to a testable model. This suggests that the critical areas for conservation are not, as would seem obvious, those areas from which the fauna has been recorded, but the likely narrow corridors of freshwater close to the scarp between the areas from which the fauna has been recorded. Any future management strategy should consider this model.

Acknowledgements

We are grateful to a number of former and present residents of Exmouth for their experience with the local caves and wells over many years, especially Len Banfield, Malcolm East and Brian Vine. For assistance in obtaining samples we thank John Bass, Darren Brooks, Malcolm East, Brian Vine and Ray Wood. Diana Jones offered me advice on the shrimps and Caroline Lawrence drew the map. Jan Birrell provided expert technical assistance. Dr B. Knott kindly provided much of the data on water chemistry. Dr D. Smith, University of Melbourne, conducted the Th/Ur analysis. The Department of Conservation and Land Management permitted work within Cape Range National Park and the Lessees permitted work on Exmouth Gulf Station. The coastal samples were collected incidentally to work in Cape Range for which the field work was funded by the Australian National Parks and Wildlife Service, The National Heritage Committee and by the Western Australian Museum. The electrophoretic work was funded by the Australian National Parks and Wildlife Service.

I thank the referees for their advice on distribution records and statistics.

Appendices

Appendix 1: Genetic data for the Blind Gudgeon, *Milyeringa veritas.*

Appendix 1a: Allele frequencies for the seven populations of gudgeon. Alleles are designated alphabetically with 'a' being the most cathodal. Where present, multiple loci are designated numerically according to increasing electrophoretic mobility.

LOCUS	allele	C-25 Kudamurra	C-149 Tulki	Well C-273 5 Mile	C-274 Pilgramunna	C-362 Javis	C-361 Mowbowra	C-27 Kubura
Enol-2	b			75			100	100
	a	100	100	25	100	100		
Fum	b	90	100	100	100	100	100	100
	a	10						
Acon-2	c					25		
	b	90	90	100	100	75	100	100
	a	10	10					
PepB	b	90	100	100	100	100	100	100
	a	10						
Ldh-1	b	50	80	67			100	100
	a	50	20	33	100	100		
Idh-1	b	90	100	100	100	100	100	100
	a	10						
Idh-2	c	20	60	93	75	100	100	100
	b	80	40		25			
	a			7				
Pgm-2	b				12			
	a	100	100	100	88	100	100	100
Mdh-3	b		40	100	37	25	100	100
	a	100	60		63	75		
Ca	b	100	100	100	87	100	100	100
	a				13			
Gpi-1	b	50	100	42	100	100		
	a	50		58			100	100
Sordh	b	80	62	100	87	75	100	100
	a	20	38		13	25		
Maximum N		5	5	7	5	2	3	3

Invariant loci: Acon-1, Ada, Adh, Ak, Ald-1, Ald-2, Ck, Enol, Est, Fdp-1, Fdp-2, Gapd, Glo, Got-1, Got-2, Gp-1, Gp-2, Gpi-2, Gpt, Ldh-2, Mdh-1, Mdh-2, Me, Mpi, PepD, Pgam, 6Pgd, Pgk, Pgm-1, Pk and Tpi.

Appendix 1b: Genetic distance matrix. Upper = Nei's Distance (corrected for small sample size, Nei 1978); lower = Fixed Differences (%).

Well	C-25	C-149	C-273	C-274	C-362	C-361	C-27
C-25	—	0.011	0.048	0.019	0.024	0.076	0.076
C-149	0	—	0.029	0.013	0.014	0.063	0.063
C-273	2	0	—	0.037	0.040	0.002	0.002
C-274	0	0	0	—	0.000	0.084	0.084
C-362	0	0	0	0	—	0.086	0.086
C-361	5	5	0	7	7	—	0.000
C-27	5	5	0	7	7	0	—

Appendix 2: Genetical data for the atydid shrimps *Stygiocaris* spp.

Appendix 2a: Allele frequencies for the six shrimp populations. Data from C-361 and C-27 are for *S. stylifera* while the remaining four localities are from *Stygiocaris lancifera.*

		Well					
LOCUS	allele	C-273 5 Mile	C-24 Milyering	C-25 Kudamurra	C-149 Tulki	C361 Mowbowra	C-27 Kubura
Acon	d				25		
	c	100	100	100	75		
	b					83	100
	a					17	
Acyc-2	b	25					
	a	75	100	100	100	100	100
Argk-1	b						6
	a	100	100	100	100	100	94
Argk-2	b				12	100	100
	a	100	100	100	88		
Est-1	b	100	100	100	100		
	a					100	100
Est-2	c	100	100	100	100		
	b					100	87
	a						13
Gapd	b					100	100
	a	100	100	100	100		
Got-1	d			12			
	c					17	
	b	75	12	75		83	100
	a	25	88	13	100		
Got-2	c					100	100
	b	37	87	87	100		
	a	63	13	13			

Appendix 2a cont.

Gpi	c	12				50	31
	b						6
	a	88	100	100	10	50	83
Gpt	c	37	25	37			
	b	63	75	63	100		
	a					100	100
Hk	b	100	100	100	100		
	a					100	100
Mpi	b					100	100
	a	100	100	100	100		
PepA	b	100	100	100	100		
	a					100	100
PepB-1	b	100	100	100	100		
	a					100	100
PepB-2	b	100	100	100	100		
	a					100	100
PepD-1	b	100	100	100	100	50	100
	a					50	
Sordh	b	100	100	100	100		
	a					100	100
Tpl	b	100	100	100	100		
	a					100	100
Maximum N		4	4	4	4	3	8

Invariant loci: Acyc-1, Ald, Enol, Fdp, Fum, Gda, Gp, Ldh and PepD-2.

Appendix 2b: Genetic distance matrix. Upper = Nei's Distance (corrected); lower = Fixed Differences (%).

Well	C-273	C-24	C-25	C-149	C-361	C-27
C-273	—	0.021	0.005	0.041	0.742	0.708
C-24	0	—	0.014	0.003	0.787	0.758
C-25	0	0	—	0.029	0.739	0.704
C-149	0	0	0	—	0.791	0.783
C-361	50	50	50	50	—	0.006
C-27	50	50	50	50	0	—

Appendix 3: Genetical data for the Amphipoda from four caves in Cape Range.

Appendix 3a: Allele frequencies of Amphipoda.

LOCUS	allele	C-18	C-64	C-103	C-163
Acon-1	b				17
	a	100	100	100	83
Acyc	b	100	50		100
	a		50	—	
Adh	b	12	100		
	a	88		—	100
Fdpase	b	50		100	100
	a	50	100		
Gapd	b		28		100
	a	100	72	100	
Got-1	b	62	78		100
	a	38	22	100	
Got-2	b				6
	a	100	100	100	94
Gpi	e				5
	d				89
	c				6
	b	75	100	100	
	a	25			
Idh	b	100	100	100	39
	a				61
Lap	b	100	50		100
	a		50	—	
Mpi	b	12			
	a	88	100	100	100
PepB-1	b		17		
	a	100	83	—	100
PepB-2	a	100	100	—	100
PepD	c				56
	b	75	100	37	44
	a	25		63	
6Pgd	a	100	100	—	100
Pgm-1	c				100
	b	100	83	100	
	a		17		

Appendix 3a cont.

Tpi	c		100		
	b	100		100	
	a				100
Maximum N		4	9	4	9

Invaraint loci: Acon2, Enol, Gp-1, Gp-2, Gpt, Ldh, Mdh-1, Mdh-2, PepA, Pgm-2 and Pk.

Appendix 3b: Genetic distance matrix. Upper = Nei's Distance (corrected); lower = Fixed Differences (%).

Cave	C-18	C-64	C-103	C-163
C-18	—	0.108	0.033	0.194
C-64	4	—	0.155	0.286
C-103	0	9	—	0.310
C-163	14	18	23	—

Appendix 4: Distances between caves and wells.

Appendix 4a: Matrix of the distance between the wells on the North West Cape peninsula. Upper right: shortest distance (km) between all pairs of wells. Lower left: distance (km) around the north of the peninsula under the assumption that the subterranean aquatic fauna does not live beneath Cape Range.

	C-24	C-25	C-27	C-149	C-273	C-274	C-361	C-362
C-24	—	17	22	9	23	21	20	69
C-25	17	—	13	26	6	38	16	86
C-27	50	35	—	29	10	40	8	87
C-149	9	26	65	—	31	12	25	60
C-273	23	6	34	31	—	44	17	91
C-274	69	38	54	1	44	—	35	48
C-361	58	42	8	66	35	77	—	80
C-362	69	86	124	60	91	48	125	—

Appendix 4b: Matrix of the distance (km) between all pairs of caves in Cape Range containing amphipods.

	C-18	C-64	C-103	C-163
C-18	—	5.8	3.8	7.5
C-64		—	9.0	11.5
C-103			—	3.3
C-163				—

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Revision of *Lerista orientalis* (Lacertilia: Scincidae) of northern Australia

G.M. Storr*

Abstract

Lerista orientalis is divided into three species, viz. *L. orientalis* from north-eastern Western Australia to north-western Queensland, *L. zonulata* from north-eastern interior of Queensland and *L. ingrami* from south-east coast of Cape York Peninsula.

Introduction

When *L. orientalis* was recently recorded from Western Australia (Greer 1990), I borrowed material in order to draw up a description and to check the suspicion that *L. orientalis* was composite (Wilson and Knowles 1988: 181). This suspicion was well-founded, for the material proved to consist of three allopatric species.

This paper is based on specimens kindly loaned by the Australian Museum (catalogue numbers prefixed by AM, Northern Territory Museum (NTM), Queensland Museum (QM), South Australian Museum (SAM) and Western Australian Museum (WAM).

Systematics

Lerista orientalis (DeVis)

Miculia orientalis DeVis 1889: 160.

Diagnosis

A small slender *Lerista* with 4 fingers, 4 toes, and immovable eyelid (a spectacle) differing from *L. zonulata* mainly in its broad dark diffuse upper lateral zone with more or less definite upper edge but no definite lower edge, and from *L. ingrami* in its greater size, overall darker colouration, more numerous superciliaries (5 vs 4 or 5) and midbody scale rows (mostly 20 vs mostly 18) and larger nasals and frontoparietals.

Description.

Snout-vent length (mm): 21-49 (N 71, mean 38.7). Length of appendages etc. (% SVL): foreleg 8-13 (N 55, mean 9.7), hindleg 17-25 (N 56, mean 20.3), tail 105-143 (N 24, mean 122.4), snout to foreleg 25.5-33 (N 58, mean 29.3).

Nasals in very short to long contact. Prefrontals widely separated. Frontoparietals in moderately short to long contact (N 54) or very short to short contact (2), about as large as interparietal. Nuchals 0-3 on each side (N 55, mean 1.9). Supraoculars 3, first two in contact with frontal. Supraciliaries 5, second and fifth smallest, first occasionally as large as third and fourth. Loreals 2, second smaller. Presuboculars 2, second much the smaller. Upper labials 6 (5 on one side of one specimen). Midbody scale rows 18 (N 1), 20

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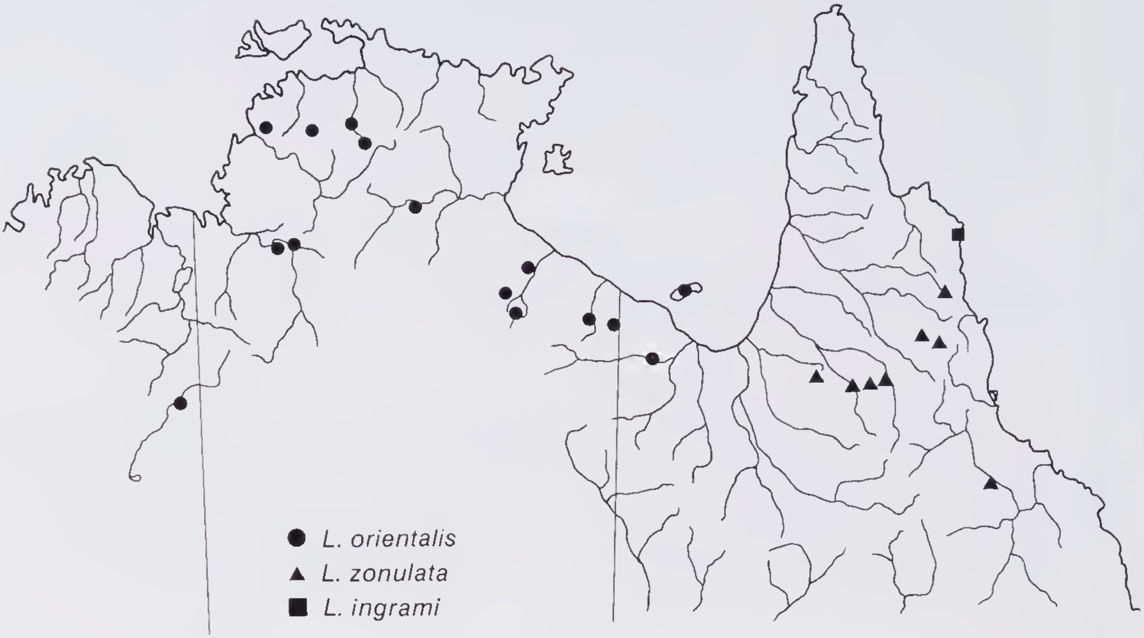

Figure 1 Map of northern Australia showing location of specimens of *Lerista orientalis, L. zonulata* and *L. ingrami.*

(43), 21 (1) or 22 (7). Lamellae under longest toe 11-15 (N 58, mean 13.0), with or without a fine weak keel.

Upper surface pale to moderately dark olive grey, olive brown or reddish brown, becoming paler and more reddish on tail, and marked with blackish brown or dark brown: stippling (often heavy) on head and tail and 4 rows of dots (sometimes faint, especially outer pair) passing through centre of dorsal scales. Upper lateral zone back to base of tail blackish brown (dark pigment sometimes confined to broad edge of scales), usually fairly sharp-edged superiorly but gradually merging inferiorly with lower lateral zone, and extending forward as a stripe through orbit, lore and nasal before becoming paler, narrowing, curving down and meeting opposite number at tip of snout. Labials barred blackish brown. Lower surfaces pale brown to brownish white; lower laterals and sometimes ventrals finely dark-edged.

Distribution

Semiarid interior of Kimberleys, Western Australia, subhumid and semiarid coastal drainages of north of Northern Territory and far north-west of Queensland (including Mornington I.), mainly in hilly country. See map, Figure 1.

Remarks

This taxon was based on a specimen (presumably from Gregory Downs) that is no longer extant, but DeVis' excellent description can only apply to this species.

Material

Western Australia: Gordon Down (NTM 0285).

Northern Territory: Stapleton National Park at Florence Falls (NTM 8664-5) and Bamboo Creek (NTM 8742-7); Ban Ban Spring (NTM 3143, 3179-80, 3210-2); Kakadu National Park in 13°12′S, 132°18′E (NTM 13920, 13924) and in 13°47′S, 132°34′E (NTM 13977); Roper Hwy, 9 km E Moroak T/O (AM 117090-3); Gregory National Park in 15°36′S, 131°07′E (NTM 13268, 13284); 50 km E Timber Creek (WAM 60201); 26 km WSW Borroloola (AM 54151, 117060); Balbirini Station in 16°44′S, 135°33′E (AM 117014-39); Mallapunyah (AM 20759); Blackfellow Springs, Calvert Hills Station (NTM 14448, 14450); Wollogorang Station, including Echo and Banyan Gorges (NTM 14407-8, 14418, 14426-7).

Queensland: Mornington I. (SAM 5360); Doomadgee (SAM 5391, 5394A-F, 5395; QM 10909, 47699, 47722, 47752, 47818, 47828).

Lerista zonulata sp. nov.

Holotype

R63747 in Australian Museum, collected on 5 July 1977 by A.E. and P. Greer at Georgetown, Queensland, in 18°17′S, 143°33′E.

Paratypes

Queensland: Mt Windsor Tableland in 16°19′S, 145°01′E (QM 38756); 10 km SW Mareeba (AM 94575-6); Chillagoe (QM 31223) and 3 km SE (AM 87801); near Petford (QM 47103), Georgetown (AM 63733-46, 63748-67) and 34 km W (AM 63724-5) and 40 km E (AM 63258); Croydon (AM 63340-50, 63361-9, 63370-4, 63677-84); Sellheim (QM 46268); Charters Towers (WAM 21485).

Diagnosis

A small slender *Lerista* with 4 fingers, 4 toes and immovable eyelid (a spectacle), differing from *L. orientalis* mainly in its sharp-edged dark upper lateral stripe, and from *L. ingrami* in its greater size, darker coloration, more supraciliaries (normally 5, *v.* 4 or 5), more midbody scale rows (mostly 20, *v.* mostly 18), larger nasals and larger frontoparietals.

Description

Snout-vent length (mm): 25-50.5 (N 90, mean 39.2). Length of appendages etc. (% of SVL): foreleg 6.5-12 (N64, mean 8.5), hindleg 15-22 (N65, mean 18.7), tail 99-139 (N36, mean 118.4), snout to foreleg 25-35 (N67, mean 28.8).

Nasals in very short to long contact. Prefrontals widely separated. Frontoparietals in moderately short to long contact (N51) or very short to short contact (5), about as large as interparietal. Nuchals 1-4 on each side (N56, mean 2.2). Supraoculars 3, first two in contact with frontal. Supraciliaries 5 (N57, second and fifth smallest, first occasionally as large as third and fourth) or 4 (N3, due to fusion of first and second). Loreals 2, second smaller. Presuboculars 2, second much the smaller. Upper labials 6. Midbody scale rows 20 (N 52), 21 (2) or 22 (5). Lamellae under longest toe 11-15 (N 61, mean 12.7), with or without a fine weak keel.

Upper surface pale to moderately dark olive brown, olive grey or greyish brown, becoming paler and more reddish on tail, and marked with dark brown or blackish brown: stippling on head (sometimes heavy) and tail and 4 (occasionally 6) rows of dots or small spots (sometimes faint) passing through centre of dorsal scales. Wide sharp-edged dark brown or blackish brown upper lateral stripe (about 2 scales wide) extending back to tail (on which it narrows and breaks up into a series of spots) and forward through orbit, lore and nasal before narrowing, curving down and meeting its opposite number at tip of snout. Upper labials and sometimes lower labials barred or dotted with dark brown. Upper surface of legs pale brown, mottled or stippled with dark greyish brown. Lower surfaces brownish white; lower lateral, lateroventral and sometimes ventral and subcaudal scales edged or dotted with greyish brown.

Distribution

Interior of north Queensland from the Mt Windsor Tableland south to Charters Towers, mainly in semiarid hilly country. See map, Figure 1.

Remarks

Because of its sharp-edged upper lateral stripe, this species is superficially similar to *L. ingrami,* but I believe that it is closer to *L. orientalis,* which it resembles in size, scalation, habitat preferences and most aspects of coloration. For colour photograph of a specimen from Chillagoe see Wilson and Knowles (1988, pl. 563).

Derivation of name

From Latin *zonula* (small belt), in reference to the upper lateral stripe.

Lerista ingrami sp. nov.

Holotype

J 32396 in Queensland Museum collected on 27 July 1976 by G.J. Ingram near beach north of mouth of McIver River, Queensland, in 15°07′S, 145°15′E.

Paratypes

Queensland: 7 km N of mouth of McIver River (QM 20644-51) and 5 km N (QM 20653).

Diagnosis

A very small, very pale, slender *Lerista* with 4 fingers, 4 toes, immovable eyelid (a spectacle) and sharp-edged dark upper lateral stripe, differing from *L. zonulata* and *L. orientalis* in its lesser size, paler coloration (especially white lower lateral and ventral surfaces), fewer supraciliaries (4 or 5, *v.* normally 5), fewer midbody scale rows (mostly 18, *v.* mostly 20) and smaller nasals and frontoparietals.

Description

Snout-vent length (mm): 20-36 (N 10, mean 25.1). Length of appendages etc. (% SVL): foreleg 9-13 (N 9, mean 10.4), hindleg 19-27 (N 9, mean 23.6), tail 93-114 (N 6, mean 103.5), snout to foreleg 28-36 (N 9, mean 32.2).

Nasals in very short to short contact (N 7) or just touching (1). Prefrontals widely separated. Frontoparietals in medium contact (N 4), very short to short contact (4) or just touching (1), smaller than interparietal. Nuchals 2-4 on each side (N 5, mean 2.6).

Supraoculars 3, first two in contact with frontal. Supraciliaries 5 (N 5, third and fourth largest) or 4 (N 5, due to fusion of first and second). Loreals 2, second smaller. Presuboculars 2, second much the smaller. Upper labials 6. Midbody scale rows 18 (N 7) or 20 (3). Lamellae under longest toe 12-15 (N 10, mean 13.6), smooth.

Upper surface very pale greyish brown, marked with dark brown: small spots on head and 4 rows of dots passing through centre of dorsal scales. Moderately wide, sharp-edged dark brown upper lateral stripe from side of rostral to base of tail, about 1½ scales wide on body, narrowing on lore, dilating at and surrounding eye and nostril, and occasionally meeting its opposite number after narrowing and curving down on front of rostral. Upper surface of legs brownish white, stippled with brown. Other surfaces (including lips and under tail) white.

Distribution

Only known from south-east coast of Cape York Peninsula near mouth of McIver River.

Remarks

The humid sandy coastal heaths between Cooktown and Cape Flattery are also the exclusive home of two other skinks, viz. *Ctenotus rawlinsoni* and *Carlia dogare* (Ingram 1979).

Derivation of name

After Dr G.J. Ingram of the Queensland Museum.

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A revision of the echinoderm genus *Bunaster* (Asteroidea: Ophidiasteridae)

Loisette M. Marsh*

Abstract

The four nominal species of *Bunaster*, previously known from very few specimens, are confined to the Philippines area, Indonesia and Australia. The holotype of *B. ritteri* has been re-examined and this species becomes the senior synonym of *B. lithodes* Fisher. *B. ritteri* is here recorded from Australian seas for the first time. *Bunaster uniserialis* and *B. variegatus*, described from north-eastern and south-western Australia respectively are confirmed as distinct species.

Introduction

The species of *Bunaster* form a homogeneous group with relatively minor differences between the species and because of their rarity there has been little opportunity to study their variation. They are restricted to the south-east Asian and Australian region, from the Xisha (Paracel) Islands in the South China Sea to the northern, north-eastern and western coasts of Australia. They are usually cryptic in habit, at least in shallow water, and are found from the shore to nearly 200 metres.

The genus, *Bunaster* and type species, *B. ritteri* Döderlein, 1896, were described from a single specimen from Amboina (Ambon, Indonesia); a second species, *B. lithodes* Fisher, 1917 was described from a single specimen from the Philippines and *B. uniserialis* H.L. Clark, 1921, also from a single specimen, from Torres Strait. The fourth species, *B. variegatus* H.L. Clark, 1938 was described from 12 specimens from south-western Australia including specimens from the Houtman Abrolhos, previously identified as *B. lithodes* (H.L. Clark 1923).

With more material now to hand it is now possible to record the range of variation in characters (particularly those likely to be size dependent) of all three species.

The holotypes of all four nominal species have been examined and the enigmatic *B. ritteri* compared with the holotype of *B. lithodes* and with other specimens formerly identified as the latter species. *B. ritteri* is shown to be the senior synonym of *B. lithodes* and is here recorded from reefs in north-western Australian waters for the first time. The close similarity between *B. uniserialis* and *B. variegatus* led to a critical comparison of the types and a series of specimens from north Queensland and south-western Australia. Apart from their geographical separation there are consistent morphological differences between the two, which are confirmed as valid species.

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Terminology and Abbreviations

Standard measurements for Asteroidea are used: R is the major radius from mouth to arm tip, r is the minor radius from mouth to the interradial margin and br is the arm width at the base of the arm. The names of the institutions from which specimens were examined are abbreviated as follows: AM, Australian Museum, Sydney; MCZ, Museum of Comparative Zoology, Harvard; Munich, the Zoologische Staatssamlung, München; WAM, Western Australian Museum, Perth.

Systematics

Bunaster

Bunaster Döderlein, 1896: 317

Diagnosis

A genus of Ophidiasteridae with small disc and elongate, more or less cylindrical arms; size small (maximum recorded R, 23 mm); abactinal and marginal plates bare, convex, with small granules between plates; marginal plates prominent, wider than long, when viewed from above, and set at an angle to the direction of the arm; intermarginal plates present; papulae in 6-10 rows; small bivalved pedicellariae usually present, excavate pedicellariae rare. Distributed from the South China Sea to Australia, from the shore to *c.* 200 metres.

Type species: *Bunaster ritteri* Döderlein, 1896: 317.

Other species included: *Bunaster uniserialis* H.L. Clark, 1921 and *B. variegatus* H.L. Clark, 1938; (*B. lithodes* Fisher, 1917 is referred to synonymy of *B. ritteri*).

Remarks

Despite their small size members of the genus are very distinctive while the species are superficially very similar to one another.

Bunaster is unlike other ophidiasterids in the strong development and angling of the marginal plates. In this respect and in the presence of intermarginal plates it resembles the Cretaceous species *Stauranderaster coronatus* (Forbes, 1848) (Stauranderasteridae). This species has entrenched pedicellariae of ophidiasterid type but as the ambulacral armature and actinal plates are not described (Spencer 1905, Spencer and Wright 1966), one can only speculate on a possible relationship and on the age and lineage of this otherwise Recent genus. Blake (1987) notes that the valvatid family Stauranderasteridae has Oreasteracean affinities but is in need of re-evaluation.

On the present evidence *Bunaster* is probably best placed in the Recent family Ophidiasteridae but the nature of the marginal plates and the presence of both bivalved and entrenched pedicellariae suggest affinities with the Oreasteridae and possibly with the extinct Stauranderasteridae.

Key to the species of *Bunaster*

1 Papulae in 10 rows, 1-4 pores per papular area, actinal plates in two series; South China Sea to Timor Sea .... *B. ritteri*
1^1 Papulae in 6-8 rows, single 2
2 Papulae in 6 rows, actinal plates in a single series; Great Barrier Reef, Queensland .... *B. uniserialis*
2^1 Papulae in 6-8 rows, actinal plates in two (occasionally 3 or 4) series; south Western Australia .... *B. variegatus*

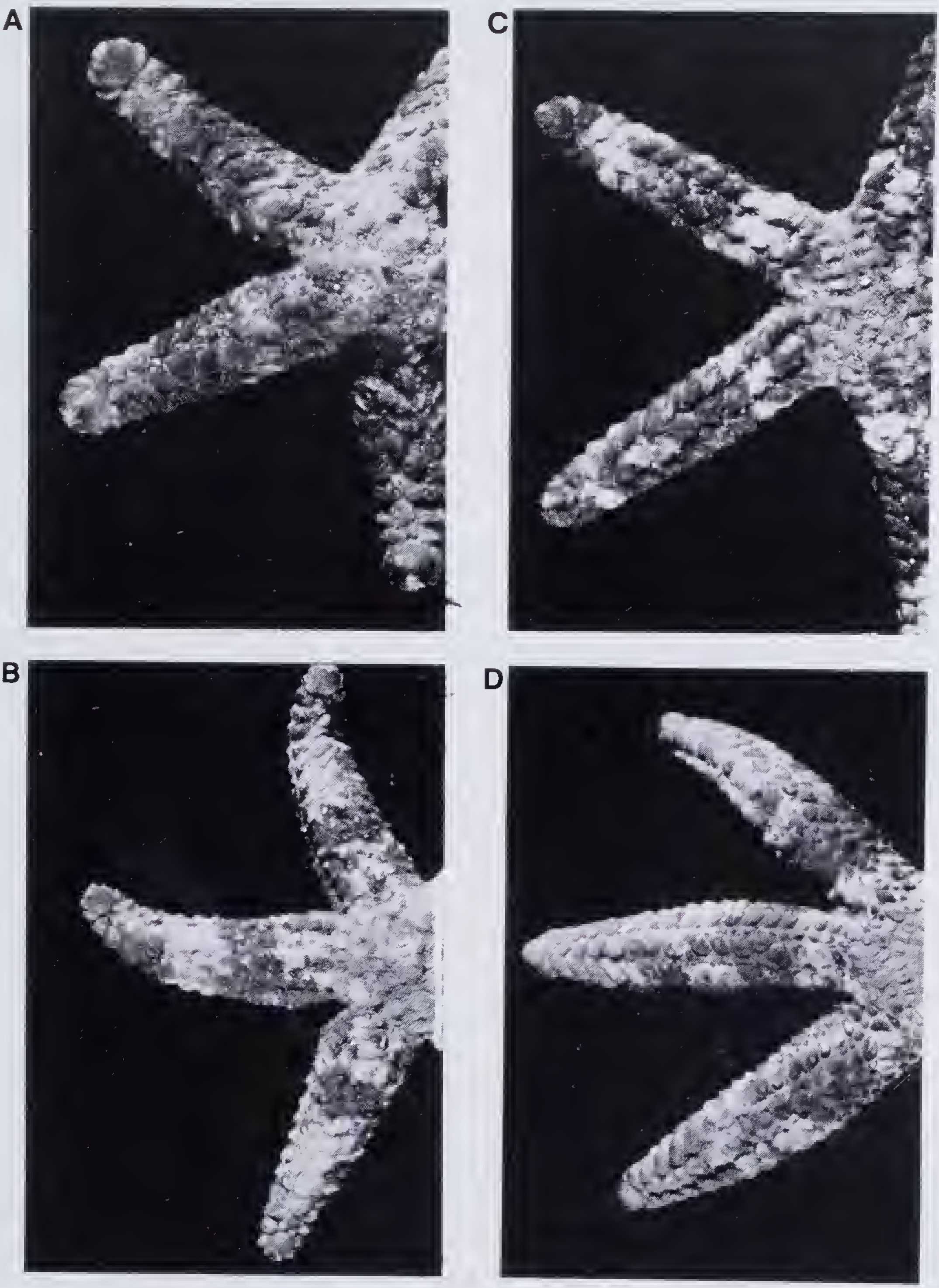

Figure 1. Abactinal views of holotypes of (a) *Bunaster ritteri* (R/r = 10.0/2.8 mm); (b) *B. lithodes* (R/r = 22.0/5.0 mm); (c) *B. uniserialis* (R/r = 11.3/2.7 mm); (d) *B. variegatus* (R/r = 21.0/5.0 mm).

Bunaster ritteri Döderlein

Table 1, Figures 1a,b, 2a,b, 3a,b, 4a,b.

Bunaster ritteri Döderlein, 1896: 317-319, pl. 22, Figures 1a-g. Clark, H.L. 1921: 69; Clark and Rowe 1971: 34-35 (distrib.), 61 (key), Figure 15f; Jangoux *et al.* 1987: 305

Bunaster lithodes Fisher, 1917: 91; Fisher, 1919: 398, pl. 95, Figures 8-8b, pl. 124, Figure 4; Clark, H.L., 1921: 69; Clark and Rowe, 1971: 34-35 (distrib.), 61 (key); Liao, 1980: 157-158, Pl. 3.

non *B. lithodes*, H.L. Clark 1923: 241 (= *B. variegatus* Clark 1938).

Material examined

The holotypes of *B. ritteri* (Munich 935/1) and *B. lithodes* (MCZ 2498); 3 spec. MCZ 3708 from coral reef Aor I. (Alor?) South China Sea, June 1938, ex Raffles Museum; 1 spec. Munich, Siboga stn 282, 27-54 m; WAM 49-88 (2), one on top of a deal coral boulder, one on the under side, on the reef flat on the north side of Cartier Island (12°32'S, 123°33'E) L. Marsh, 20 Sept. 1986; WAM 50-88, under boulder on sea-grass covered reef flat north of West Island, Ashmore Reef, Timor Sea (12°14'S, 122°58'E) L. Marsh, 18 Sept. 1986; WAM 385-90 (3), Xisha Islands, South China Sea (16-17°N, 111-113°E approx.), Liao Yulin.

Photographs of *B. lithodes* Fisher, USNM E 10238 from Alor I., South China Sea.

Diagnosis

Disc convex, arms tapering, round in section, maximum known R of 23.0 mm. Abactinal plates separated by elongate granules, fairly closely spaced; papulae 1-3 (occ. 4) per area in 10 rows. Actinal plates in two series; enlarged granules at the base of the subambulacral spines vary from a few to a complete series along the ray; granules present between furrow and subambulacral spines. Distributed from the South China Sea to the Timor Sea, on coral reefs and to 54 metres.

Description

Disc convex, arms tapering, round in section, R/r = 10.0/2.8 mm (3.6/1), br = 2.6 mm (holotype of *B. ritteri*), R/r of 22.0/5.0 mm, (4.4/1), br = 6.0 mm (holotype of *B. lithodes*) (Figure 1a,b) to 23.0/6.0 (3.8/1), (WAM 385-90 (1 of 3)). Abactinal and marginal plates very convex, resembling "in miniature, irregular boulders set in coarse pebbly mortar" Fisher (1919). Abactinal plates appear bare, separated by one or more series of elongate granules, fairly closely spaced. Papulae 1-3 (occ. 4) per area in 10 rows; carinal plates in a somewhat irregular series but some elongate and angled to the direction of the arm; an irregular series of up to 14 dorsolateral plates lie either side of the carinals; marginal plates 10-11 (holotype of *B. ritteri*), 17-18 (holotype of *B. lithodes*) to 18-19 in WAM 385-90 with up to 16 intermarginal plates in one, occasionally two series; surface texture of the plates with microscopic roughness (Figures 3a,4a); actinal intermediate plates convex, in two series of similar sized plates or with larger plates in the outer row (Figure 2a,b); subambulacral spines separated from each other and from the furrow series by granules some of which, at the base of the subambulacral spines, are enlarged and tend to form a distinct row on some rays; small white bivalved pedicellariae among granules near many papular pores (Figure 4a). Spatulate tongs-shaped pedicellariae are embedded in some superomarginal and disc plates of the holotype of *B. lithodes* (Fisher, 1919 pl 95, Figures 8a, b) and two specimens from the Xisha Islands (WAM 385-90,

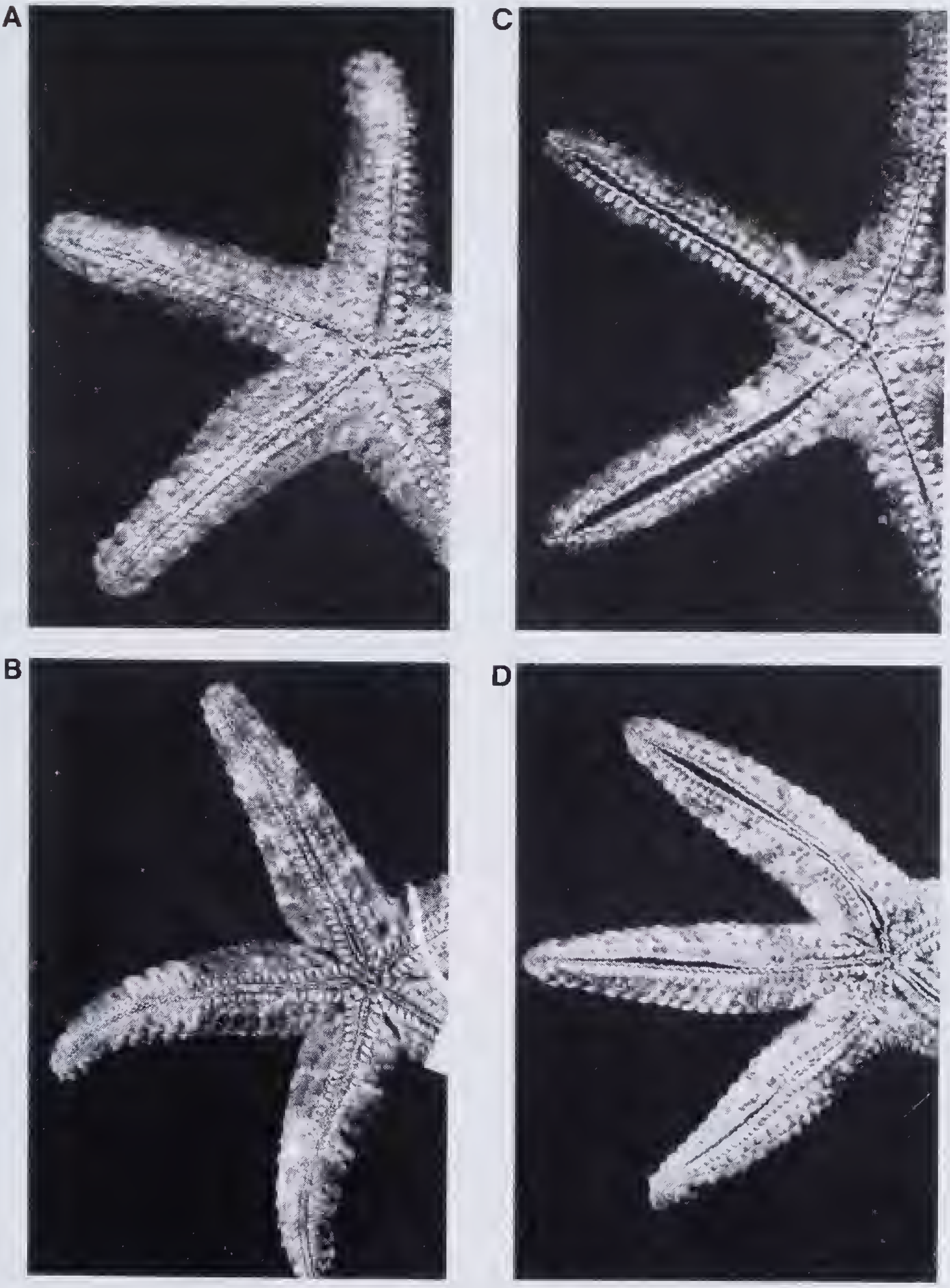

Figure 2. Actinal views of holotypes of (a) *Bunaster ritteri;* (b) *B. lithodes;* (c) *B. uniserialis;* (d) *B. variegatus.*

Figure 4b). Colour (alive) mottled shades of greenish grey, dried these are shades of brown, peaks of some plates white, skin where visible, usually white.

Variation

The holotypes of B. *ritteri* and *B. lithodes* have been examined together with ten other specimens. The variation in size dependent characters is shown in Table 1.
The specimens range in size from R/r of 10.0/2.8 mm to 23.0/6.0 mm, the R/r ratio varies from 3.6 to 4.7/1; marginal plates range from 13 in the smallest to 18-19 in the largest (WAM 385-90); dorsolateral plates range from 6 to 16 and intermarginals from 4 to 16; actinal plates in two rows in all specimens, the outer row usually with larger plates at least basally; papulae are in 10 rows in all specimens with 1-2 papulae per area in the smallest to 3 (occasionally 4 on the disc) in the largest; papulae in a single actinal row, two intermarginal and two dorsolateral rows (making a total of 10 rows); subambulacral spines elongate in the holotype of *B. lithodes* and in specimen USNM E 10238 but shorter, more almond shaped in WAM specimens and the holotype of *B. ritteri*; enlarged granules at the base of the subambulacral spines vary from a few to a complete series along the ray; granules between the bare plates are everywhere small and close packed; small white bivalved pedicellariae are abundant, but entrenched tongs-shaped pedicellariae are rare.

Holotype

Zool. Staatssammlung, Munich, ref. 935/1 (dry).

Type Locality

Amboina (Ambon, Indonesia).

Habitat

Coral reefs. The Australian specimens were found on and under boulders on reef flats. The Siboga specimen is from 27-54 metres.

Distribution

Xisha (Paracel) Islands in the South China Sea; Philippines; Indonesia; Ashmore and Cartier reefs in the Timor Sea.

Remarks

Bunaster ritteri has been distinguished from the other species of *Bunaster* by the presence of curious "ball and socket" organs (Fisher 1919; Clark and Rowe 1971). Examination of the holotype shows that these enigmatic structures are actually partly inflated papulae (Figure 3a). The white granules described by Döderlein are small bivalved pedicellariae (Figure 4a).

Fisher (1919) noted the difference in shape of the subambulacral spines between the holotypes of *B. ritteri* and *B. lithodes* but examination of a series of specimens shows a good deal of variation in this character and in the relative size of actinal plates of the two series. Fisher (1919) notes that the granules between the naked areas of the plates are smaller and more numerous in the holotype of *B. lithodes* than in that of *B. ritteri* but this character too is subject to some individual variation.

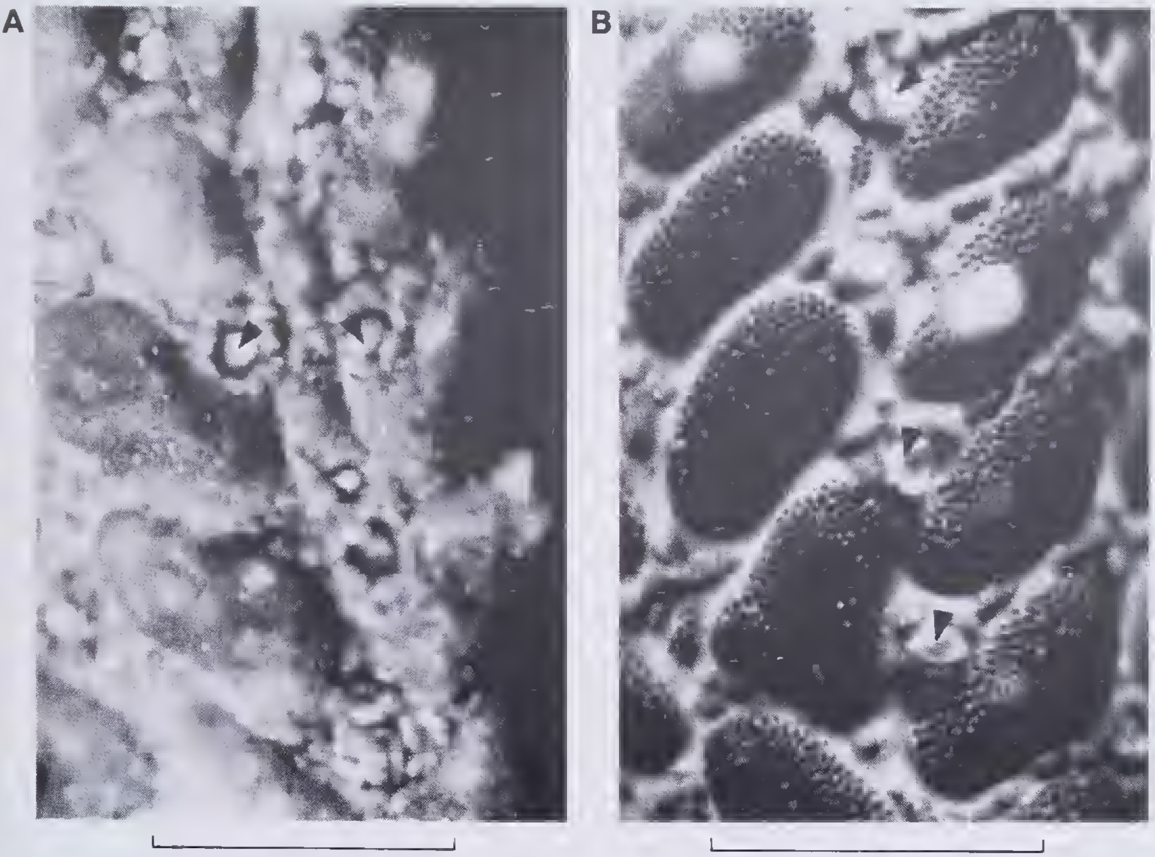

Figure 3. Detail of abactinal and superomarginal plates showing surface texture, interstitial granules and partly inflated papulae (arrowed) (a) *Bunaster ritteri* (holotype); (b) *B. uniserialis* (AM J9690). Carinal plates on left of each photograph, superomarginals on right, scale bar = 1 mm.

No characters can be found to separate *B. lithodes* from *B. ritteri* so that the former becomes a junior synonym of the latter.

B. ritteri is distinguished from *B. uniserialis* by the presence of 10 rows of 1-3 (occ. 4) papulae and two rows of actinal plates and from *B. variegatus* by the 10 rows of 1-4 papulae and the more irregular convexity of the abactinal plates. The granules separating the bare plates form a more complete cover in *B. variegatus* than in *B. ritteri*. The distribution of *B. ritteri* does not overlap that of either *B. uniserialis* or *B. variegatus*.

***Bunaster uniserialis* H.L. Clark**

Table 1, Figures 1c, 2c, 3b, 4c.

Bunaster uniserialis H.L. Clark, 1921: 69-71, pl. 7 Figure 2, pl. 36, Figures 5-7; H.L. Clark 1946: 118; Clark and Rowe 1971: 34-35 (distrib.), 61 (key).

Material examined

The holotype (MCZ 2313) and 16 specimens from the Great Barrier Reef, Queensland. AM J9237, 5 m, Wistari Reef, Capricorn Gp, G.B.R., Queensland, N. Coleman, 14 July 1975; AM J17304, no loc., 3 m; AM

J19401, 25 m on overhanging wall, outer slope, Osprey Reef, Coral Sea (13⁰56′S, 146⁰32′ E) I. Loch, 17 Dec. 1984; AM J21513 fore reef, on crest, 1 m, Robertson Reef, G.B.R., J. Davidson, 21 Nov. 1986; AM J21514,

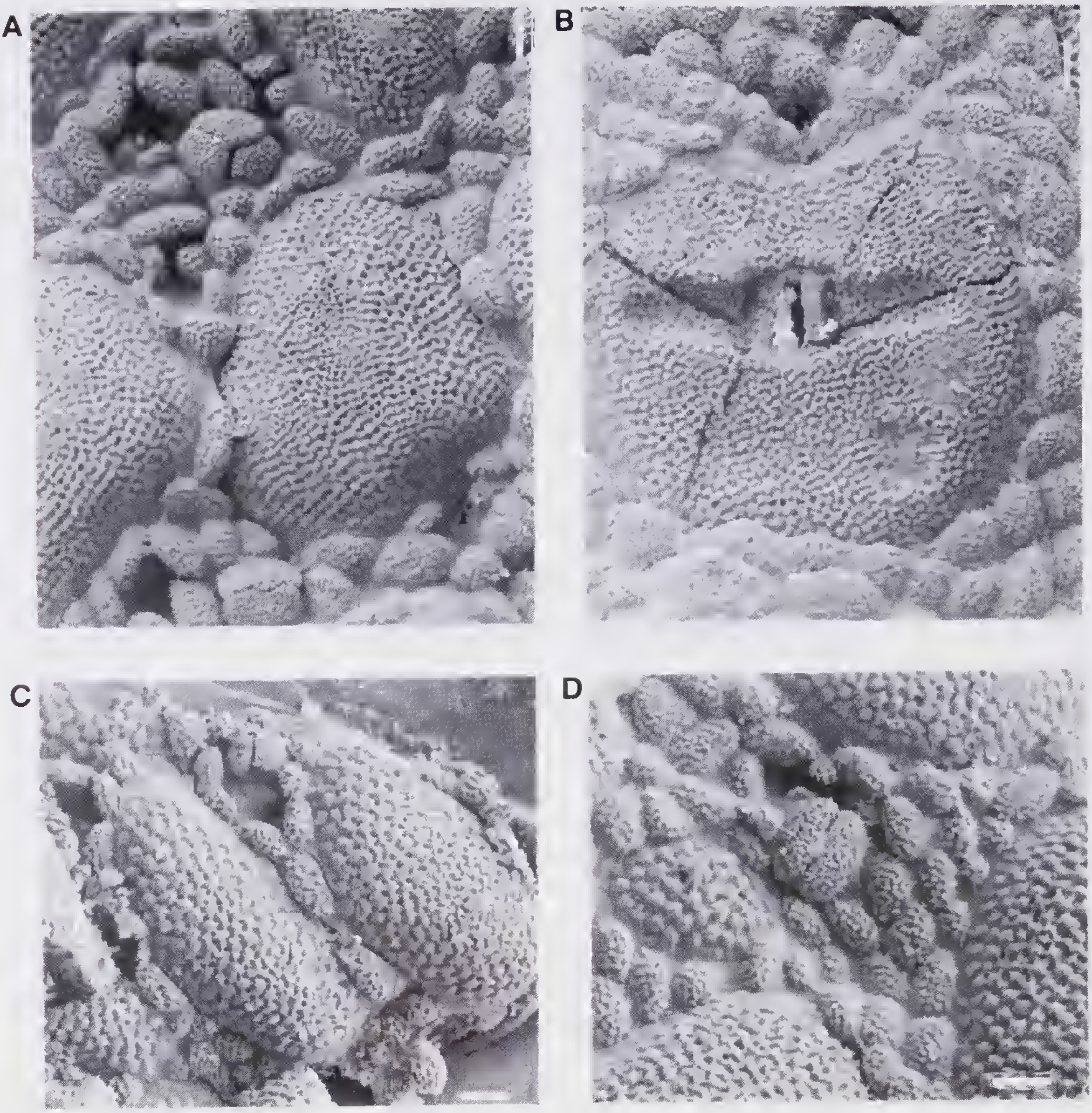

Figure 4. SEM photographs of abactinal plates, intersitial granules and pedicellariae of (a) *Bunaster ritteri* (WAM 49-88), 2 and 3 valved pedicellariae (arrowed); (b) *B. ritteri* (WAM 385-90), alveolus of entrenched pedicellaria in a disc plate (damaged); (c) *B. uniserialis* (WAM 426-90) bivalved pedicellaria (arrowed); (d) *B. variegatus* (WAM 1542-74), bivalved pedicellaria (arrowed). Scale bar = 100 microns.

fore reef, on crest, 0 m, Old Reef, G.B.R., J. Davidson, 30 Nov. 1986, ; AM J21515, fore reef, on crest, 1 m, Hope Reef, G.B.R., J. Davidson, 7 Sept. 1986; AM J 21516, AM J21517, fore reef, on crest, 0 m and at base of fore reef 13 m, Square Reef, G.B.R., J. Davidson, 23 Nov. 1986; AM J21518, fore reef, on crest, 2 m, Lodestone Reef, G.B.R., J. Davidson, 19 July 1986: AM J 21519, fore reef, on crest, 0 m, Keeper Reef, G.B.R., J. Davidson, 18 July 1986; AM J16815, 3m, Carter Reef, G.B.R., L. Vail and A. Hoggett, 16 Oct. 1982; AM J9242, 18 m, Heron I., Qld, N. Coleman, 19 Nov. 1974; AM J9245 (2), 18 m in hole in coral bommie, Heron I., Qld, N. Coleman, July 1975; AM J9690, under coral slab on reef flat, Macgillivray's Reef, Lizard I., Qld, N. Coleman, 13 Nov. 1975; WAM 426-90, 4 m, Showers Reef, G.B.R., J. Davidson, 9 Sept. 1986.

Diagnosis

Abactinal surface flat, rays slender, quadrangular in section, maximum known R of 11.3 mm. Abactinal plates separated by rounded well spaced granules; papulae single in 6 rows. Actinal plates in a single series; enlarged granules at base of subambulacral spines in a continuous row, no granules between subambulacral and furrow spines. Only known from the Great Barrier Reef, Queensland.

Description

Abactinal surface flat, rays slender, quadrangular in section, maximum known size, R/r = 11.3/2.7 mm, (4.2/1), br = 2.8 mm (holotype) (Clark gives R/r of 11.0/2.3 mm, (4.8/1) (Figure 1c); papulae single, in 6 rows; carinal series of somewhat irregular convex plates, some elongate, angled; dorsolateral plates small, 4-11 in a row; marginal plates up to 15 with up to 5 intermarginal plates; actinal intermediate plates in a single series (Figure 2c); surface texture of bare plates coarse (Figures 3b,4c); granules between plates rounded and well spaced, showing white skin between; enlarged granules at the base of subambulacral spines in a continuous row, no other granules between these and the furrow spines; subambulacral spines sometimes pointed; small, white, bivalved, pedicellariae among the granules (Figure 4c), none to many, similar in shape to those of *B. ritteri*; colour of holotype alive, variegated maroon, brown and bluish-white (Clark 1921 pl. 7 Figure 2); dried specimens are shades of brown or violet.

Variation

The holotype, with R of 11.3 mm is the largest specimen so far recorded. It has 14-15 superomarginals and inferomarginals, 8-9 dorsolateral plates, 5-6 intermarginals, a single row of actinal plates, 6 rows of single papulae and a row of enlarged granules between the furrow and subambulacral spines. Other specimens examined range from R/r of 5.5/1.5 mm to 9.6/2.5 mm with R/r ratio from 3.4 to 5.2/1; with 10-15 marginal plates, 4-11 dorsolateral plates, 1-6 intermarginals (Table 1). All have a single series of actinal plates, 6 rows of single papulae and a coarse surface texture on the bare plates. All have well spaced granules between the plates and lack granules (apart from the row of enlarged ones) between the furrow and subambulacral spines. Pedicellariae are variable in abundance, sometimes lacking. Some specimens from Heron Island are violet coloured when dry, others are various shades of brown, disc sometimes rust, sometimes with light bands on arms. Bosses on plates and skin between plates, white.

Holotype

MCZ No. 2313.

Table 1. Comparison of size dependent characters of the three species of *Bunaster*. Size classes (or size of single specimens) are R in mm. Mean values for the characters are given, the range is given in brackets.

Bunaster species	No. of specimens	Size classes	Supero-marginal plates	Carinal plates	Inter-marginal plates	Plates in second acti-nal series	Rows papulae	Papulae per area
B. ritteri	1 (Holo.)	10.0	13	6-7	4-5	3-4	8-10	1-2
	2	11-15.9	14.5(14-15)	9.3(7-12)	7(6-8)	7(6-8)	10	1.8(1-3)
	7	16-20.9	16.8(16-18)	11.1(6-14)	9.5(8-12)	10.4(6-16)	10	2.3(1-4)
as *B. lithodes*	1 (Holo.)	22.0	17-18	15-16	15-16	15	10	3
B. ritteri	1	23.0	18-19	16-17	16	15	9-10	2-5
B. uniserialis	1	5.5	13	6-8	4	0	6	1
	14	6-10.9	13(11-15)	7.1(4-11)	3.9(1-6)	0	6	1
	1 (Holo.)	11.3	14-15	8-9	5-6	0	6	1
B. variegatus	2	2-5.9	10.0(9-11)	4.0(3-5)	2.5(2-3)	0	0-6	1
	13	6-10.9	13.3(12-15)	5.8(4-9)	3.7(1-6)	2.5(0-4)	6	1
	25	11-15.9	15.2(12-17)	7.0(5-12)	5.0(3-10)	5.3(2-8)	6.0(6-8)	1
	12	16-20.9	16.0(14-17)	7.1(4-12)	5.4(3-11)	6.4(3-11)	6.6(6-8)	1
	2 (incl. Holo.)	21.0	17.7(16-20)	10.0(8-14)	9.2(5-4)	10.5(6-14)	7.0(6-8)	1

Type locality

South-western reef, Mer, Murray Islands, Torres Strait, coll. H.L. Clark, 18 Oct. 1913.

Habitat

B. uniserialis is a coral reef species occurring cryptically on reef flats, on seaward reef crests and outer reef slopes of the Great Barrier Reef from a depth of 0 to 25 m (from the specimens available).

Distribution

Known only from the Great Barrier Reef, Queensland, Australia from Mer, Torres Strait (09°56′S, 144°04′E) to Wistari Reef, Capricorn Group (23°29′S, 151°53′E) and Osprey Reef in the Coral Sea.

Remarks

H.L. Clark named this species *uniserialis* in reference to the single series of abactinal plates (the carinals) on the rays although he also notes the presence of inconspicuous dorsolateral plates. The name is more appropriately applied to the single series of actinal plates which is constant in all the specimens so far known. *B. uniserialis* appears to be smaller than the other species except *B. ritteri*, the holotype of which, although smaller than that of *B. uniserialis*, has two series of actinal plates and 10 rows of papulae, compared with a single row of actinal plates and 6 rows of papulae in *B. uniserialis*. The surface texture of the plates is coarser in *B. uniserialis* than in *B. ritteri* and the granules between the plates are more widely spaced.

B. uniserialis resembles *B. variegatus* of the same size in having single papulae in 6 rows. It differs in having a single row of actinal plates whereas *B. variegatus* even with R of only 6.7 mm has a few plates of a second row. It also differs from *B. variegatus* in having coarser texture on the bare plates, much sparser granulation between the plates and no granules except the row of enlarged ones between the furrow and subambulacral spines.

Although *B. uniserialis* is superficially very similar to small *B. variegatus* the differences noted above clearly separate them.

Bunaster variegatus H.L. Clark, 1938

Table 1, Figures 1d, 2d, 4d.

Bunaster variegatus H.L. Clark, 1938: 134-136, Pl. 22, Figure 1; H.L. Clark 1946: 118-119; Marsh 1976: 218 (Table).

B. lithodes H.L. Clark 1923: 241.

Material examined

In addition to the holotype and 11 paratypes, 42 specimens all from south-western Australia: WAM 161-71, under intertidal granite boulders, north side of Cape Naturaliste, B.R. Wilson, 28 Dec. 1967; WAM 53-88, 183-176 m, stn. DM 1/72/22, S.W. of Cape Naturaliste 33°35.1′S, 114°31.4′E, B.R. Wilson on HMAS *Diamantina*; WAM 54-88, 183 m, stn. DM 1/72/71, west of Lancelin, 31°00′S, 114°52′E, B.R. Wilson on HMAS *Diamantina*; WAM 156-73(2), under rocks at 8 m, Hall Bank, Fremantle, N. Coleman, 9 April 1972; WAM 28-80, 9-12 m, Hall Bank, Fremantle, S.M. Slack-Smith, C. Bryce, L.M. Marsh, 25 Jan. 1980; WAM 1542-74, 55-88, 56-88, under rocks, 0-1 m, Bathurst Pt, Rottnest I., L.M. Marsh, 10 March 1960; WAM 57-88, under rock, Armstrong Pt, Rottnest I., R. Slack-Smith, 5 Jan. 1965; WAM 59-88, from weed and rock, edge of reef flat pool, Armstrong Pt, Rottnest I., L. Marsh, 19 April 1975; WAM 60-88, under rock on platform, North Point, Rottnest I., E.P. Hodgkin, 7 March 1964; WAM 58-88, under ledge, reef at Nancy Cove, Rottnest I., L.M. Marsh, 14 March 1976; WAM 10-73, Pelsaert I., Houtman Abrolhos, N.N. Wilson, 8 Jan. 1968; WAM 284-77, Houtman Abrolhos, Br. Green, Feb. 1971; WAM 519-76, reef flat, Half Moon Reef, Houtman Abrolhos, L.M. Marsh, 8 April 1976; WAM 375-88, reef flat, Half Moon Reef, Houtman Abrolhos, S.M. Slack-Smith, 8 March 1988; WAM 358-88, 1-6 m, Jackson I., Pelsaert Gp, Houtman Abrolhos, S.M. Slack-Smith and L.M. Marsh, 3 March 1988; WAM 51-88(2), 52-88, reef flat, Easter Gp, Houtman Abrolhos, Aquinas College, 23 Aug. 1970, 30 Aug. 1972; WAM 575-77(2) reef flat, Beacon I., Wallabi Gp, Houtman Abrolhos, L.M. Marsh, 30 Aug. 1977; WAM 780-84 Beacon I., S.M. Slack-Smith and C. Bryce, 23 March 1983; WAM 1804-74 reef flat, North I., Houtman Abrolhos, Aquinas College, 27 Aug. 1974; WAM 45-80, from coral, 15-18 m, outside outer bar, South Passage, Shark Bay, 26°08′S, 113°10′E, L.M. Marsh, 15 April 1979; WAM 654-88, from dead *Acropora* on coral pinnacle, 6-9 m, Goss Passage, Wallabi Gp, Houtman Abrolhos, L.M. Marsh, 18 March 1987; WAM 656-88, 2-10 m, Goss Passage, off Beacon I., Wallabi Gp, Houtman Abrolhos, L.M. Marsh and R. Babcock, 20 March 1987; WAM 83-78, 192-179 m, S.W. of Mandurah, 32°43′S, 114°48′E, DM 1/72/29, 17 Mar. 1972; WAM 679-88, reef platform, W. side Garden I., L.M. Marsh, 17 Nov. 1948; WAM 712-88, 146-142 m, W.S.W. of Cape Leeuwin, 34°25′S, 114°36.5′E, DM 1/72/17, 16 March 1972; WAM 713-88(4), 190-174 m, W.S.W. of Cape Leeuwin, 34°25.5′S, 114°35′E, DM 1/72/16, 16 March, 1972; WAM 714-88, 161-165 m, N.W. of Bunbury, 33°15′S, 114°36′E, DM 1/72/25, 17 March 1972; WAM 715-88(2), 190-161 m, N.W. of Bunbury, 33°14′S, 114°27′E, DM 1/72/19, 16 March 1972; AM J6937(2), Wooded I., Easter Gp, Houtman Abrolhos, Percy Sladen Trust Exped., 1913 or 1915; AM J7436, Rottnest I., E.P. Hodgkin; AM J7838, Houtman Abrolhos, W.A., S. White, March 1970.

Diagnosis

Disc moderately convex, arms tapering, with a maximum known R of 21.0 mm. Abactinal plates separated by closely spaced granules; papulae single in 6-8 rows. Actinal plates in two series, enlarged granules at base of subambulacral spines of variable occurrence, rarely forming a series; granules form a continuous cover between subambulacral and furrow spines. Only found in south-western Australia from shore to *ca.* 200 metres.

Description

Disc moderately convex, arms tapering, with a maximum known size (the holotype) of R/r = 21.0/5.0 mm (4.2/1), br = 6 mm (Clark gives R/r of 23/6 mm (3.8/1) (Figure 1d); 6-8 rows of single papulae; abactinal and marginal plates oval to irregular in shape, more regular in shape and arrangement than in *B. ritteri*, carinal and marginal plates angled, 3-14 dorso-laterals, 9-20 marginals, 2-14 inter marginals, in a single row; surface texture of bare areas of plates finer than that of *B. uniserialis* but coarser than that of *B. ritteri* (Figure 4d); granules between bare areas of plates closely spaced, forming a continuous cover; actinal intermediate plates in two series in specimens with R of more than 7 mm (Figure 2d); enlarged granules at base of subambulacral spines of variable occurrence, rarely forming a series; granules form a continuous cover between subambulacral and furrow spines; small, white, bivalved pedicellariae, the same shape as those of *B. ritteri*, of variable occurrence, none to many (Figure 4d); colour, alive, variable, often shades of old rose, often with disc pink, arms cream with dark brown or pink bands or blotches, specimens may be pure white, tan or dark brown.

Variation

The holotype has R/r of 21.0/5.0 mm (4.2/1), 19-20 superomarginals, 19-20 inferomarginals, 10-14 dorslateral plates, 10-14 intermarginal plates, papulae single, in 8 rows, actinal plates in two rows, the outer with about 14 plates. These figures differ somewhat from those in the original description; in addition a few pedicellariae (not recorded by Clark, 1938) were observed.

The 53 other specimens examined range in size from R/r of 2.9/1.0 mm to 21.0/5.6 mm, mean R is 12.8 mm and the R/r ratio varies from 2.9/1 to 4.7/1 with a mean of 3.97/1. The number of superomarginal plates is size dependent ranging from 9-20 with 7-20 inferomarginals; the inferomarginals are frequently the same in number as the superomarginals but are sometimes one less and occasionally more. Specimens with R of 13 mm or more usually have about 16 supero- and inferomarginals. The variation in size dependent characters is shown in Table 1.

Intermarginal plates vary from 2 in the specimen with R of 2.9 mm to 10-14 in the holotype. The number is quite variable even among specimens of the same size.

The dorsolateral series of plates range from 3 in the specimen with R of 2.9 mm to 10-14 in the holotype. They are usually rather small and inconspicuous but occasionally are nearly as large and prominent as the carinals.

A second row of actinal plates is present in all but the smallest specimens with R of 4.2 mm or less. A specimen with R of 6.7 mm has 1-3 plates in the second row but one of 7.8 mm has only one. Specimens with R of 8 mm have 3-4 plates. A few of the larger specimens, with R of 15 mm or more have either a third series of small plates between the main row and the adambulacrals, or a few plates of a third outer row, however, most have the inner row the longest with the largest plates and a short second (outer row) of small plates.

The papulae are single even in the largest specimen, the holotype, and generally in 6 rows. Seven of the 54 specimens have 8 rows at least on some rays (including the holotype), with the extra rows on the actinal surface between the two rows of actinal plates. Inter-marginal papulae are always in a single row and there is one row either side between the carinal and superomarginal plates.

An enlarged granule sometimes occurs next to some of the subambulacral spines and occasionally forms a partial row, particularly in small specimens. All except the smallest specimen with R of 2.9 mm have close-set granules between the subambulacral and furrow spines.

Pedicellariae are present in 35 of the 54 specimens examined including the holotype. Clark (1938) did not observe pedicellariae in any of the paratypes but they are present in two of the Rottnest paratypes (WAM 18/22-31). The pedicellariae are similar in form to the bivalved pedicellariae of *B. ritteri* and *B. uniserialis*. No entrenched pedicellariae have been found.

The colour in life is variable from pure white to dark brown but many have a deep pink (old rose) disc with the arms either the same shade or darker with some predominantly white plates forming one or two indistinct light bands on the arms. There is sometimes also a darker band on the middle of the arms. A few specimens are entirely dark brown, one is light tan, others have various combinations of cream, dark brown and pink. The convexities of the abactinal plates are often white as are the pedicellariae. Twenty-two of the 54 specimens were entirely white, when alive. The actinal surface is always lighter than the abactinal varying from white or cream to mottled fawn or pink. Unlike most asteroids the colour is retained with little fading after drying from fixation in formol saline and is also retained in alcohol (in one case after 40 years).

Holotype

MCZ no. 3214

Type Locality

Bunker Bay, Cape Naturaliste, Western Australia, coll. E.W. Bennett, in a shallow intertidal pool with loose rocks, a little muddy sand and clusters of short brown algae.

Paratypes

MCZ 3213(2) Bathurst Pt, Rottnest I.; MCZ 3215 Bunker Bay; WAM 18/22-31 Bathurst Pt, Rottnest Island. The registration number indicates five specimens but eight are present: nine are recorded by Clark (1938) who states that all "except the very young, with R less than 12 mm may be considered paratypes". Five of this series are larger than 12 mm in R so perhaps the registration numbers applied only to these. However all eight specimens are in one lot marked paratypes in H.L. Clark's hand.

Habitat

Cryptic, on the underside of boulders or coral slabs, or in crevices of rock or coral from intertidal pools to 190 metres.

Distribution

South-western Australia from Shark Bay (26°S) to west-south-west of Cape Leeuwin (34°25′S).

Remarks

Bunaster variegatus is distinguished from *B. ritteri* by having single papulae in 6-8 rows (1-4 papulae in 10 rows in *B. ritteri*). The abactinal plates are more regular in shape and less 'bouldery' than in *B. ritteri* and their surface texture is coarser. *B. variegatus* also differs in colour from *B. ritteri*.

B. variegatus is distinguished from *B. uniserialis* by the presence of a second row of actinal plates in specimens with R of 6 mm or more, with a third row sometimes present in very large specimens. *B. variegatus* also differs from *B. uniserialis* in having a very closely packed covering of flattened granules between the plates and between the subambulacral and furrow spines. Enlarged granules at the base of subambulacral spines occur in about half the specimens but nowhere do they form a complete row as in *B. uniserialis*.

Like *B. uniserialis* the papulae are single, usually in six rows but up to 8 rows are found in large specimens of *B. variegatus*. The three species have allopatric distributions.

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A large pterodactyloid pterosaur from the Late Cretaceous (Late Maastrichtian) of Western Australia

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Abstract

An incomplete right ulna of a large pterodactyloid pterosaur is described from the Late Cretaceous Miria Formation (Late Maastrichtian), Giralia Range, Western Australia. The bone represents the first pterosaur known from Western Australia, and the largest and geologically youngest pterosaur from Australia, and the youngest Mesozoic terrestrial tetrapod yet found in Australia. Comparisons with other pterosaurs give estimates of wingspan for the Western Australian pterosaur at between 3.6 (cf. *Santanadactylus*) to 4.9 metres (cf. *Pteranodon*). The presence of a ridge dividing the medial condyle on the proximal face of the ulna suggests that the bone belongs to an azhdarchid; if so this is the first record of the family Azhdarchidae in Australia.

Introduction

The fossil record of pterosaurs in Australia is rather poor, and has been limited to Early Cretaceous occurrences. A number of specimens, referred tentatively to ?*Ornithocheirus* sp. from the Albian Toolebuc Formation of Queensland, were described by Molnar and Thulborn (1980) and Molnar (1987). Rich and Rich (1989) described a small crushed pterosaur bone from the Aptian-Albian of south-Western Australia. The specimen was tentatively identified as a tibiotarsus of what would be a rather small pterosaur, but is similar to the crushed metatarsals of *Pteranodon* from North America and is a metatarsal of a large pterosaur. This paper describes the proximal end of the ulna of a pterosaur from the Miria Formation (Late Maastrichtian) of Western Australia. The specimen, which has been previously discussed and figured in Long (1990, p. 78), is the first pterosaur from Western Australia, Australia's largest pterosaur, and the only Late Cretaceous pterosaur from Australia. It may also be the youngest known pteranodontid. Finally the specimen is also of interest in being Australia's only Late Maastrichtian terrestrial tetrapod as the otherwise youngest Mesozoic vertebrates are sauropod dinosaur bones from the base of the late Cretaceous (Winton Formation, central north Queensland, Coombs and Molnar 1981).

Discovery of the specimen

The specimen (WAM 60.57) was found in 1960 by E. Car of the Western Australian Museum as three bone fragments washed out of the Miria Formation in its type section at Toothawarra Creek (Figure 1). As this is the only Cretaceous unit exposed in the area and the rock still attached to the bone matches that of the Miria Formation, there is no

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doubt as to the exact age and stratigraphic source of the bone. In early 1990 one of us (JAL) recognised the bone fragments in the collection as belonging to one specimen and restored the bone. It was recognised as being unusual in its slender shaft proportions but an identification could not be assigned, so a cast of the bone was sent to Dr. Ralph Molnar of the Queensland Museum. Molnar suggested it might be a pterosaur bone, so further casts were sent to Dr. Peter Wellnhofer of Munich and one of us (SCB), and shortly afterwards the bone was confirmed to be a pterosaur ulna.

Geological setting

The Miria Formation (Miria Marl, Condon *et. al.*, 1956; Hocking *et. al* 1987) has been recently studied in detail by honours students in the Geology Department of the University of Western Australia. The unpublished dissertations which describe foraminifers from the Miria Formation confirm its Late Maastrichtian age, earlier suggested by microfossil studies by several workers (Edgell 1957; Belford 1958, McGowan 1968, Apthorpe 1979) and from diverse ammonite faunas described by Henderson & McNamara (1985a). Other fossils from the Miria Formation includes the nautiloid *Cimomia tenuicostata* (Glenister *et. al.* 1956), as well as undescribed brachiopods, echinoids, sponges, corals, bryozoans and sharks teeth. Other vertebrate remains which have come from the Miria Formation include one bone (WAM 90.10.2)

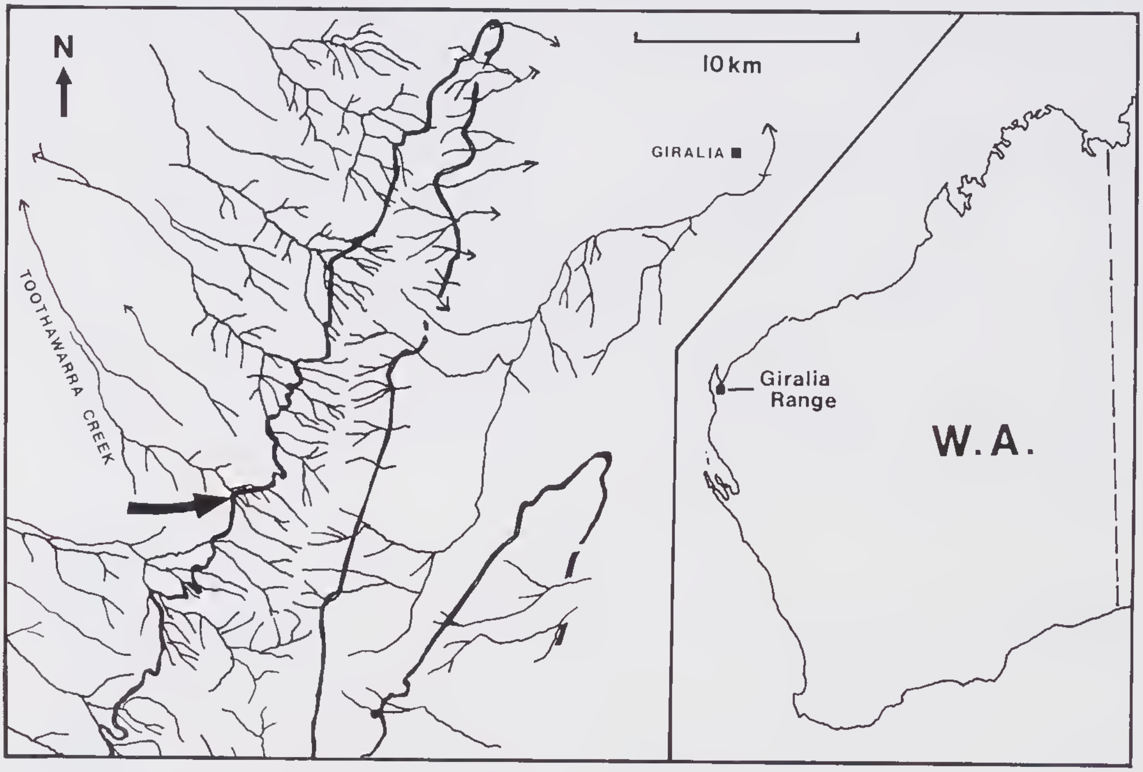

Figure 1. Locality map showing outcrop of the Miria Formation and where the pterosaur bone was found (arrow). After Henderson and McNamara (1985a).

tentatively assigned as a saurischian (possibly a theropod humerus) as well as several unidentifiable lumps of reptilian bone. The Late Maastrichtian age of the Miria Formation makes it the youngest Mesozoic terrestrial vertebrate site in Australia.

The deposition of the Miria Formation began in the wake of a Late Maastrichtian marine transgression (Apthorpe 1979), resulting in quiet shelf deposits in the northern Carnarvon Basin. Its lithology is a cream coloured calcarenite, 0.6-2 metres thickness, with abundant phosphatic grains and nodules. These suggest the unit has been condensed, with fragmentary fossil preservation indicating periods of higher water energy which winnowed the sequence (Henderson & McNamara 1985b).

Description of the pterosaur bone

The specimen (Figure 2) is an incomplete right ulna consisting of the proximal end and some shaft. Parts of the proximal end are broken and missing and as preserved it has a maximum width of 53.5 mm and a thickness of 31 mm. The shaft is broken at approximately the middle of the ulna where it is oval in cross-section and measures 22.5 mm by 17.8 mm. The length of the specimen is 134 mm. The anterior surface (Figure 2c) is pitted by weathering. The cortical bone has flaked off in many places, and where it is missing the internal cast shows impressions of small ridges and struts. The cortical bone is up to 1.0 mm thick along the shaft and is thinner toward the expanded proximal end.

In proximal view the bone is roughly D-shaped (Figure 2a). The medial and lateral condyles extend across the entire anterior half of the proximal end. The posterior parts of both condyles are missing as is the tuberosity for the insertion of M. triceps brachii. The condyles face proximally and a little anteriorly but because they are incomplete, it is difficult to accurately describe their orientations. The medial condyle has a slight ridge running diagonally across it. The anteromedial margin of the medial condyle and approximately 15 mm of bone distal to it are broken away. Lateral to this is a depression for the proximal end of the radius. In the middle of the depression between the condyles are the pneumatic foramina. It is not possible to determine if there were foramina on the proximal surface. The biceps tubercle is 18 mm from the medial condyle. It is suboval 7 mm by 3 mm, rises about 1.5 mm above the shaft, and is angled slightly. It is not possible to identify any other features on the anterior surface because of weathering and loss of cortical bone. The posterior surface of the ulna is not badly damaged, but does not show many features. There is a muscle scar on the posterolateral surface that is directed proximally and is part of the insertion of the M. triceps brachii. There is a similar scar on the posteromedial surface that is angled toward the medial epicondyle of the humerus and probably is from the medial collateral ligament.

Comparisons

Hooley (1914) reviewed the pterosaur fauna of the Cambridge Greensand of England which includes at least four genera of pteranodontids and non-pteranodontids. He divided the proximal ulnae into three groups. Group A ulnae have a robust ridge on the anterior surface of the shaft which provides a platform to support the radius and M. biceps brachii inserts on the side of the ridge rather than on the biceps tubercle. Group B

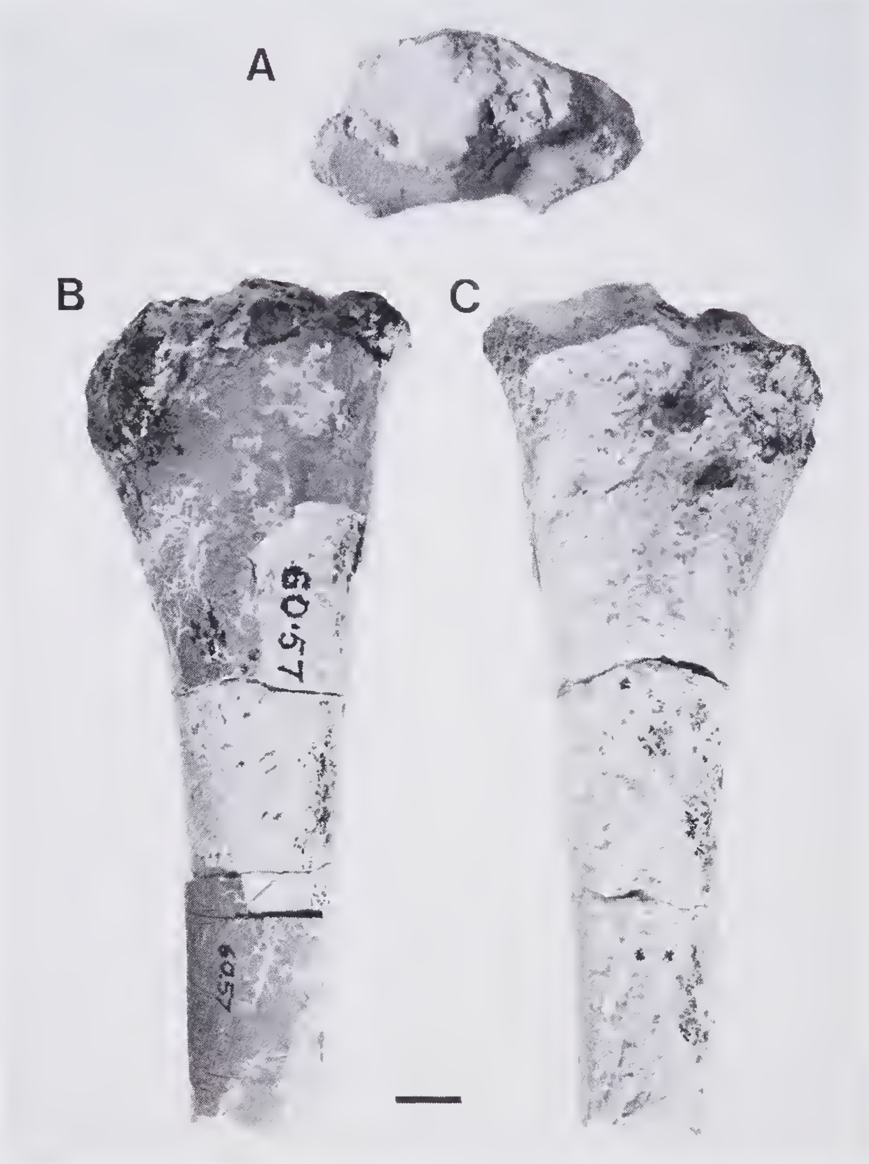

Figure 2. Right proximal ulna of ?azhdarchid pterosaur from Western Australia, WAM 60.57. A, in proximal view. B, in posterior view. C, in anterior view. Bar scale 1cm.

ulnae lack the ridge, have a biceps tubercle, and have a circular pit on the proximal surface posterior to the condyles. Group C ulnae, represented by a single specimen, are similar to Group B ulnae but lack the pit on the proximal end. All three types of ulnae have a pneumatic foramen on the anterior surface between the condyles. WAM 60.57 is similar to Group B ulnae but the damage to the proximal end makes it impossible to determine if a pit was present. Unfortunately, it is not clear if Hooley's groupings correspond to cladistic groups.

Cretaceous pterodactyloids include four major clades, the Dsungaripteridae, Nyctosauridae, Pteranodontidae and Azhdarchidae (Bennett 1989). Comparisons of WAM 60.57 with representatives of those clades are more useful in determining the relationships of WAM 60.57 than considering other pterosaur ulnae, but difficulties arise due to the scarcity of casts or good figures of other specimens. The proximal ulna of dsungaripterids is known only from *Dsungaripterus weii.* The ulna has a straight shaft, thick walls, and does not have noticeable pneumatic foramina. The condyles are extended anteriorly above the shaft and are angled anteriorly. The margins of the condyles are massive and rounded. The condition of the biceps tubercle is not known because the anterior surface of the shaft is damaged. WAM 60.57 differs from the ulna of *Dsungaripterus weii* in having thin walls, the condyles do not extend as far above the shaft and are angled more proximally, and the margins of the condyles are sharp, not massive and rounded. Ulnae of two indeterminate large pterodactyloids share certain similarities and differ from all other ulnae discussed here in certain details. They are proximal ulnae referred to *Araripesaurus* sp. (Wellnhofer 1985, figure 44, 45; 1988) and a proximal ulna referred to *Ornithocheirus* sp. from the Early Cretaceous of France (Buffetaut & Wellnhofer 1983). In both specimens the shaft is posterodorsally curved, the condyles appear to be angled anteriorly, and the biceps tubercle is rather indistinct, although this may be due to immaturity or abrasion. The *Araripesaurus* sp. ulnae have small foramina on the proximal surface and a large pneumatic foramen on the anterior surface between the condyles, while the *Ornithocheirus* sp. ulna has a number of small pneumatic foramina on the proximal surface posterior to the condyles. The *Araripesaurus* sp. ulnae are associated with humeri that display the primative morphology with a straight mid-section to the shaft. Therefore, the specimen cannot be pteranodontid or nyctosaurid (Bennett 1989), and it may well be dsungaripterid. Whatever taxa these ulnae represent they differ from WAM 60.57 in the posterodorsal curvature of the shaft, the anteriorly directed condyles, and the indistinct biceps tubercle.

The proximal ulna of pteranodontids is known from *Ornithodesmus latidens* (Hooley 1913), *Santanadactylus pricei* (Wellnhofer 1985) and *Pteranodon* (Eaton 1910). The shaft is relatively straight and the condyles are directed proximally. The ulnae of *Santanadactylus pricei* and *Pteranodon* have distinct biceps tubercles. That of *Pteranodon* has a longitudinal groove in the middle, while that of *Santanadactylus pricei* does not. The ulna of *Ornithodesmus* (Hooley 1913) has a robust ridge extending from the foramen distally along the shaft. The ridge forms a platform that supports the radius. The ridge presumably takes the place of the biceps tubercle, and like the Greensand ulnae mentioned above, the M. biceps brachii inserted on the side of the ridge. *Pteranodon* and *Ornithodesmus latidens* have a large pneumatic foramen just distal to and between the condyles, while *Santanadactylus pricei* lacks a pneumatic foramen on the anterior surface between the condyles, and instead has a large pneumatic foramen just proximal to the biceps tubercle. *Pteranodon* also has a nutrient foramen distal to the biceps tubercle.

WAM 60.57 is like the ulna of pteranodontids in the relatively straight shaft and proximally directed condyles. It is like *Pteranodon* and *Santanadactylus pricei* in

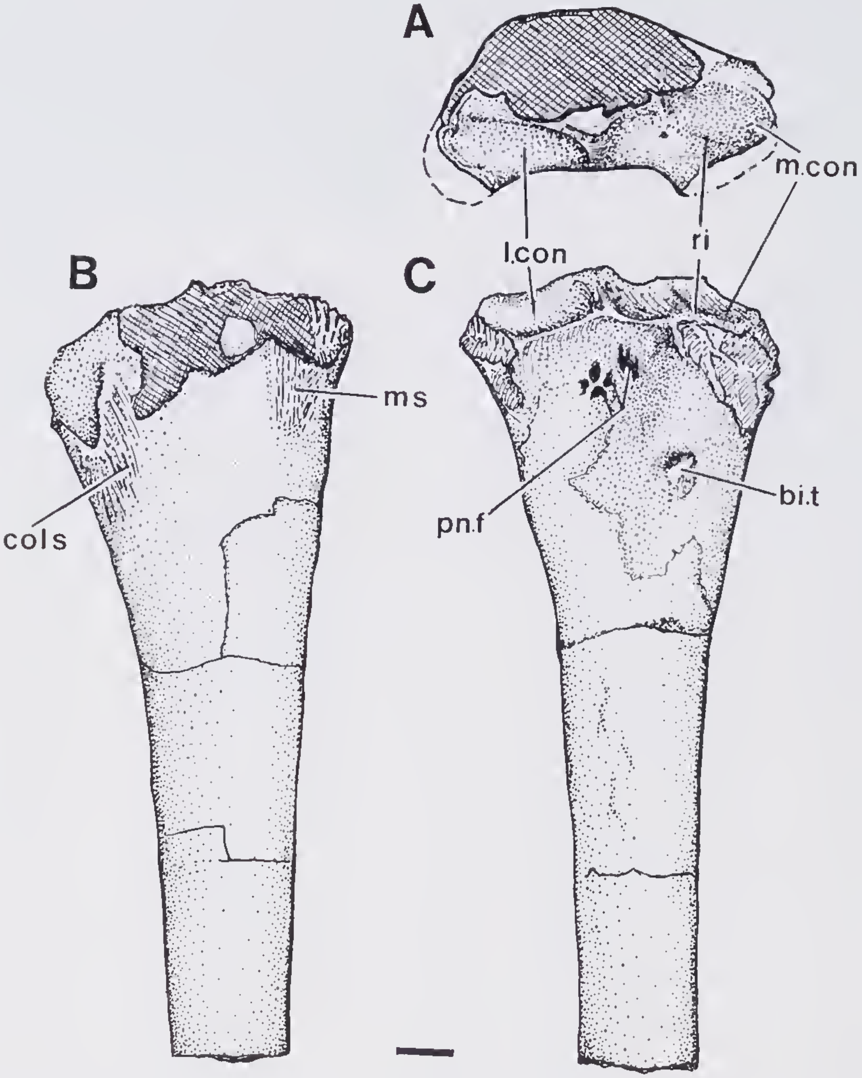

Figure 3. Right proximal ulna of ?azhdarchid pterosaur from Western Australia, WAM 60.57. A, in proximal view. B, in posterior view. C, in anterior view. Abbreviations: bi.t., biceps tubercle; col.s., collateral ligament scar; l.con, lateral condyle; m.con., medial condyle; m.s., muscle scar; pn.f. pneumatic foramina; ri, ridge. Bar scale 1cm.

possessing a distinct biceps tubercle and lacking a ridge to support the radius. It is like *Pteranodon* and *Ornithodesmus* in the position of the pneumatic foramina, although it has a number of small foramina instead of a single large foramen.

The ulna of nyctosaurids is not well known, and is represented only by badly crushed specimens of *Nyctosaurus gracilis*. The ulna has a straight shaft, proximally directed condyles, a distinct biceps tubercle, and a large single pneumatic foramen on the anterior surface between the condyles. The ulna is similar to that of *Pteranodon* except it lacks a groove in the biceps tubercle. WAM 60.57 differs from the ulna of *Nyctosaurus* in that it has a number of pneumatic foramina on the anterior surface instead of single large foramen. In addition, WAM 60.57 is considerably larger than the largest known nyctosaur, *Nyctosaurus lamegoi,* from the Maastrichtian of Brazil (Price 1953).

The ulna of azhdarchids has not been described. However, specimens of *Arambourgiania* (Nessov and Jarkov 1989, = *Titanopteryx* Arambourg preoccupied) from Jordan and *Quetzalcoatlus* from Texas include proximal ulnae. The ulna of *Arambourgiania* (BMNH 9228) has a relatively straight shaft, proximally directed condyles, a distinct biceps tubercle, one or two rather small pneumatic foramina on the anterior surface between the condyles, and a weak ridge running along the medial condyle. The ulna of *Quetzalcoatlus* is similar to that of *Arambourgiania,* but lacks pneumatic foramina on the anterior surface, and it is not known if it had a ridge on the medial condyle. WAM 60.57 is very similar to the ulna of *Arambourgiania* and is virtually the same size. It differs from *Arambourgiania* in that it has a number of pneumatic foramina on the anterior surface just distal to the condyles, and its biceps tubercle is relatively smaller.

The ulna of *Pterodactylus* has not been described in sufficient detail for comparisons, but the ulna of *Rhamphorhynchus* presumably displays the primitive condition of the pterodactyloid ulna. The form is very similar to the general form seen in *Santanadactylus, Pteranodon, Nyctosaurus, Quelzalcoatlus* and WAM 60.57. The proximal end has condyles facing proximally, the shaft tapers to a relatively straight mid-section with a subcircular to suboval cross-section, and it does not have a ridge extending down the shaft supporting the radius. There are no visible pneumatic foramina and the shaft is relatively smaller in diameter and has relatively thicker walls than those of large pterodactyloids.

Size

It is difficult to estimate the size of a pterosaur from a single limb element, but it is routinely done. Comparisons of WAM 60.57 with complete ulnae of *Pteranodon* and *Santanadactylus pricei* suggest that the 134 mm long section is between one half to two-fifths of the total length. Therefore the complete ulna probably measured between 27 and 34 cm. The wing proportions of large pterodactylids are variable. Extrapolating from an estimated length of 30 cm the wingspan in life (flexed as in flight) would be: 3.6 m based on the proportions of *Santanadactylus araripensis* (Wellnhoffer 1985), 3.8 m based on the proportions of *Quetzalcoatlus* (Langston 1981) or 4.9 metres based on the proportions of *Pteranodon* (Bennett, unpublished data).

Discussion

On the basis of its large size and stratigraphic position it is clear that WAM 60.57 is a pterodactyloid. It is probably not a dsungaripterid because it is not thick-walled and the condyles do not face anteriorly. It is probably not a nyctosaurid because it is much larger than the largest known nyctosaurid, and the group is not known outside the Americas. WAM 60.57 is very similar to *Arambourgiania* from Jordan and both have a ridge dividing the medial condyle that is not noted on the ulnae of dsungaripterids, pteranodontids or nyctosaurids. It is not certain that the ridge is a phylogentically important character. If it is not there is nothing to suggest that the ulna is not a pteranodontid, however, on the basis of the ridge dividing the medial condyle the Australian ulna is tentatively referred to the Azhdarchidae.

This is the first record of a pterosaur from Western Australia, and the only late Cretaceous occurrence from Australia. If the specimen is an azhdarchid, it is the first record of an azhdarchid from Australia. Azhdarchids are known from Early Cretaceous of England, and the Late Cretaceous of Central Asia, Jordan, Senegal, New Jersey, Texas and Wyoming in North America (Bennett 1989). If the specimen were a pteranodontid it would be the only member of that clade post mid-Campanian.

The form of the pterodactyloid ulna changed little through the Cretaceous. As the size of the pterodactyloids increased, relatively large joints were needed and the shaft became pneumatic. Consequently the ulna became relatively stouter. The dsungaripterid ulna is derived in possessing a posterodorsal curvature of the shaft from the proximal end and the rather anteriorly directed condyles. The ulna of *Ornithodesmus* and Hooley's Group A ulnae are derived in the possession of a robust ridge supporting the radius and taking the place of a biceps tubercle. However, all other ulnae of larger pterodactyloids, including WAM 60.57, are similar and vary in what appear to be rather minor details. It is surprising that the ulnae of pteranodontids and azhdarchids would be similar because the humeri of the two clades are very different. Perhaps better knowledge of the two groups will reveal differences.

Phylogenetically important morphological variation of pterosaur postcranials is not yet well understood, although recent attempts to characterise such variation have made progress (Padian 1984; Howse 1986; Wiffen & Molnar 1988; Bennett 1989). The above review of variation in the proximal ulna indicates that there is considerable difference between taxa in the size and location of pneumatic foramina. It is not known whether this variation is of phylogenetic importance. In large samples of *Pteranodon* the size and position of the pneumatic foramina are relatively constant, however, further study of this and other aspects of postcranial variation in pterosaurs is needed.

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A new species of *Rattus* from Gunung Mutis, South West Timor Island, Indonesia.

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Abstract

A new species of murid rodent is described from a single, aged individual, collected in montane forest at *ca.*1900 m elevation on Timor. It is small bodied, with a bicoloured tail, 3 pairs of mammae and a distinct skull morphology. It is tentatively placed in the genus *Rattus*.

Introduction

Since September 1987 there have been seven collaborative expeditions to Nusa Tenggara by the Western Australian Museum and the Museum Zoologicum Bogoriense. These expeditions have greatly increased knowledge of the distribution of species of terrestrial vertebrates in this region (Kitchener *et al.* 1990a, b) and several new species have been discovered. These include one nyctophiline and one cynopterine bat (Kitchener *et al.* 1991a; Kitchener and Maharadatunkamsi 1991) and the first unquestionably native species of *Rattus* in Nusa Tenggara (Kitchener *et al.* 1991b). Additionally, a specimen of the endemic murid *Paulamys* c.f. *P.naso*, known previously only from fossil dentary fragments, was collected on Flores Island (Kitchener *et al.* 1991c).

On the last expedition, a single specimen of a distinctive small rodent was collected in a remnant patch of montane forest on the slopes of Gunung Mutis, South West Timor. This specimen clearly represents a new species, however we remain uncertain as to its generic affiliations. It is tentatively allocated to the genus *Rattus*. Although the new species is the first extant native rodent recorded from Timor, a number of fossil murids (including *Coryphomys buehleri* Schaub, 1937) are recorded from several Pleistocene and Holocene localities on the island (Hooijer 1965; Glover 1971; Musser 1981b).

Methods

Measurement and descriptions: external measurements and weight were recorded from WAM M34827 in the field prior to its fixation in formalin. Cranial and dental measurements were taken with digital calipers to the nearest one hundred millimetre. Measurement points are illustrated in Musser (1970) and described in Musser and Newcomb (1983). The terminology of cranial bones and foramina is that of Musser (1981a, b).

Phylogenetic analysis: Phylogenetic relationships were examined between WAM M34827 and 16 genera including *Rattus* and some closely related genera listed in Table

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11 of Musser (1981a), as well as *Bunomys, Paulamys* and *Komodomys*. Minimum length cladograms were constructed using the tree-building phylogenetic computer package HENNIG 86 (Farris, 1988). The search for the most parsimonious tree was conducted using the exhaustive branch and bound algorithm, based on the Wagner method.

The character matrix consists of 15 skull characters and two characters related to number of molar roots (see Appendix). These correspond to the first 16 characters in Musser (1981a; Table 11), except that his character number 11 was divided into two separate characters by separating the shape of the pterygoid fossa from the presence or absence of sphenopterygoid vacuities. Character state data for most genera are taken from Musser (1981a); for *Paulamys* from Kitchener *et al.* 1991; for *Bunomys* from descriptions in Musser (1981a) and *Komodomys* from Musser and Boeadi (1980). Wherever possible, previous character state assessments were checked against actual specimens of the taxa involved.

The tree was rooted using a hypothetical ancestor scored as plesiomorphic for all 17 characters.

Colour: Pelage and skin colour where they follow Ridgway (1912) are capitalised.

Systematics

Rattus timorensis sp. nov.

(Figures 1-7)

Holotype

Western Australian Museum catalogue number WAM M34827*; adult female; skin prepared as 'cabinet specimen'. Carcass fixed in 10% formalin and preserved in 70% ethanol; liver, kidney, blood samples in ultrafreeze at Western Australian Museum.

Type Locality

West facing valley between two ridges near the top of Gunung Mutis at altitude *ca.* 1900 m; *ca.* 7 km east of Desa Nenas (*ca.* 9°31′S, 126°16′E) (Figure 1).

Diagnosis

Rattus timorensis is distinguished from all other species of *Rattus* by a combination of its small size (112 gm); 1 postaxillary and 2 inguinal pairs of mammae; bicoloured tail with white ventral surface; skull with long narrow rostrum; poorly developed ridging along dorsal margins of interorbital, postorbital and temporal regions; absence of sphenopterygoid vacuity; relatively large bulla; anterior expansion of infraorbital canal; and relatively short projection of palatal bridge posterior of M^3.

It differs from *Komodomys rintjanus* by its smaller body size; soft dark brown fur rather then semi-spinous, sandy coloured fur on dorsum; 6 rather than 10 mammae; dorsal profile of skull not strongly arched; dorsal ridges outlining interorbital region poorly developed; lacrimal bones small, smoothly curved, rather than large and

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*Final disposition of specimen will be Museum Zoologicum Bogoriense.

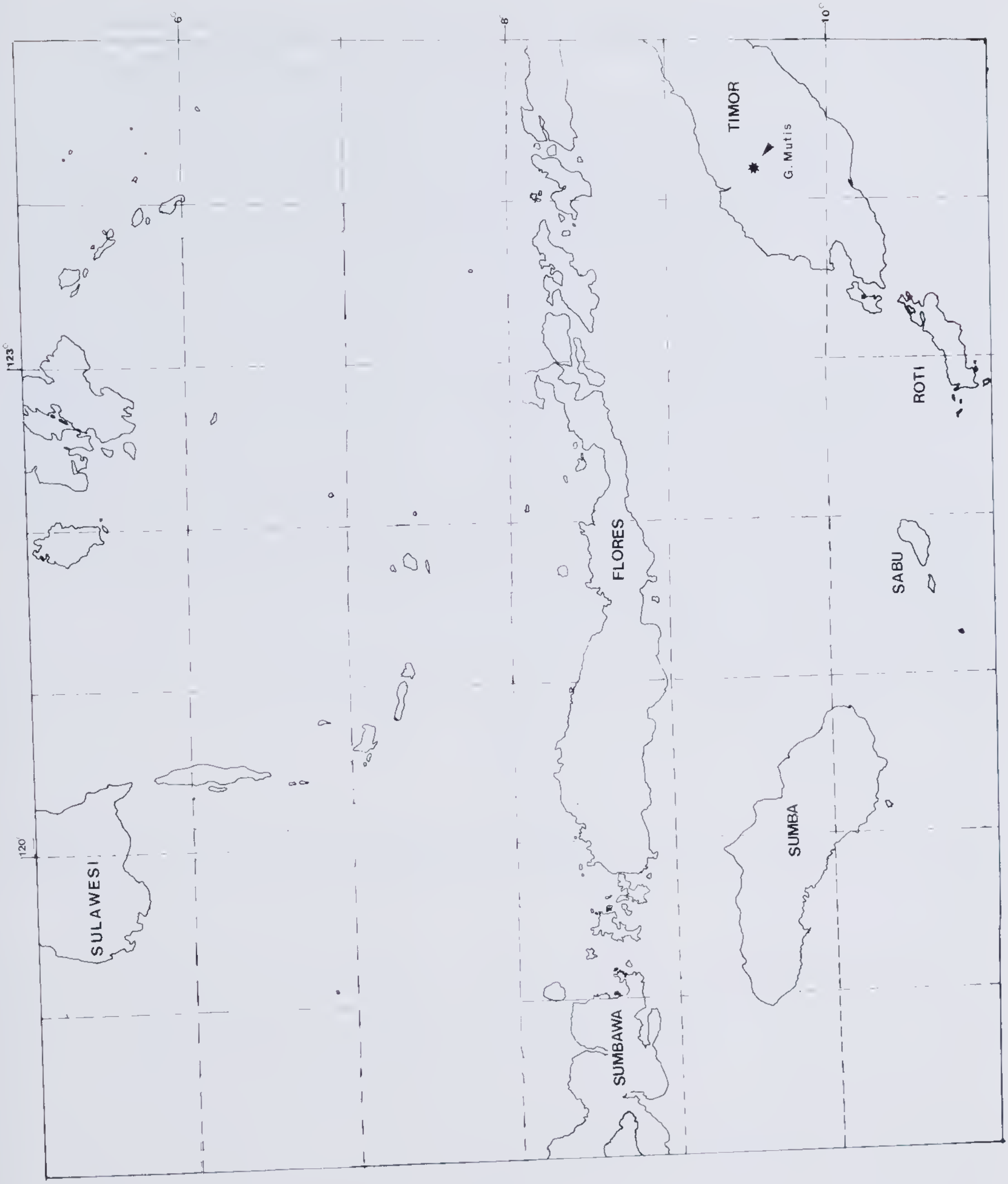

Figure 1. Map of Nusa Tenggara showing collection locality of *Rattus timorensis* holotype.

Figure 2. Photograph of Gunung Mutis showing the patch of mixed montane forest (arrowed) in which the holotype of *Rattus timorensis* was collected.

squarish; zygomatic plates with leading edge more gently sloping anteriorly; interparietal larger; incisive foramen broader; palatal bridge extending slightly further posterior of M^3 posterior face (0.9 v. 0.5); sphenopterygoid vacuities absent; teeth smaller relative to palatal bridge.

It differs from the similarly-sized *Paulamys* cf. *P.naso* (e.g., snout to vent length 157 *v.* 164 and weight 112 *v.* 122 gm) in having considerably shorter hind foot (30 *v.* 39.3) and ear (20.5 *v.* 24.2); a broader skull: e.g., zygomatic breadth relative to greatest skull length (0.50 *v.* 0.45); upper incisors wider at tips (2.2 *v.* 1.9); incisor foramen longer (8.9 *v.* 7.4) terminating posterior to M^1 anterior face rather than anterior to it, palatal bridge extending slightly further past M^3 posterior face (0.9 *v.* 0.5); sphenopterygoid vacuity absent; and infraorbital canal wider.

It differs from *Bunomys* spp. in having 6 rather than 4 mammae; incisive foramen terminating posterior to M^1 anterior face; palatal bridge extending beyond M^3 posterior face; and infraorbital canal wider.

It differs from *Coryphomys buehleri*, the only described fossil murid from Timor, in its much smaller size (M_{1-3} 6.3 *v.* 19.9 in *C.buehleri;* Schaub 1937).

Description

Measurements (in mm) of the holotype WAM M34827 are as follows: tip of rhinarium to vent length 157; distal tip of tail to vent length (broken) 77+; hind foot length 30; ear length 20.5; greatest skull length 38.72; condylobasal length 36.53; zygomatic breadth 19.37; interorbital breadth 6.10; nasal length 14.97; nasal breadth 3.86; rostrum length 14.43; rostrum breadth 6.28; braincase breadth 16.40; braincase height 12.57; zygomatic plate breadth 3.94; interparietal breadth 9.43; interparietal length 4.84; breadth across upper incisor tips 2.16; diastema length 11.08; palatal length 20.89; postpalatal length 12.86; palatal bridge length 6.71; palatal bridge breadth at M^1 3.64; palatal bridge breadth at M^3 4.31; mesopterygoid fossa breadth 2.53; incisive foramen length 8.91; incisive foramen breadth 2.26; bulla length 7.31; bulla height 6.57; M^{1-3} length (cusp) 6.62; M^{1-3} length (alveolar) 6.90; M^1 breadth (cusp) 2.15; M^1 breadth (alveolar) 1.87; M^2 breadth (cusp) 1.95; M^2 breadth (alveolar) 1.66; M^3 breadth (cusp) 1.55; M^3 breadth (alveolar) 1.15; M_{1-3} length (crown) 6.30; dentary condyle to dorsal incisor base 23.32; dentary height below M^1 anterior labial cusp 5.56. Body weight 112 gm.

Skull and dentary (Figure 3)

Skull small (greatest length 38.7) but moderately robust; cranium with broad zygoma; infraorbital canal wide and flared when viewed dorsally, slightly asymmetrical with left side leading edge more flared; interorbital region moderately wide (6.1); lacrimal small, smoothly rounded; neurocranium suboval dorsal outline, moderately inflated and deep (12.6); interparietal moderately large (4.8 x 9.4); ridges absent from dorsal margins of interorbital region, this region outlined by very faint beading which extends along postorbital margin to most anterior corner of parietal; rostrum long relative to greatest skull length (0.37), narrow; from interorbital region to nasal tip relatively straight in lateral profile; nasals narrow, distal ends slightly flared and rounded; zygomatic plate moderately wide, leading edge slopes gently forward; bulla relatively widely spaced, moderately long relative to greatest skull length (0.19); eustachian tube projects anteromedially to level of bulla anterior edge; incisive foramina long (8.9), narrowing slightly posteriorly, extending to a point almost level to anterior edge of M^1 anterolingual root; premaxilla-maxilla suture in anterior one third of incisive foramen; palatal bridge short, extends only 0.9 posterior to M^3 cusp posterior face; ventral surface generally smooth with several tiny vascular foramina; posterior palatal foramen oval, level with M^2 and M^3 interface, sited in moderately deep palatal grooves that extend the length of palatal bridge; squamosal dorsal to bulla complete, not divided by squamosal-mastoid foramen; stapedial foramen moderately large; sphenopalatine foramen small, oval, *ca.* 1.9 anterior to small slit-like dorsal palatine foramen; zygomatic arch squamosal roots originate low on sides of braincase, without posterior horizontal ridge to mastoid; braincase sides almost vertical; postglenoid vacuity moderately wide, separates dorsal and anterior margins of periotic and bulla from squamosal; alisphenoid canal lateral part open, not covered by strut of alisphenoid bone; mesopterygoid fossa moderately wide, 60% of palatal breadth at M^3; perforated by large sphenopalatine

Figure 3. Photograph of vegetation close to place where *Rattus timorensis* holotype was collected.

vacuities that are visible laterally in orbit; pterygoid fossa wide, slants toward midline; sphenopterygoid vacuities absent on both sides. Dentary with strong masseteric ridge terminating close to and above masseteric foramen; angular process relatively deep and strongly produced.

Dentition and palate (Figures 4 and 6)

Upper molars small relative to palatal bridge; M1, M2 and M3 with 5, 4, 3 roots respectively, these roots located as for *Rattus.* The wear on these molars is such that it is not possible to evaluate much of the occlusal cusp pattern. However, the size of the upper and lower molars gradually reduce in size from M1 to M3; comparison with equally worn teeth of *R. rattus diardi* suggests M^1 cusp t7 and M^2 cusp t3 absent.

The palate (Figure 6) is closely similar to that of *Rattus norvegicus* as described by Kutuzov and Sicher (1952).

Pelage and skin

The predominant colour of dorsal pelage is Olive Brown. This derives from Chaetura Drab (dark brown) of the guard hairs mixing with the Tawny Olive (orange brown) tip to hairs. The basal hair on head is *ca.* 9 long increasing to 13 at neck, and to 19 on back and rump. Occasional longer guard hairs on head; these more abundant on neck, (up to

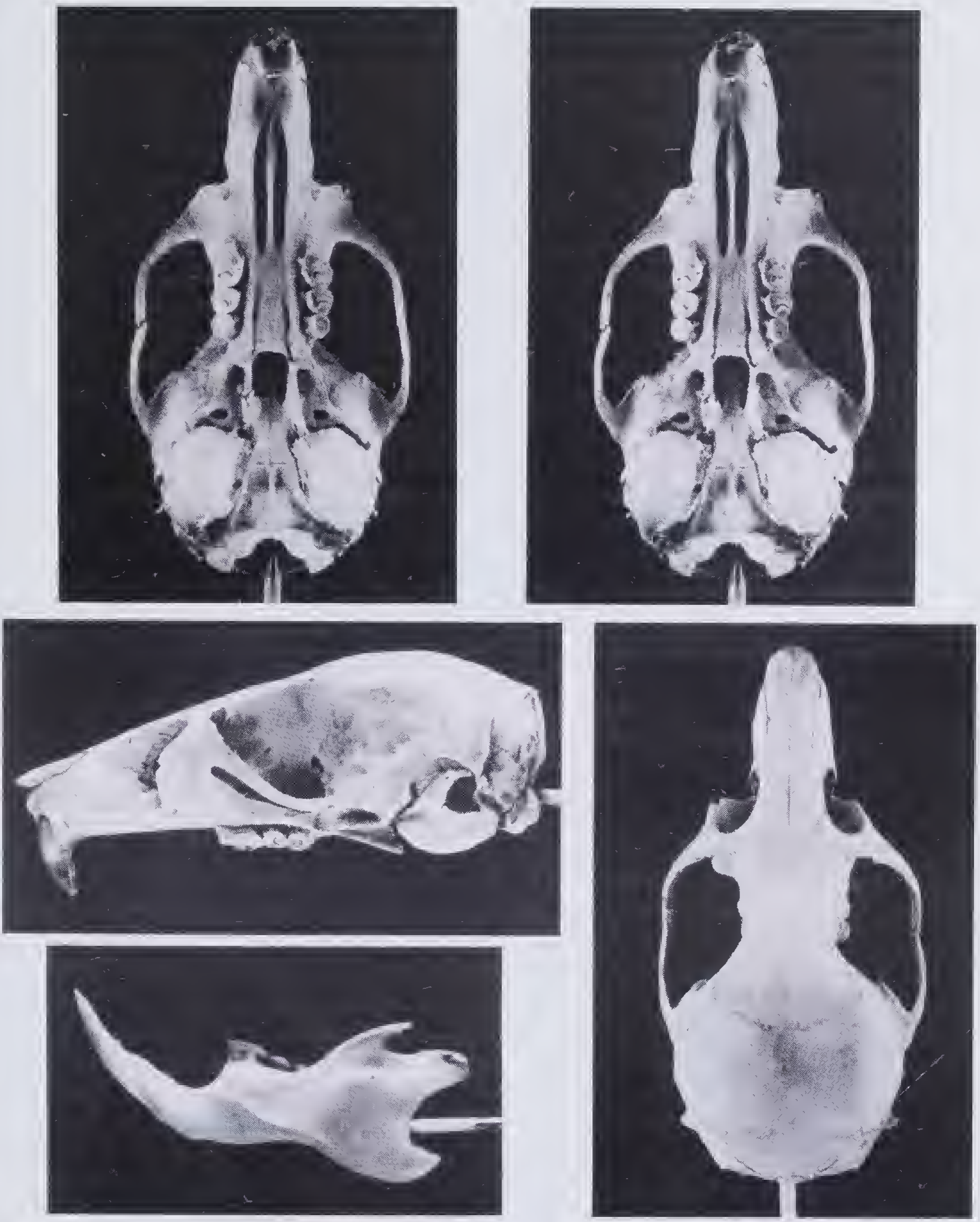

Figure 4. Photograph of skull dentary and teeth of *Rattus timorensis* holotype; ventral aspect of skull as stereopairs.

Figure 5. Photograph of *Rattus timorensis* holotype.

Figure 6. Photograph of soft palate and plantar surface of pes of *Rattus timorensis* holotype.

25 long), and on back and rump (up to 35 long); guard hairs on rump Chaetura Drab tipped with Light Cinnamon Buff. Flanks Tawny Olive peppered with Cinnamon Buff, merging gradually into Light Buff venter. Basal portion of ventral fur (*ca.* 12 long) Neutral Gray, this showing through apical wash on the chest and throat. Forearm fur predominantly Neutral Gray tipped with white or Light Buff; wrist and manus laterally white, dorsally Neutral Gray of skin prominent through short white hairs; toes white dorsally; palmar surface Light Ochraceous-Salmon (orange pink). Dorsal surface of pes to base of toes Neutral Gray of skin prominent through short white hairs; toes white-skinned with long white hairs slightly overhanging claws; plantar surface Light Ochraceous-Salmon.

Tail broken and heavily scarred; "bicoloured" with colour of skin prominent: dorsally deep Neutral Gray, ventrally White; hairs short (*ca.* 2.5): dorsally Chaetura Drab, ventrally white. 14 scales per cm at basal part.

Ears short (20.5), evenly rounded, skin Dark Mouse Gray, lightly furred with short hairs Chaetura Drab externally and Light Buff internally.

Vibrissae

Facial vibrissae long: *ca.* 30 Pairs of long (to 60), mystacials, the lateral and ventral ones white, the central and dorsal ones black brown; *ca.* 2 pairs of moderate length (to 20) dark brown interramals; 2 pairs of dark brown genals (20 long); 2 pairs of long (to 30) dark brown supraorbitals and one pair of short (to 7) dark brown submentals; forearm with 7 short (up to 12 long) white ulnar carpals. Antebranchial and calcaneal vibrissae not evident.

Pes and manus (Figure 7)

Typically *Rattus* like. Manus claws long (4.1); pollex with nail; all palmar pads prominent; three interdigital pads: outer and inner kidney-shaped, central pad triangular-shaped; thenar pad approximately one-half area of hypothenar, both large. Pes claws moderately long (4.8); pads, smooth but with sub-epidermal lamellae; inner plantar pad elongate, *ca.* 4 long; outer plantar pad 1.2 behind nearest interdigital pad and approximately three-quarters size of this front pad; outer interdigital pad broadly kidney shaped with smaller posterolateral subcircular accessory pad.

Etymology

Rattus timorensis is named after the island on which it was collected.

Remarks

The genus Rattus

Recent years have seen considerable refinement of the generic concept *Rattus*, resulting in a sharp reduction in the number of contained species from over 600 (e.g., Chasen 1940; Ellermen 1949; Tate 1951) to little more than 50 (Musser and Newcomb 1983; with additions by Musser and Heaney 1985). This reduction results principally from the work of Misonne (1969), Musser and Boeadi (1980), Musser *et al.* (1979), Musser (1981 a, b, c' 1982 a, b) and Musser and Newcomb (1983) through whose collective efforts many of the more discrete generic groupings have been set apart from *Rattus*. Additionally, Musser (1971), Musser (1973 a, b; 1986), Musser and Califia (1982) and Taylor *et al.* (1982) have revised a number of groups within *Rattus*, leading to the detection of many junior synonyms.

While monophyly of those taxa currently included within *Rattus* is still not resolved (Musser and Newcomb 1983) and possibly will not be until the wider application of modern genetic techniques, the 'core' specics of *Rattus* (i.e., those that appear to be closely related to its type species, *R. rattus*) have been diagnosed by Musser and Boeadi (1980: 397) to have the following combination of characters: cranium and mandibles with basic configuration of *R. rattus* and *R. argentiventer;* incisive foramen long and terminate between first molars; palatal bridge long, terminates well beyond toothrow; sphenopalatine vacuities large such that anterior process of basisphenoid and presphenoid appear suspended in air; bulla relative to cranium of medium to large size; incisor anterior face with orange pigment; toothrows narrow relative to palatal bridge;

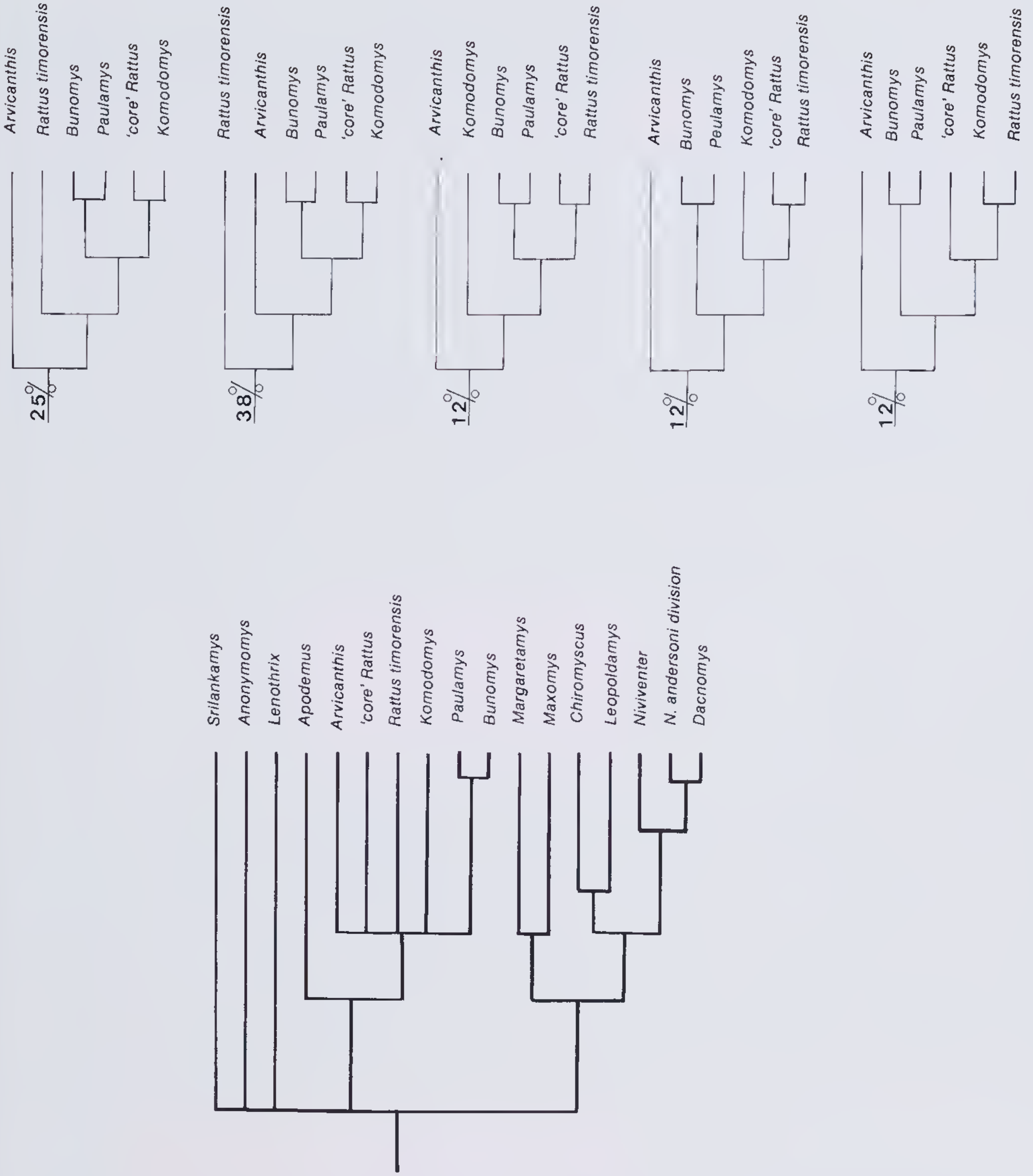

Figure 7. Cladogram of relationship between *Rattus timorensis* holotype; 'core' members of *Rattus* and other related genera. The consensus tree from the 24 equally parsimonious trees is in bold; other equally parsimonious combinations for the clade involving *Rattus timorensis* are shown, along with their proportional representation in the total sample.

M^1 with 5 tooth roots; M1-3 occlusal pattern as in *R. rattus* and *R. argentiventer;* M3 reduced relative to M1 and M2; and the extent to which M^1 overlaps M^2 overlaps M^3. This diagnosis is further amplified for the 'core' *Rattus* species in Musser and Newcomb (1983: 345-349).

As discussed by Musser and Newcomb (1983), strict adherence to this diagnosis would effectively preclude a number of the Sulawesian, Sundaic and Australo-Papuan species currently included within *Rattus.* On the other hand, sufficient broadening of the generic diagnosis to accomodate these taxa would result in a considerable blurring of the generic distinction between *Rattus* and its close relatives.

Based on the available evidence, *Rattus timorensis* likewise appears to lie close to, though probably not strictly within, the genus *Rattus sensu stricto.* Regrettably the holotype has extremely worn molars so that it is not possible to discern their cusp morphology, however it differs from 'core' *Rattus* species in having a relatively long narrow rostrum; a relatively short palatal bridge which extends only 0.9 mm beyond the posterior edge of M^3 and does not form a long and wide shelf beyond the teeth; a bicoloured tail, contrasting with the more typical even brown colour; poorly-developed ridging along the dorsal margins of the interorbital, postorbital and temporal regions of cranium; a wide infraorbital region; 3 pairs of mammae; and in lacking sphenopterygoid vacuities.

In order to obtain a relatively objective picture of phylogenetic affinities, we examined the cladistic relationship between WAM M34827 and species of *Rattus, Paulamys, Bunomys, Komodomys* and 12 other murid genera (see Musser 1981a, b; Kitchener *et al.* 1991). The data set (see Appendix) consists of various characters proposed by Musser (1981a) as of value for primary evaluation of *Rattus* and related genera. These characters were related to the skull and numbers of molar roots only; cusp morphology could not be scored for WAM 34827.

An exhaustive branch and bound analysis produced a series of twenty-four, equally parsimonious phylogenetic trees, each with a Consistency Index of 0.51. A Strict Consensus tree derived from this series (Figure 7) shows *Rattus timorensis* in an unresolved polychotomy with *Arvicanthus,* 'core' *Rattus, Komodomys, Paulamys* and *Bunomys.* In the majority (63%) of the 24 trees produced (Figure 7) *Rattus timorensis* lies outside the clade including 'core' *Rattus, Komodomys, Paulamys* and *Bunomys.* When placed within that clade, however, *R.timorensis* is the sister taxon to 'core' *Rattus* in 6 trees, and to *Komodomys* in 2 trees. A similar analysis using the full (cranial + dental) character set, but with *R. timorensis* scored as unknown for all dental characters, gave a smaller number of trees with fewer variants but an essentially similar Strict Concensus topology. Because the greater resolution implied by the fewer trees is not gained through any additional information on *R.timorensis,* we prefer to accept the less fully resolved outcome of the cranial analysis.

The phylogenetic analysis indicates that we should be cautious in placing WAM M34827 in the genus *Rattus,* and we do so only with considerable reservation. Revision of its generic status must await firstly the recovery of a younger specimen of this taxon to enable clarification of its molar cusp morphology, and secondly, the results of an ongoing immunological (Microcomplement Fixation) study, incorporating material from this specimen, which is being carried out by Dr C. Watts and his colleagues at the South Australian Museum.

Within the current taxonomic scope of *Rattus sensu* Musser and Newcomb (1983), *R.timorensis* is superficially similar to such widely separated taxa as *R. hoogerwerfi,* a species from the mountains of N. Sumatra (see Musser 1986), members of the *'Stenomys'* group (*R. verecundus* and *R. niobe*) in the New Guinean Region, and a newly discovered, endemic *Rattus* species from Flores Island (Kitchener *et al.* 1991b).

Rattus hoogerwerfi is about the same size as *R.timorensis* (body length 170-196 *v.* 157) however its tail is markedly different (the distal half, rather than the ventral half, is white) and its pelage is long and soft, but brightly coloured and brown according to Chasen (1939), rather than a darker brown. It shares with *R. timorensis* the feature of a relatively short palatal projection posterior to M^3, however from the work of Musser and his colleagues this is very likely a plesiomorphic state within Muridae. *Rattus timorensis* differs from *R. hoogewerfi* in a number of skull features: zygomatic width slightly greater relative to greatest skull length (0.50 *v.* 0.47); rostrum longer relative to greatest skull length (0.37 *v.* 0.32); rostrum narrower relative to rostrum length (0.43 *v.* 0.51); bulla longer relative to greatest skull length (0.19 *v.* 0.15); braincase height greater relative to greatest skull length (0.33 *v.* 0.28); absence of dorsal ridges outlining interorbital region and extending laterally to postorbital and temporal region; and M^{1-3} alveolar length shorter (6.9 *v.* 7.5-8.5).

Members of the Australo-Papuan *"Stenonys"* group *(R. verecundus and R. niobe)* and *Rattus* sp.nov. from Flores I. share with *R.timorensis* the feature of weakly developed dorsal ridges outlining the interorbital and more posterior cranial regions. Additionally, *R. verecundus* and *R. niobe* also have relatively long rostra relative to greatest skull length (e.g., *R. timorensis v. R.verecundus:* 0.37 v. 0.36 (0.35-0.37) N=6, measurements from WAM M25088, M25100, M25103, M25106, M25130, M25143).

On a more detailed level, *R. timorensis* is very obviously distinct from each of these species. For example, it differs from *R. verecundus* and *R. niobe* (see Taylor *et al.* 1982) in being generally larger in body and skull measurements; in having longer bullae relative to greatest skull length (0.19 *v.* <0.15); incisive foramen much longer; sphenopterygoid vacuity absent. It differs from the Floresian *Rattus* sp. (see Kitchener *et al.* 1991) in being larger in most body and skull measurements; in having a much longer rostrum and longer incisive foramina; relatively larger bulla; sphenopterygoid vacuity absent; ridges outlining interorbital region considerably reduced to a slight beading; rostrum considerably narrower dorsoventrally; zygomatic plate anterior edge more gently curved; neurocranium more ovate in dorsal profile.

Habitat and conservation status

The unique specimen of *R.timorensis* was collected in a triangular-shaped patch (*ca.* 30 ha.) of mixed montane forest, situated between two sharp ridges defining the southwestern face of Gunung Mutis (Figure 2, arrowed). Dominant tree species include *Podocarpus imbricatus* and several small-leafed angiosperms. The shrublayer is relatively dense and includes *Daphniphyllum* spp., *Prunus arborea* and *Ilex* sp. Tree ferns to 3 m are abundant in moister situations. The ground layer includes dense stands of bracken and a "fishtail" fern; litter is sparse on steeper stopes but considerably thicker in sheltered positions. The area shows little evidence of direct human exploitation, but is traversed by horse and cattle trails

The animal was trapped in a 'breakback' trap, placed among a system of 'runs' and 'burrows' in the wall of a moist, densely-shaded gully; the trap was baited with uncoooked meat. Ten specimens of *Rattus exulans* were captured in the immediate vicinty, from a combined trapping effort of 75 Elliot and 30 'breakback' trap-nights.

Adjacent, drier slopes of Gunung Mutis support extensive tall forests of *Eucalyptus urophylla,* in which the understorey is generally less dense though of similar floristic composition. Further downslope there are extensive stands of the *Eucalyptus urophylla* tall forest within which are found occasional elements of the montane forest community. Extensive, grassed clearings occur at *ca.* 1650m and *ca.* 1800m (the higher clearing is partly shown in Figure 2); these support grazing herds of Banteng cattle and horses, and are clearly of anthropogenic origin. Burning both around the margins of these clearings as well as within the main forest stands appears to be resulting in a progressive destruction of the mixed montane forest, and its replacement by the *Eucalyptus urophylla* community. The mixed montane community is therefore under considerable ecological threat. *Eucalyptus* forests are likewise dominant on all other high peaks in the Nenas area, and in wider Southwest Timor as a whole. Trapping in these areas resulted in capture of *Rattus exulans* and *R. rattus sumbae.*

Whether *Rattus timorensis* is confined to the mixed montane forest habitat is not known for certain, however there can be little question as to the endangered status of this newly discovered species.

Acknowledgements

We are grateful for the companionship on the October 1990 expedition to Timor of Ron Johnstone, Western Australian Museum, Linc Schmitt, Western Australian University, and Richard Curtis, Western Australian Department of Public Health. The hospitality and assistance of the people of Desa Nenas is also warmly acknowledged.

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Photographs taken in the laboratory were by Norah Cooper, Western Australian Museum.

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Appendix

DATASET A: CRANIAL AND ROOT CHARACTERS ONLY

ANCESTOR	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
CHIROMYSCUS	1 1 1 0 0 0 0 1 0 0 1 1 0 0 0 1 0
NIVIVENTER	0 1 1 0 0 0 0 1 0 0 0 0 0 0 1 1 0
N. ANDERSONI	0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 1 1
DACNOMYS	0 1 0 0 0 0 0 1 0 0 0 0 0 0 1 1 1
LEOPOLDAMYS	0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0
MAXOMYS	0 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0
SRILANKAMYS	0 0 1 0 0 0 0 0 0 0 0 0 0 1 0 0 0
ANONYMOMYS	0 0 1 0 0 0 0 1 0 0 0 0 0 0 0 0 0
MARGARETAMYS	0 1 1 0 1 0 0 1 0 0 0 0 0 0 0 0 0
LENOTHRIX	0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0
APODEMUS	0 0 0 1 0 0 1 1 0 1 0 0 1 0 0 0 0
ARVICANTHIS	0 0 0 1 1 1 1 1 0 1 1 1 1 0 1 1 0
RATTUS	0 1 1 1 1 1 1 1 1 1 1 1 1 0 1 1 0
PAULAMYS	0 0 1 1 1 1 1 0 0 0 1 1 1 0 1 1 0
BUNOMYS	0 0 1 1 1 1 1 0 0 0 1 1 1 0 1 1 0
R. TIMORENSIS	0 0 1 1 1 1 1 1 1 1 0 1 1 0 1 1 ?
KOMODOMYS	0 1 1 1 1 1 1 1 0 1 1 1 1 0 1 1 0

DATASET B: ALL CRANIODENTAL CHARACTERS

ANCESTOR	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
CHIROMYSCUS	1 1 1 0 0 0 0 1 0 0 1 1 0 0 0 1 0 1 1 0 0 1 1 1 0 1 0 1 1 1
NIVIVENTER	0 1 1 0 0 0 0 1 0 0 0 0 0 0 1 1 0 1 1 0 0 1 1 1 0 1 0 1 1 1
N. ANDERSONI	0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 1 1 0 1 0 0 1 1 1 0 1 0 1 1 1
DACNOMYS	0 1 0 0 0 0 0 1 0 0 0 0 0 0 1 1 1 0 1 0 0 1 1 1 0 1 0 1 1 1
LEOPOLDAMYS	0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 1 1 1 0 1 0 1 1 1
MAXOMYS	0 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 1 1 1 0 1 0 1 1 1
SRILANKAMYS	0 0 1 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 1 0 0 0 1 1 0 1 0 1 1 0
ANONYMOMYS	0 0 1 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 0 1 0 1
MARGARETAMYS	0 1 1 0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 1 1 0 0
LENOTHRIX	0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 1 0 0 0 1 1 0 0 0 0
APODEMUS	0 0 0 1 0 0 1 1 0 1 0 0 1 0 0 0 0 0 0 1 1 0 0 0 0 1 0 0 0 0
ARVICANTHIS	0 0 0 1 1 1 1 1 0 1 1 1 1 0 1 1 0 0 1 0 0 1 0 0 0 1 0 1 0 0
RATTUS	0 1 1 1 1 1 1 1 1 1 1 1 1 0 1 1 0 0 1 0 0 1 0 0 0 1 0 1 0 0
PAULAMYS	0 0 1 1 1 1 1 0 0 0 1 1 1 0 1 1 0 0 1 0 0 1 0 1 0 1 0 1 0 0
BUNOMYS	0 0 1 1 1 1 1 0 0 0 1 1 1 0 1 1 0 0 1 0 0 1 0 1 0 1 0 1 0 0
R. TIMORENSIS	0 0 1 1 1 1 1 1 1 1 0 1 0 1 1 ? 0 ? ? 0 ? ? ? ? ? ? ? ? 1 0
KOMODOMYS	0 1 1 1 1 1 1 1 0 1 1 1 1 0 1 1 0 0 1 1 0 1 0 0 0 1 0 0 1 0

NOTES ON DATASETS

Character states designated as follows: 0 = PLESIOMORPHIC STATE
1 = APOMORPHIC STATE
? = STATE UNKNOWN

Characters are listed from left to right; all are binary. For dataset A, the 17 characters correspond to Musser's (1981a; Table 11) characters 1-16 except that his character 11 is divided into two characters (11 and 11a). With the exception of *R. timorensis*, the character state for character 11a is the same as for Musser's character 11. For dataset B, the 30 characters correspond to Musser's characters 1-29, with character 11 divided into two as per dataset A.

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Description of a new deepwater clingfish (Gobiesocidae) from New South Wales

J. Barry Hutchins*

Abstract

A new species of deepwater clingfish, *Kopua kuiteri*, is described from New South Wales. It is distinguished from the only other member of the genus, *K. nuimata* Hardy, by the lower dorsal and anal fin-ray counts (6 and 7 versus 10-11 and 8-9 respectively), the absence of papillae in region D of the ventral sucking disc (present in *K. nuimata*), and the lower number of sensory pores on each side of the head (2 versus 7 respectively). These differences are discussed in the context of interspecific variation in other Australian and New Zealand genera.

Introduction

The monotypic gobiesocid genus *Kopua* Hardy is known only from deep water off the north island of New Zealand. Its type species, *K. nuimata* Hardy, 1984, was described from six specimens (19-28 mm SL) collected at depths between 160 and 337 m. Unlike other New Zealand clingfishes, *K. nuimata* is characterised by the unique condition of large eyes separated by a very narrow interorbital. In addition, the ventral sucking disc has a peculiar shape caused by a long and truncate posterior fringe.

During an investigation by the present author in 1982 aimed at discovering the number of clingfish species in southern Australian waters, an unusual specimen from deep water off Bermagui in New South Wales was examined. Its distinctive features included a large eye, very narrow interorbital, and a long, somewhat truncate posterior fringe to the ventral disc. At the time, this specimen was thought to represent an undescribed genus and species. When *Kopua nuimata* was described two years later, there was little doubt that the Australian specimen would also prove to be a member of this genus. However, a closer examination showed that the New Zealand and Australian forms differed considerably in respect to two characters thought to be important for distinguishing gobiesocid genera (*K. nuimata* has many more cephalic sensory pores than the Australian specimen and the pattern of papillae on the ventral sucking disc is different). It was decided to await more Australian material in the off chance that the single specimen was deformed. However, in the intervening years, no additional specimens have been found. Furthermore, after the examination of large numbers of gobiesocids, it is now considered unlikely that the single specimen is abnormal. The purpose of this paper, therefore, is to describe the Australian specimen as a new species of *Kopua,* and to comment on the importance of the differences between it and *K. nuimata.*

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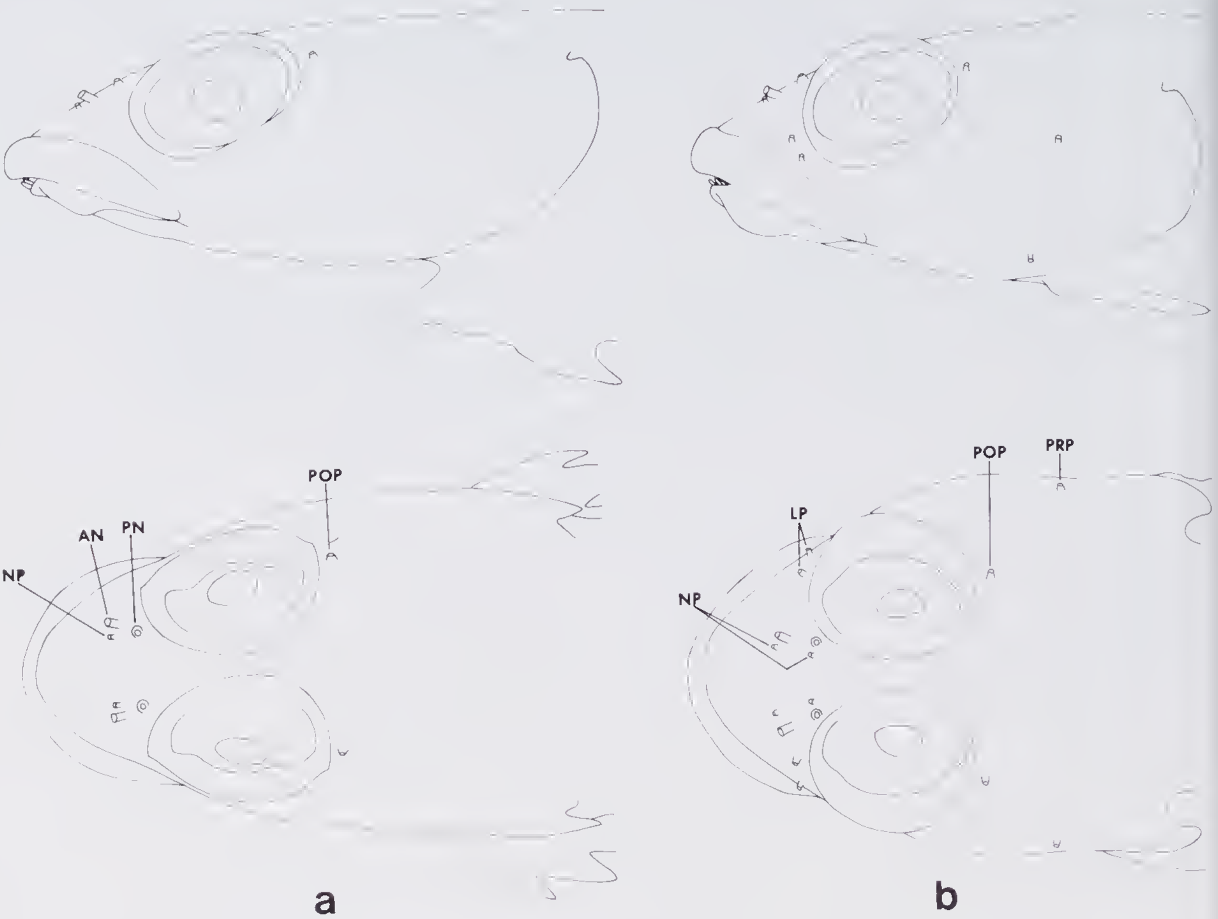

Figure 1. Lateral and dorsal view diagrams of the heads of both species of *Kopua* showing the differences in their cephalic pore systems: a. *K. kuiteri* sp. nov., holotype, 37 mm SL; b. *K. nuimata,* NMNZ P.13110, 28 mm SL (abbreviations: AN-anterior nostril; LP-lacrymal pore; NP-nasal pore; PN-posterior nostril; POP-postocular pore; PRP-preopercular pore).

The methods used follow Hutchins (1983). The material examined is housed at The Australian Museum, Sydney (AM), National Museum of New Zealand, Wellington (NMNZ), and Western Australian Museum, Perth (WAM).

Systematics

Kopua kuiteri sp. nov.

Figures 1a, 2, and 3

Holotype

AMS I.22886-001, 37 mm SL, off Bermagui, New South Wales (36°25'S, 150°04'E), inside empty cowry shell, collected by bottom trawl at 92-110 m , R. Kuiter, 3 August 1980.

Diagnosis

This species is placed in the genus *Kopua* because of the large eyes, extremely narrow interorbital, and its distinctively shaped ventral sucking disc. It is separated from *Kopua nuimata,* the only other known member of the genus, by its lower fin-ray counts, the lack of cephalic sensory pores in the preoperculomandibular and lacrymal series, and the absence of a posterior patch of papillae on the anterior half of its ventral sucking disc (region D).

Description

As only a single specimen of this species is known, its measurements are included in the following account, accompanied by the proportional meristics in parentheses.

Dorsal fin rays 6; anal fin rays 7; pectoral fin rays 23; pelvic fin rays I,4; caudal fin rays 14 (segmented rays only); vertebrae 34 (from radiograph); branchiostegals 6.

Body moderately robust, subcylindrical anteriorly, compressed posteriorly, depth 5.2 mm (7.1 in SL) and width 6.9 mm (5.4 in SL); caudal peduncle very short but deep, length 0.9 mm and depth 3.9 mm; head moderately wide posteriorly and compressed, head length 15 mm (2.5 in SL) and head width 8.3 mm (1.8 in its length); snout somewhat triangular in dorsal view, rounded anteriorly, length 3.6 mm (4.2 in head length); nostrils moderate in size, tubular, posterior one much shorter than anterior, both without flaps; posterior nostril level with or slightly anterior to front border of eye; eye large, diameter 4.3 mm (3.5 in head length); bony interorbital very narrow, width 0.7 mm (21.4 in head length).

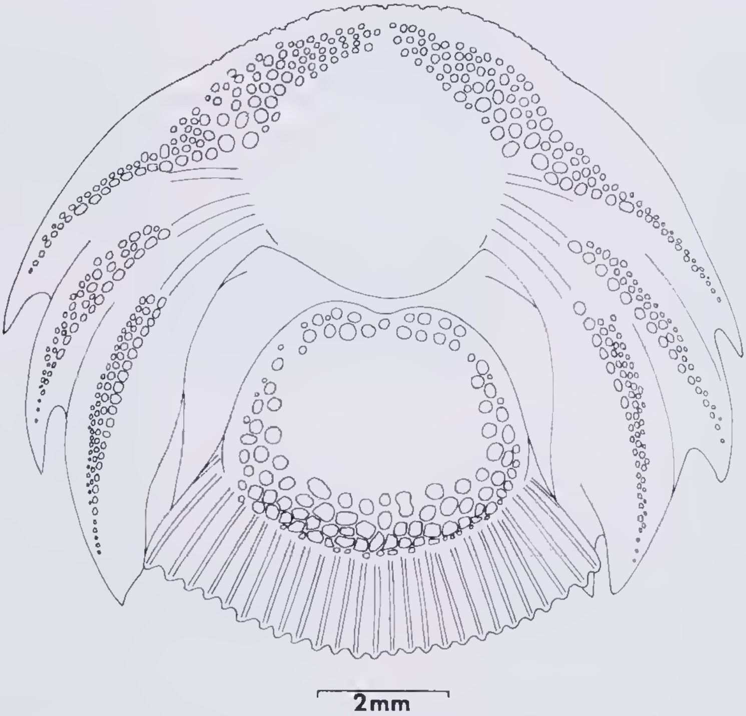

Figure 2. Ventral sucking disc of *Kopua kuiteri* sp. nov., holotype, showing arrangement of papillae on ventral surface (anterior end faces top of page).

Skin smooth and scaleless; lateral line sensory system consists of moderate-sized open pores and minute papillae, the former found only on the head (Figure 1a); each pore has a short tubular opening served by a canal in underlying bones; two pores only on each side of head, one postorbital and one nasal; papillae arranged in longitudinal series laterally on body, more scattered on head, although linear series of about six papillae from nostrils to behind corner of mouth, and line of three on lower jaw adjacent to lip fold (due to the difficulty in detecting these papillae, they are not described further here).

Gill opening wide, membranes joined across isthmus but not attached to it; upper attachment of gill membrane opposite second or third pectoral fin ray; upper attachment of pelvic fin membrane opposite 12th pectoral fin ray; axial dermal flap very small, upper attachment opposite 17th-18th pectoral fin ray; ventral disc double, somewhat circular, moderately large, both length and width 10.3 mm (3.6 in SL); striated posterior fringe long, with distinctly squared posterolateral corners (Figure 2); disc papillae arranged as in Figure 2.

Mouth distinctly subterminal, with large fleshy lips; lip fold of lower jaw not continued across symphysis; teeth in both jaws conical, erect, moderate in size, and bluntly rounded, those anteriorly more flattened and incisorlike; upper jaw with single row of lateral teeth, forming two rows anteriorly (some scattered smaller and more acute teeth posterior to anterior rows); lower jaw with similar teeth to upper, except some lateral teeth noticeably larger and anterior rows forming a tooth patch on either side of symphysis, anteriormost projecting forward, those behind smaller, erect and more pointed; palatine and vomerine teeth absent; gill filaments on all four gill arches; gill rakers short and pointed (unable to be counted).

Bases of dorsal and anal fins short, that of dorsal equal to and originating slightly more anterior to that of anal fin; snout to origin of dorsal fin 27 mm (1.4 in SL); urogenital opening centred between origin of anal fin and rear margin of ventral disc; a prominent genital papilla present.

Subopercular element present, forming terminal bone posteriorly on side of head, but not spinelike; condition of dorsal postcleithral, ventral postcleithral, and pelvis not known.

Colour of holotype in alcohol: overall pale yellowish brown, with blackish brown eyes.

Figure 3. *Kopua kuiteri* sp. nov., holotype, AMS I.22886-001, 37 mm SL, lateral view.

Colour when fresh (based on colour transparencies of the freshly collected holotype): ground colour pale yellowish brown, with numerous irregularly shaped orange to reddish-orange blotches on head and body, those on latter tending to form cross-bands on back and sides (Figure 3); head with several reddish lines and dashes continued from lower border of eye to ventral surface; a pale purple ringlike mark on side of head about half way between eye and pectoral fin base, subequal in size to pupil; dorsal and anal fins with reddish rays, those of other fins pale red to hyaline, all integuments hyaline; eye orangish, more blackish dorsally, with a pale ring enclosing black pupil.

Distribution

Kopua kuiteri is known only from the type locality off southern New South Wales.

Comparisons

Kopua kuiteri and *K. nuimata* share several important features: both have a similar-shaped ventral disc, a small axial dermal flap, a large eye and very narrow interorbital, teeth which are very close in both their shape and arrangement, and both lack flaps on the rim of the anterior nostril. In addition, both species are the only gobiesocids known to inhabit relatively deep waters in the Australian and New Zealand region. However, *K. kuiteri* possesses only two sensory pores on each side of the head, whereas *K. nuimata* has 7 (Figures 1a and 1b). *Kopua kuiteri* lacks the posterior nasal pore, all lacrymal pores, and all preoperculomandibular pores, whereas *K. nuimata* has an anterior and a posterior nasal pore, two lacrymal pores, and two preopercular pores (both species have only one postorbital pore and lack all mandibular pores). In addition, *K. kuiteri,* unlike *K. nuimata,* has no papillae in region D of its ventral sucking disc. The lower dorsal and anal fin-ray counts for *K. kuiteri* are also significant (6 and 7 respectively, versus 10-11 and 8-9 for *K. nuimata*).

Remarks

Hardy (1984) described *Kopua nuimata* as a new genus and species of deepwater gobiesocid from New Zealand. The discovery of the first Australian deepwater species, herein described as *K. kuiteri,* now extends the range of the genus across the Tasman Sea. No other Australian or New Zealand gobiesocid genus has so far been shown to have a distribution encompassing this region. Although *K. kuiteri* possesses most if not all of the distinguishing features of the genus (see Comparisons above), its major differences when compared to the New Zealand species are difficult to explain in the context of presumed gobiesocid evolution. Hutchins (1983) and Shiogaki and Dotsu (1983) both suggested that the arrangement and number of cephalic sensory pores were important for indicating relationships in the family. A survey of all Australian and New Zealand clingfishes by the present author reaffirmed this (for example, all four species of the Australian *Aspasmogaster* share identical pore patterns (Hutchins 1984), as do the three species of the Australian *Parvicrepis,* both species of the Australian *Lepadichthys,* the two species of *Trachelochismus* from New Zealand, and the two species of *Modicus* from New Zealand). However, the five species currently making up the Australian genus *Cochleoceps* can be separated into three groups based on the number of preoperculomandibular pores, two species with six, two with four and one with five (see

Hutchins 1983). These groupings are also supported by other character differences, which appears to indicate that more than one genus is represented (Hutchins, in preparation). Furthermore, the pattern of papillae on the ventral disc was shown by Briggs (1955) to be a good indicator of relationships. On the other hand, the present study has shown that considerable differences in the cephalic pores and ventral disc papillae exist between the two species of *Kopua*. Consequently, it would appear that these characters are not good indicators of close relationship in all cases, especially for a taxon inhabiting both sides of the Tasman. Other gobiesocids from Australia and what appears to be their New Zealand counterparts have previously been placed in separate genera belonging to different subfamilies on the basis of certain character differences (Briggs 1955). For example, Briggs placed the Australian monotypic *Creocele* and the New Zealand monotypic *Diplocrepis* in separate subfamilies based on the different number of gills (four and three respectively) (this arrangement has been criticised by other workers, e.g. Springer and Fraser 1976, and Hardy 1983). Allowing for this discrepancy, in addition to some differences in the number and pattern of the cephalic pore system, the two closely resemble each other in overall morphology, both internally and externally. Obviously other characters besides the number of gills and the arrangement of both the cephalic pores and ventral disc papillae need to be investigated. Further studies might show that the Australian and New Zealand gobiesocids have more in common than was earlier believed.

Additional material examined.

Kopua nuimata, NMNZ P.13110, paratype, 28 mm SL, Rangatira Knoll, NW of White Island, 292-337 m, RV Tangaroa, 23 January 1981; NMNZ P.9928, paratypes, 3: 25-27 mm SL, Middlesex Bank, NW of Three Kings Islands, 206-221 m, RV Tangaroa, 31 January 1981.

Acknowledgements

Specimens were kindly provided on loan by J.R. Paxton (AM) and A. Stewart (NMNZ). I am particularly grateful to R.H. Kuiter for supplying colour transparencies of the holotype showing its life coloration. Technical assistance was provided by K. Smith (WAM).

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Revision of *Lerista microtis* (Lacertilia: Scincidae)

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Abstract

'Lerista microtis arenicola' is now regarded as a full species and is redescribed. *'L. m. microtis'* is divided into three subspecies, *L. m. microtis* and *L. m. intermedia* of southern Western Australia and *L. m. schwaneri* of far western South Australia; and *L. viduata*, a new species from the southern Western Australia is described.

Introduction

Only eight *'Lerista m. microtis'* and three *'L. m. arenicola'* were available for my generic revision (Storr 1972). Since then many more specimens of these taxa have been collected, permitting a re-assessment of their status. In view of its substantial differences from *L. microtis* (and their possible sympatry in South Australia), *L. arenicola* is raised to a full species. *L. microtis* itself is divided into three subspecies, and a new species is separated from it.

This paper is based on 108 specimens in the Western Australian Museum (catalogue numbers not prefixed) and eight specimens kindly loaned by the South Australian Museum (catalogue numbers prefixed by SAM).

Systematics

Lerista microtis (Gray)

Moca microtis Gray, 1845, *Cat. Liz. Brit. Mus.*, p. 23.

Diagnosis

A small *Lerista* with 5 fingers, 5 toes and movable eyelid. It is distinguishable from *L. arenicola* by its wide sharp-edged black upper lateral stripe, from *L. viduata* by its white midlateral stripe and from *L. bougainvillii* (Gray) of south-eastern Australia by its 3 (rather than 4) supraoculars, 6 (rather than 5) supraciliaries, lesser size and longer limbs.

Lerista microtis microtis (Gray)

Figure 1

Diagnosis

A small short-legged subspecies, with few dorsal markings apart from black laterodorsal stripe or spots and with strong complex lateral pattern including whitish dorsolateral, midlateral and ventrolateral stripes.

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Figure 1. A *Lerista m. microtis* from Torbay Head, photographed by R.E. Johnstone.

Description

Snout-vent length (mm): 20-52 (N 72, mean 38.7). Length of appendages etc (%SVL): foreleg 13.5-20 (N=46, mean 16.3), hindleg 23-35 (N 45, mean 29.7), tail 104-134 (N 23, mean 121.7), snout to foreleg 25-38 (N 45, mean 31.1).

Nasals narrowly separated (N 27), just touching (5) or in short contact (13). Prefrontals widely separated. Frontoparietals in long contact, about as large as interparietal. Supraoculars 4, first two in contact with frontal. Supraciliaries 6, first largest. Loreals 2. Presuboculars 2 (including lower of two preoculars). Upper labials 7 (44) or 8 (2). Nuchals 2-5 on each side (N39, mean 3.2). Midbody scale rows 18 (N 4), 20 (26) or 22 (3). Lamellae under fourth toe 16-22 (N 38, mean 19.5).

Dorsally medium to dark olive grey or brown, usually with little pattern; commonly some black flecks and a narrow to wide laterodorsal stripe or series of spots. Narrow greyish white or brownish white dorsolateral stripe on body, becoming wider and more diffuse on tail. Very wide, sharp-edged black upper lateral stripe from snout to tail, on which it becomes paler, narrower and ragged-edged. Narrow to moderately wide white midlateral stripe from upper lip to base to tail. Usually a narrow to moderately wide black lower lateral stripe from in front of foreleg to behind hindleg. Usually a white or greyish white ventrolateral stripe from in front of foreleg to hindleg. Under tail and legs pinkish white; rest of lower surfaces greyish white or pinkish white, scales sparsely to heavily stippled and/or edged with grey or black.

Distribution

Humid and subhumid south-west of Western Australia: Darling Range from Dwellingup south to the Collie River; and south coast from Augusta east to Bremer Bay and inland to the Manjimup district. See map, Figure 2.

Remarks

The specimen from Torbay Head (Figure 1) has the back unusually pale and strongly patterned. For other extreme see colour photograph of an Albany specimen in Wilson and Knowles (1988 : 300, pl. 555).

Material

South-west Division (WA): 5km E Dwellingup (40118) and 28km SE (80833); Waroona (88478); 15km NW Collie (76271, 81282) and 25km W (49275-7); 3.5km NE Augusta (90185-6); Canebrake Road, 23km N Scott River (36047-8); Scott River (49955); 18.5km E Black Point (90210) and 13km ESE (90200); 33km NE Nyamup (96796-8); Perup (56751, 97420, 97424); 10km S Manjimup (86944); 10km S Pemberton (89959); Meerup (47895); near Mt Chudalup (90189, 95254, 95304); south-east corner of Broke Inlet (68160); near Walpole (57415, 78317); near Bow Bridge (93544-5); William

Figure 2. Map of southern Western Australia and far western South Australia, showing location of specimens of *L. m. microtis, L. m. intermedia, L. m. schwaneri, L. arenicola* and *L. viduata.*

Bay (76268); near Denmark (31063, 31195, 90241); Torbay Head (51777); near Albany (53329-30, 56082-6); Two Peoples Bay (36382, 44991, 44996, 69824); 6km ENE Manypeaks (75624); Waychinicup Inlet (61386); near Cheyne Beach (10755, 36017, 62240, 67795); Bremer Bay (33410); Hood Point (93863-7).

Lerista microtis intermedia subsp. nov.

Holotype

89408 in Western Australian Museum, collected by R.Elston in 1982 at Culham Inlet, Western Australia, in 33°55′S, 120°04′E.

Paratypes

South-west Division (WA): Barrens Beach (89292); East Mt Barren (95394, 95401-2); Culham Inlet (78227, 89404-7, 89409); Hopetoun (56058).

Eucla Division (WA): Quaggi Beach (97333-4); Rossiter Bay (42590); Wickham I. (97579); Israelite Bay (31103, 66875, 67207, 67214) and 8km NE (17623).

Diagnosis

A medium-sized subspecies, differing from *L. m. microtis* mainly in coloration: dorsal ground colour paler but more heavily dark-spotted, spots tending to align on back into 3 diffuse stripes, and dark upper lateral stripe narrower; and differing from *L. m. schwaneri* in having fewer midbody scale rows and its smaller size.

Description

Snout-vent length (mm): 22-57 (N 21, mean 43.1). Length of appendages etc. (%SVL): foreleg 14-20 (N 20, mean 16.8), hindleg 26-35 (N20, mean 30.3), tail 110-134 (N6, mean 121.8), snout to foreleg 25-38 (N20, mean 31.5).

Nasals narrowly separated (N 12), just touching (4) or in very short contact (3). Prefrontals widely separated. Frontoparietals in long contact, about as large as interparietal. Supraoculars 4, first two in contact with frontal. Supraciliaries 6, first largest, fourth often nearly as large as first. Loreals 2. Presuboculars 2. Upper labials 7. Nuchals 2-4 (N 15, mean 3.2). Midbody scale rows 18 (N 1), 20 (14), 21 (1) or 22 (1). Lamellae under fourth toe 18-24 (N 19, mean 20.2).

Dorsally pale to medium olive grey or brown, stippled and flecked with black or blackish brown, markings on back tending to align into 3 narrow, more or less diffuse stripes. Usually an indistinct greyish or brownish white dorsolateral stripe. Narrow to wide, sharp-edged blackish upper lateral stripe from snout to tail, on which it becomes paler. Narrow white or whitish midlateral stripe from upper lip to tail. Narrow black or dark greyish brown lower lateral stripe from ear to hindleg. Occasionally a narrow indistinct pale ventrolateral stripe on body. Under tail and legs pinkish or greyish white, with or without dark flecks; rest of lower surfaces greyish white, scales sparsely to heavily stippled and/or edged with dark grey.

Distribution

Semiarid and subhumid south coast of Western Australia from East Mt Barren east to Israelite Bay, including Wickham I. in the Archipelago of the Recherche.

Remarks

For a colour photograph of an Israelite Bay specimen see Storr *et al.* (1981: pl. 13, no. 3).

Lerista microtis schwaneri subsp. nov.

Holotype

25088 in South Australian Museum, collected on 15 December 1983 by K. Jordan on Franklin Is (west), South Australia, in 32°27′S, 133°39′E.

Paratypes

South Australia: St Peter I. (SAM 31513); Goat I. (SAM 21869, SAM 27434); West Coast (SAM 1599).

Diagnosis

A large long-legged subspecies, differing from *L. m. intermedia* mainly in its larger nasals and more numerous midbody scale rows, and from *L. microtis microtis* by its larger size, more numerous midbody scale rows and more complex dorsal pattern.

Description

Snout-vent length (mm): 32-61 (N 5, mean 46.7). Length of appendages etc. (%SVL): foreleg 16-22 (N 5, mean 19.0), hindleg 28-35 (N 5, mean 31.2), snout to foreleg 28-38 (N 5, mean 32.4).

Nasals in very short to short contact. Prefrontals widely separated. Frontoparietals in long contact, about as large as interparietal. Supraoculars 4, first two in contact with frontal. Supraciliaries 6, first largest. Loreals 2. Presuboculars 2. Upper labials 7. Nuchals 2-4 (N 5, mean 2.8). Midbody scale rows 22 (N 3) or 24 (2). Lamellae under fourth toe 18-25 (N 5, mean 20.9).

Dorsally pale olive grey or brown, masked with black or blackish brown: dense stippling on head, flecks and 3 narrow diffuse stripes on back, and stippling on tail. Medium to wide, sharp-edged black or blackish brown upper lateral stripe from snout to tail, on which it becomes ragged-edged. Medium to wide, white or brownish white midlateral stripe from upper lip to proximal part of tail. Narrow black or blackish brown lower lateral stripe from just in front of foreleg to hindleg. Lower surfaces whitish, ventrals grey-edged.

Distribution

Only certainly known from Nuyts Archipelago off semiarid upper west coast of Eyre Peninsula, South Australia.

Remarks

For photograph of a Goat I. specimen see Schwaner and Miller (1984 : 215, figure 1).

The 'west coast' specimen was donated in 1930 by Constable Halloran of Fowlers Bay. If it were collected locally, *L. m. schwaneri* and *L. arenicola* would be sympatric here.

Derivation of name

After Dr T.D. Schwaner, formerly Curator of Reptiles in the South Australian Museum.

Lerista arenicola Storr

Lerista microtis arenicola Storr (1972: 61)

Diagnosis

A moderately small, pale *Lerista* with 5 fingers, 5 toes and movable eyelid, differing from *L. microtis* in its greater size and narrow ragged-edged black upper lateral stripe.

Description

Snout-vent length (mm): 30-66 (N 18, mean 49.1). Length of appendages etc. (%SVL): foreleg 14-21 (N 18, mean 17.5), hindleg 22-35 (N 18, mean 30.2), tail 105-132 (N 9, mean 117.0), snout to foreleg 26-35 (N 18, mean 30.5).

Nasals narrowly separated (N 2) or in very short to moderately long contact (16). Prefrontals widely separated. Frontoparietals in long contact, about as large as interparietal. Supraoculars 4, first two in contact with frontal. Supraciliaries 6, first largest. Loreals 2. Presuboculars 2. Upper labials 7. Nuchals 1-4 (N 18, mean 2.9). Midbody scale rows 20 (N 2), 21 (2) or 22 (14). Lamellae under fourth toe 17-23 (N 18, mean 18.7).

Dorsally usually pale olive grey or greyish brown (becoming greyish or pinkish white on tail), flecked with black, flecks on back tending to form a fine laterodorsal line. Narrow to wide, pale grey or greyish white dorsolateral stripe often discernible on body. Narrow, ragged-edged or diffuse, black upper lateral stripe from snout to proximal half of tail. Wide white midlateral stripe from upper lip to base of tail. Very narrow, ragged-edged or diffuse, black or dark grey lower lateral stripe. Under tail and legs pinkish white; rest of lower surfaces usually greyish white, ventrals grey-edged.

Distribution

Semiarid and arid sandy shores of Great Australian Bight: from Twilight Cove east to Eucla, Western Australia; and from Head of Bight east to Fowlers Bay, South Australia.

Remarks

For colour photograph of specimen from 13km W Eyre see Storr *et al.* (1981 : pl. 13, no. 4). Two of the specimens from Eyre (91438 and 92055) have the back and venter much darker than in other specimens.

Material

Eucla Division (WA): Eyre (60815, 91438, 92055) and 13km W (66914-22); old Eucla (24608, SAM 23032). South Australia: Head of Bight (SAM 5860); 12.5km NE Colona (SAM 25654); Fowlers Bay (24586-7).

Lerista viduata sp. nov.

Holotype

96771 in Western Australian Museum, collected on 27 October 1986 by B. Maryan in the Ravensthorpe Range, Western Australia, in 33°33'S, 119°06'E.

Diagnosis

A dark, weakly patterned Lerista with 5 fingers, 5 toes and movable eyelid, differing from *L. microtis* and *L. arenicola* in its more widely separated nasals, shorter limbs and little lateral pattern (especially absence of white midlateral stripe).

Description (of only available specimen)

Snout-vent length (mm): 43. Length of appendages etc. (%SVL): foreleg 12, hindleg 21, tail 116, snout to foreleg 30.

Nasals moderately widely separated. Prefrontals widely separated. Frontoparietals in long contact, about as large as interparietal. Supraoculars 4, first two in contact with frontal. Supraciliaries 6, first and fifth largest. Loreals 2. Presuboculars 2. Upper labials 7. Nuchals 3. Midbody scale rows 22. Lamellae under fourth toe 18.

Dorsally olive grey, darkest on tail. Head and tail stippled with black. Back with 4 series of small black spots or short dashes, inner (paravertebral) pair larger. Black upper lateral stripe from snout to tail, upper edge sharp, lower edge indefinite. Lateral surfaces, upper surface of limbs and venter dark grey, spotted black. Throat whitish, scales grey-edged. Under tail whitish, stippled with black.

Distribution

Only known from the Ravensthorpe Range in the semiarid southern interior of Western Australia.

Figure 3. Holotype of *Lerista viduata* photographed in life by D. Robinson.

Derivation of name

Latin for widowed, in allusion to its dark coloration and loss of white midlateral stripe.

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SHORT COMMUNICATIONS

Rec. West. Aust. Mus. 1991, **15**(2): 479-481

Arthrodire predation by *Onychodus* (Pisces, Crossopterygii) from the Late Devonian Gogo Formation, Western Australia

John A. Long*

During late September - early October 1990 a joint expedition by the Australian National University Geology Department and the Western Australian Museum collected a large number of well-preserved fossil fishes from the Gogo Formation, outcropping approximately 100km east of Fitzroy Crossing. Amongst the new finds is a well-preserved example of the predatory crossopterygian fish *Onychodus* sp. The specimen (WAM 90.11.1; Figure 1) is of special interest though because the bones of an arthrodire (Pisces, Placodermi) were found enclosed within the cranial bones of the *Onychodus* showing the first direct evidence of active predation on arthrodires by *Onychodus*. The nature of fossilisation of the fish remains in the Gogo Formation is such that, after death, the onset of concretion formation was rapid, preventing damage to many of the delicate perichondral cartilage bones of the gill-aches (Long 1988). Because the skull bones and most of the body of the *Onychodus* were not all present in the concretion, it is concluded that the specimen was partially disrupted after its death. This is not unusual because the skull roof bones of this specimen were only loosely connected, and none were in articulated position. It appears that the *Onychodus* choked on the placoderm and fell to the bottom where it was either partly scavenged or decomposed before a larger section of the head, including the gullet with the placoderm remains, was quickly buried in the sediment.

The placoderm plates were oriented with the anterior of the animal facing the same direction as the anterior of the *Onychodus* specimen. This indicates that the prey was captured by the tail, and then dragged back into the mouth by the large stabbing tooth whorl at the front of the mouth. The placoderm plates lack any markings indicative of a bite by the stabbing symphysial teeth, suggesting that *Onychodus* lunged at the soft fleshy tail of the placoderm rather than grabbing it anteriorly by the dermal armour. Furthermore the placoderm plates, although slightly displaced from their life position, had not been damaged by crushing from the powerful jaws of the *Onychodus,* indicating that the prey item was probably swallowed whole. The *Onychodus* has a lower jaw length of 105mm, suggesting an overall fish length of at least 600mm by comparison with estimates based on other complete *Onychodus* specimens from Gogo. The placoderm is one of the several undescribed new eubrachythoracid arthordires currently under study by workers at the British Museum of Natural History. It is represented by both posterior and anterior ventrolateral plates, a spinal plate and some indeterminate bone fragments. It has a ventral trunkshield about 85mm long, indicating a total fish length of about

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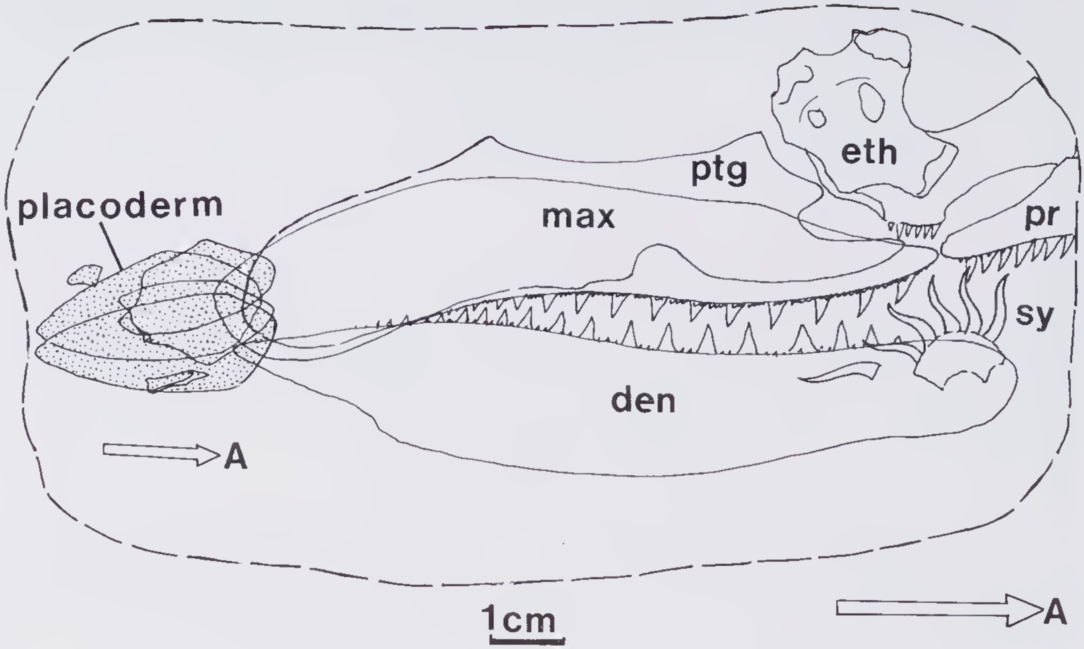

Figure 1. Sketch showing the orientation of some of the large *Onychodus* skull bones and predated arthrodire plates within the shape of the original concretion. Arrows indicate the anterior direction of both specimens.

310mm by comparison with the well-known placoderm *Coccosteus cuspidatus* (Miles & Westoll 1968). This suggests that *Onychodus* was an effective predator capable of attacking and swallowing whole prey items of a size nearly more than half its own body length, unless of course, this case is an exception which resulted in the death of the predator. Figure 2 shows a reconstruction of *Onychodus* catching an arthrodire by its tail.

A description of the Gogo *Onychodus* is currently being prepared by Dr S. M. Andrews (Royal Scottish Museum), and until this work is published the anatomical features of the feeding mechanism cannot be discussed in detail. However, it can be seen from the new specimen, which shows the anterior ossification of the braincase intact, that the skull was highly kinetic and the snout could be raised independently of the largely unossified posterior neurocranial component (the oto-occipital). The cavities within the snout for housing the large symphysial toothwhorls indicate that when *Onychodus* closed its mouth the stabbing teeth would have almost touched the top of the skull roof. The presence of a ligament attachment area on the posterior face of the symphysial tooth whorl suggests that *Onychodus* may have been able to rotate the symphysial tooth-whorls. Thus it was able to lunge out, catch prey and then retract the tooth-whorl to drag the prey back into the buccal cavity.

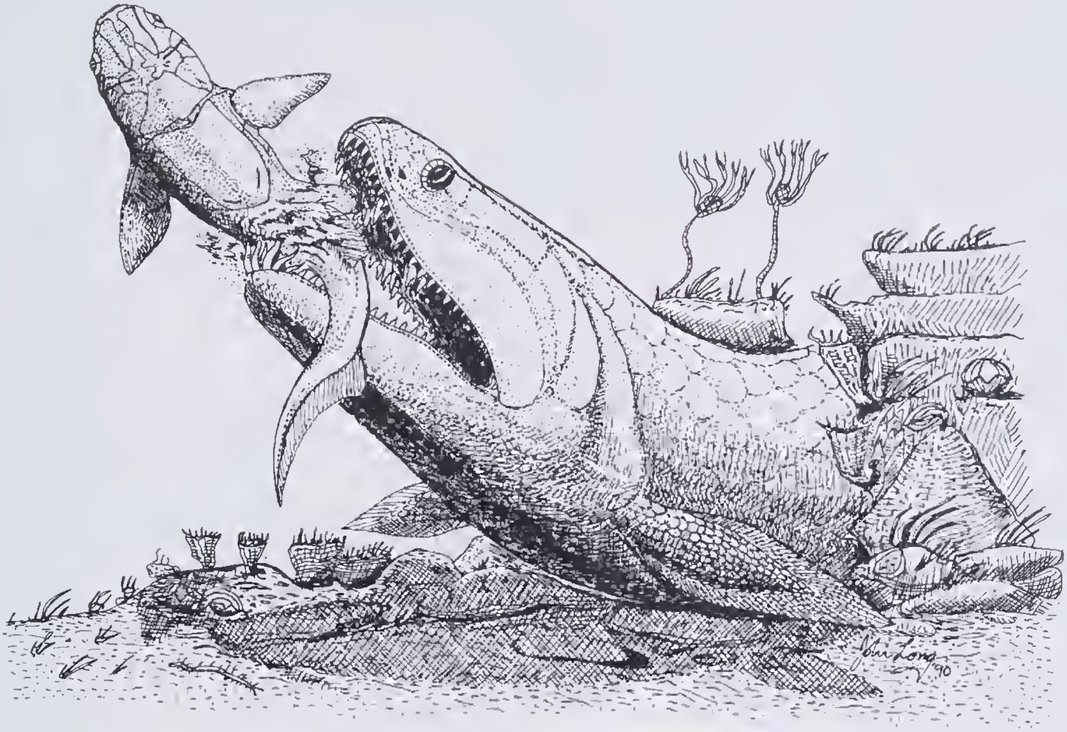

Figure 2. Restoration of an *Onychodus* catching a placoderm fish by the tail using its symphysial tooth whorls and full kinesis of the braincase.

Acknowledgements

Sincere thanks to Prof. Ken Campbell from the Geology Department, A.N.U., for providing funds to allow the author to participate in the 1990 Gogo expedition and collect new material for the Western Australia Museum. Prof. Campbell and Dr Ken McNamara kindly read and commented on the manuscript.

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Rec. West. Aust. Mus. 1991, 15(2): 483-485

A new subspecies of *Lerista planiventralis* (Lacertilia: Scincidae) from Western Australia

G.M. Storr*

Abstract

The new skink comes from the Onslow region.

Lerista planiventralis maryani subsp. nov.

Holotype

104406 in Western Australian Museum, collected by B. Maryan and R. Browne-Cooper on 10 March 1990 at 11km NW Barradale Roadhouse, Western Australia, in 22°48′S, 114°53′E.

Paratypes (all in WA Mus.)

North-west Division (WA): Onslow (104331); 11km NW Barradale (100881, 104482).

Diagnosis

A *Lerista* with ventrolateral flange, 2 fingers, 3 toes and movable eyelid, similar to *L. p. planiventralis* but differing from it and *L. p. decora* in its fewer midbody scale rows (17-18, v. 20-24) and more temporals (usually 3, v. normally 2).

Description

Snout-vent length (mm): 42-61 (N 4). Length of appendages etc. (%SVL): foreleg 7-9, hindleg 23-30, tail 89-92 (N 2), snout to foreleg 24-30.

Nasals widely separated. Prefrontals widely separated. Frontoparietals in short contact (N 2), just touching (1) or very narrowly separated: much shorter than interparietal. Nuchals 0-3 (mean 1.2). Supraoculars 3, first two in contact with frontal. Supraciliaries 5, second and fifth smallest. Upper labials 6. Temporals 1 + 2 (N 3), upper secondary usually largest, lower secondary usually smallest (in one specimen fused to upper secondary). Midbody scale rows 17 (N 3) or 18 (1). Lamellae under longest toe 13-14.

Coloration on red sandridge near Barradale. Dorsal and upper lateral surfaces of head pale brown marked with blackish grey: smudges on top of head and streak from nostril to temple. Back brownish red (becoming paler on flanks and upper surface of hindlegs and pale brown on tail), marked with greyish brown: 4 rows of faint spots on back

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* Western Australian Museum, Perth, Western Australia 6000

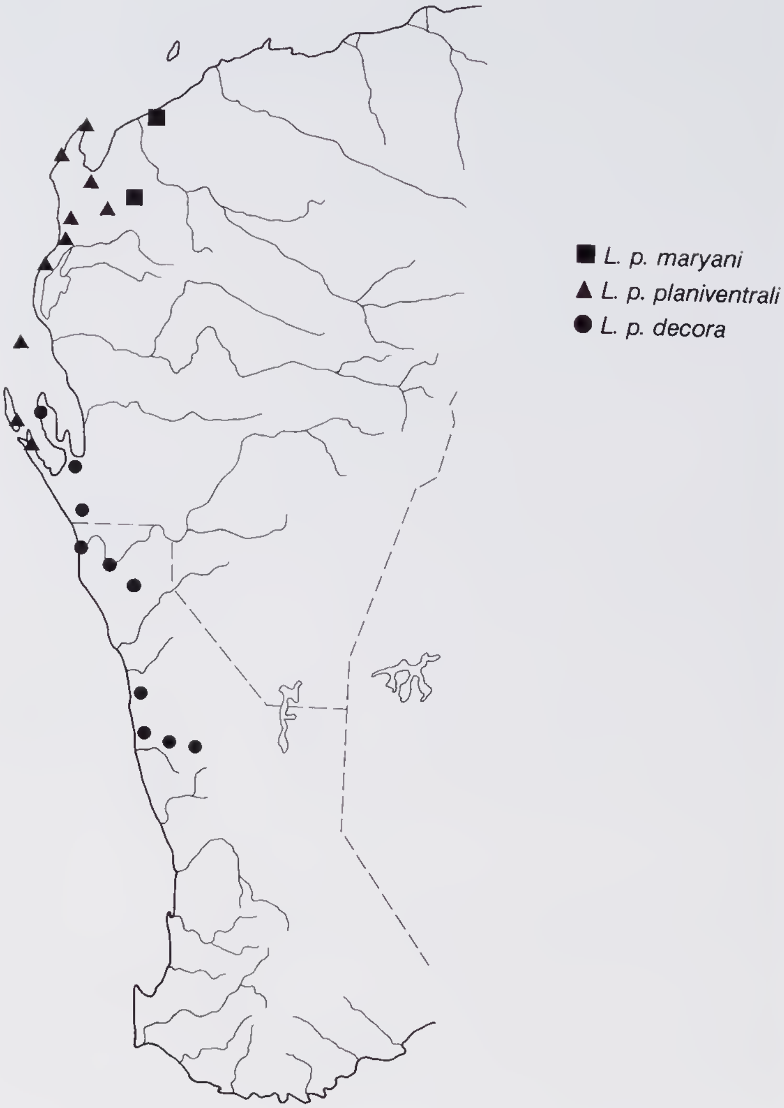

Figure 1 Map of western Western Australia showing location of specimens of subspecies of *Lerista planiventralis*.

(central pair continuing on to tail, where slightly more conspicuous) and narrow diffuse upper lateral stripe extending back on to tail and anteriorly continuing with loreotemporal streak. Lower surfaces and upper surface of forelegs white.

Coloration on pink sands near coast at Onslow. All upper surfaces pale brown to brownish white.

Figure 2 Holotype of *Lerista planiventralis maryani* photographed in life by B. Maryan.

Distribution

Arid north-west coast and hinterland of Western Australia from Onslow south to Barradale. See map, Figure 1.

Remarks

For description of *L. p. planiventralis* and *L. p. decora* see Storr (1978: 312-316).

Derivation of name

After Perth naturalist B. Maryan.

Reference

Storr, G.M. (1978). Taxonomic notes on the the reptiles of the Shark Bay region, Western Australia. *Rec. West. Aust. Mus.* **6**: 303-318.

Received 10 August 1990 Accepted 21 November 1990 Published 28 June 1991

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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.

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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.

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Synonymies should be given in the short form (taxon, author, date, page) and the full reference cited at the end of the paper.

Manuscripts

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 positions 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.

In papers dealing with historical subjects references may be cited as footnotes. In all other papers references must be cited in the text by author and date and all must be listed alphabetically at the end of the paper. The names of journals are abbreviated according to *World List of Scientific Periodicals.* The use of 'unpublished data' or 'personal communication' is discouraged.

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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.

The senior author is sent two sets of galley proofs (one to be retained) and one set of page proofs which must be returned promptly.

The senior author will receive fifty free offprints of the paper. Additional offprints can be ordered at page proof stage.

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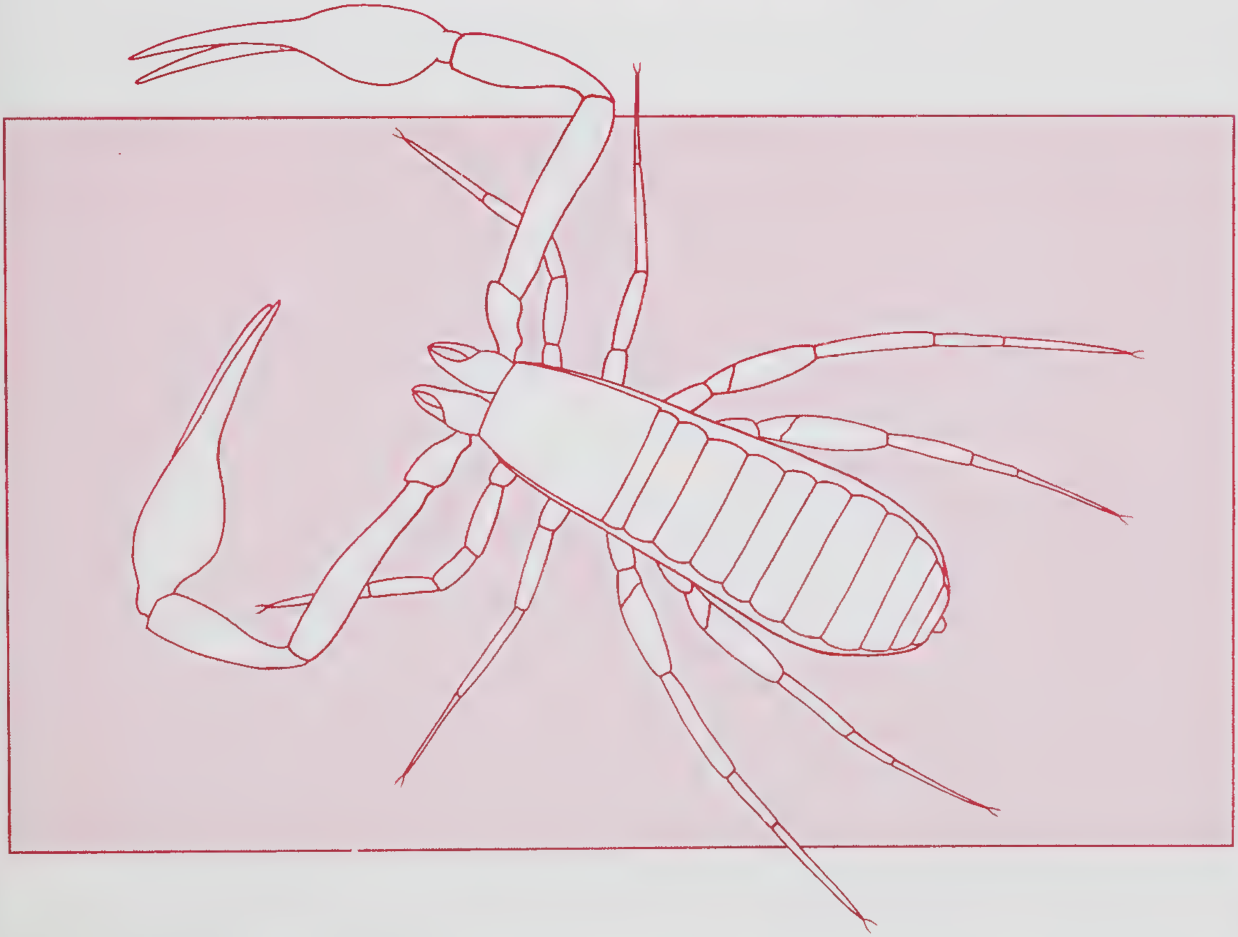

RECORDS

OF THE

WESTERN AUSTRALIAN MUSEUM AND ART GALLERY.

THE time has arrived when it has become necessary to issue Records, as is done by the older Museums.

These will deal almost entirely with the Natural History of this State. They will contain the results of Original Research, of Collecting Expeditions, and will also include brief notes on other matters connected with this Institution.

Hitherto this information has been published through the medium of various Australian, British and foreign publications.

BERNARD H. WOODWARD,

Director.

1st January, 1910.

WESTERN AUSTRALIAN MUSEUM PUBLICATIONS
1891 — 1991

MONOGRAPHS

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RECORDS of the Western Australian Museum

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Cover: Family Hyidae Chamberlin. Undescribed genus and species from caves in Cape Range.
Illustration: Mark Harvey

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The cavernicolous pseudoscorpions (Chelicerata: Pseudoscorpionida) of Cape Range, Western Australia

Mark S. Harvey*

Abstract

The pseudoscorpions collected from caves in Cape Range, Western Australia are described. Six species are recorded: *Austrochthonius easti*, sp. nov., *Tyrannochthonius butleri*, sp. nov., *T. brooksi*, sp. nov. (Chthoniidae), *Ideoblothrus woodi*, sp. nov., *I. papillon*, sp. nov. (Syarinidae) and an undescribed genus and species of Hyidae. The origins of the fauna are discussed.

Introduction

Although several cave-dwelling pseudoscorpions have been described from eastern Australia (Beier, 1967; Beier, 1968; Beier, 1969; Beier, 1975; Beier, 1976; Chamberlin, 1962; Dartnall, 1970; Harvey, 1989; Muchmore, 1982b), little is known of those from Western Australia. Several species from the Nullarbor Plain and the Yanchep region were recorded by Beier (1969), and a single species from the Margaret River region by Beier (1971). Recent field work in Cape Range by Dr W.F. Humphreys and his associates has uncovered a rich cavernicolous fauna, with six new species. Five of these species are described below, while the sixth will be treated in a forthcoming review of the Hyidae (Harvey, in preparation).

Materials and Methods

All material is lodged in the Western Australian Museum (WAM), and many are mounted on microscope slides in Euparal. Terminology follows Chamberlin (1931).

Systematics

Family Chthoniidae Daday

Genus *Austrochthonius* Chamberlin

Remarks

Australian species of *Austrochthonius* have been collected from south-eastern Australia (*A. australis* Hoff and *A. cavicola* Beier), south-western Australia, north-western Australia and north-eastern Australia. Beier (1966) incorrectly attributed material from south-western Australia to *A. australis,* and these populations represent a

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distinct, undescribed species (Kennedy, 1989). Likewise, the species from north-western Australia and north-eastern Australia are undescribed (Harvey, 1991b).

Austrochthonius easti, sp. nov.

(Figures 1-7)

Holotype

♂, Dry Swallett Cave, C-18, Cape Range, Western Australia, 22°05'24"S, 113°59'30"E, under stone, 26 June 1989, M.S. Harvey (WAM 91/272, slide).

Paratypes

Western Australia, Cape Range: 1 tritonymph, Loop Cave, C-222, 21°56'26"S, 114°05'44"E, 10 July 1989, M. East (WAM 91/273); 1 deutonymph, Trionomo Cave, C-103, 22°07'26"S, 113°59'18"E, 19 August 1989, B. Jones (WAM 91/274).

Diagnosis

This species differs from the two other described Australian species of *Austrochthonius* by the presence of 2 small eyes; *A. australis* Hoff possesses 4 corneate eyes, and *A. cavicola* Beier is totally blind.

Description

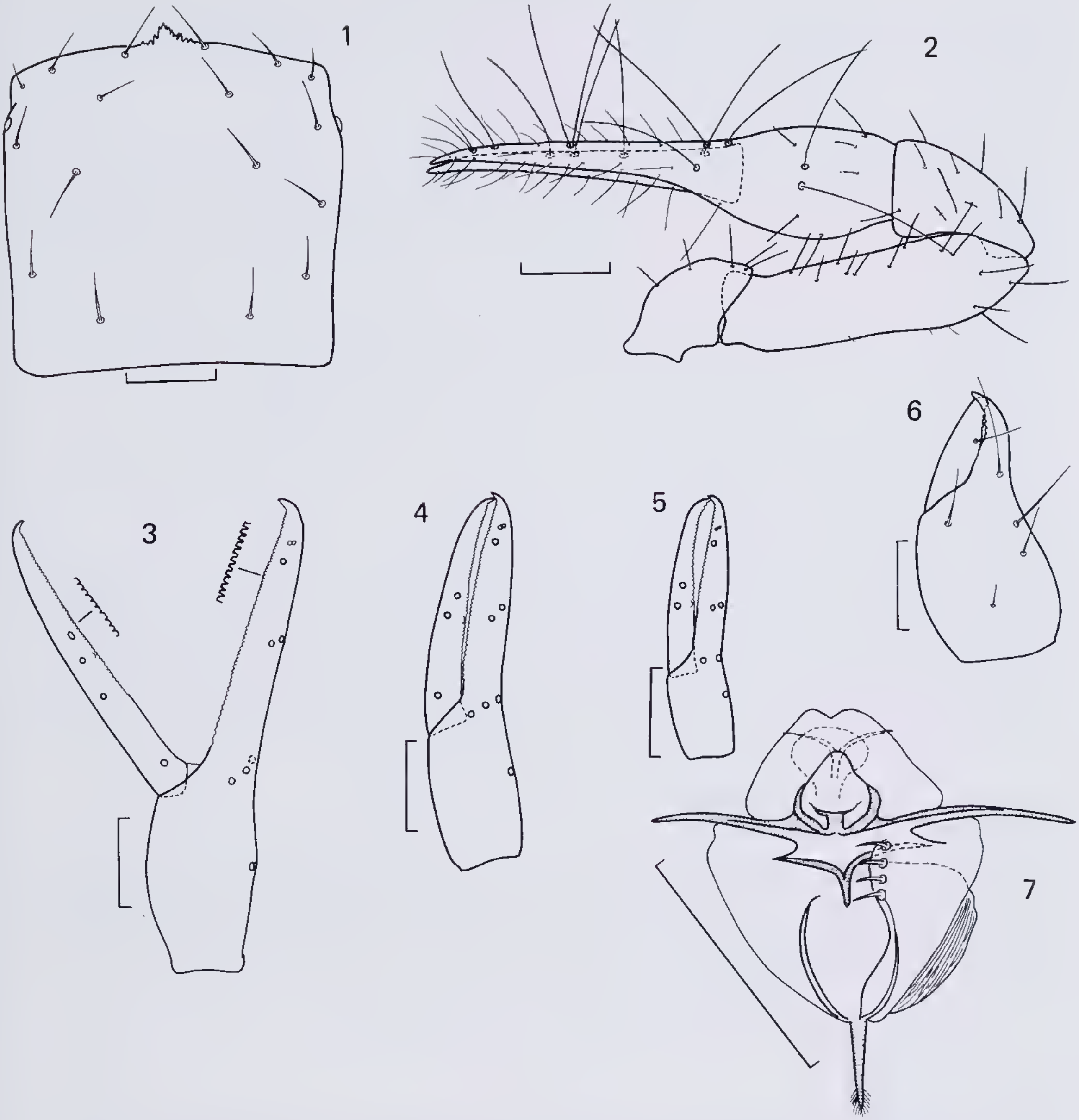
Male

Colour light red-brown. Setae straight and acicular. Pedipalp (Figure 2): trochanter 1.67, femur 3.40, tibia 1.80, chela 4.17, hand 1.33 times longer than broad, movable finger 2.06 times longer than hand. Fixed chelal finger and hand with 8 trichobothria, movable chelal finger with 4 trichobothria (Figure 3); *ib* and *isb* situated on dorsum of hand; *sb* closer to *t* than to *b*; *st* closer to *t* than to *sb*. Venom apparatus absent. Chelal teeth contiguous: fixed finger with 62 teeth; movable finger with 59 teeth. Chelicera (Figure 6): with 5 setae on hand; movable finger with 1 seta; galea represented by mound; fixed finger with 14 teeth; movable finger with 18 teeth; flagellum composed of 11 bipinnate blades. Carapace (Figure 1) 0.92 times as long as broad; lateral margins slightly convex; with 2 small eyes, posterior eyes absent; epistome serrate; with 18 setae arranged 6: 4: 4: 2: 2; without furrows. Tergites and sternites undivided. Tergal chaetotaxy: 4: 4: 4: 4: 6: 6: 6: 6: 6: 5: 0: 0. Sternal chaetotaxy: 12: (2)22[8](2): (2)7(2): 8: 8: 7: 8: 8: 7: 4: 2. Coxal chaetotaxy: 5: 3+cs: 5: 5; coxa II with 4 small pinnate coxal spines; pedipalpal coxa with 2 apical setae. Genitalia as in Fig. 7. Legs: femur IV 2.29 times longer than broad; heterotarsate; arolium slightly shorter than claws; claws simple.

Dimensions (mm): Body length 1.19. Pedipalps: trochanter 0.15/0.09, femur 0.34/0.10, tibia 0.18/0.10, chela 0.50/0.12, hand length 0.16, movable finger length 0.33. Chelicera 0.30/0.14, movable finger length 0.15. Carapace 0.34/0.37. Anterior eye diameter 0.02. Leg I: basifemur 0.18/0.05, telofemur 0.10/0.05, tibia 0.12/0.04, tarsus 0.20/0.03. Leg IV: femur 0.32/0.14, tibia 0.24/0.07, basitarsus 0.10/0.05, telotarsus 0.20/0.03.

Tritonymph

Pedipalps: trochanter 1.63, femur 3.71, tibia 1.67, chela 4.00, hand 1.30 times longer than broad, movable finger 2.08 times longer than hand. Fixed chelal finger with 7



Figures 1-7. *Austrochthonius easti,* sp. nov., holotype ♂ unless otherwise stated: 1, carapace. 2, right pedipalp, dorsal. 3, left chela, lateral. 4, left chela, lateral, paratype tritonymph. 5, left chela, lateral, deutonymph paratype. 6, left chelicera, dorsal. 7, ♂ genitalia, ventral. Scale lines = 0.1 mm.

trichobothria, movable chelal finger with 3 trichobothria (Figure 4); *isb* and *sb* absent. Chelicera with 5 setae on hand; 1 on movable finger. Carapace 0.94 times longer than broad; 2 very small eyes present.

Dimensions (mm): Body length 1.11. Pedipalps: trochanter 0.13/0.08, femur 0.26/0.07, tibia 0.15/0.09, chela 0.40/0.10, hand length 0.13, movable finger length 0.27. Carapace 0.30/0.32. Chelicera 0.25/0.14, movable finger length 0.14.

Deutonymph

Pedipalps: trochanter 4.00, femur 3.20, tibia 1.67, chela 4.00, hand 1.29 times longer than broad, movable finger 2.00 times longer than hand. Fixed chelal finger with 6 trichobothria, movable chelal finger with 2 trichobothria (Figure 5); *esb, isb, sb* and *b* absent. Chelicera with 4 setae on hand; 1 on movable finger. Carapace 0.95 times longer than broad; 2 very small eyes present.

Dimensions (mm): Body length 0.62. Pedipalps: trochanter 0.08/0.05, femur 0.16/0.05, tibia 0.10/0.06, chela 0.28/0.07, hand length 0.09, movable finger length 0.18. Carapace 0.21/0.22. Chelicera 0.16/0.09, movable finger length 0.09.

Etymology

This species is named for Malcolm East, who collected one of the specimens.

Remarks

This small species is not highly modified for cave existence, but the loss of the posterior eyes and reduction of the anterior eyes suggests that it is a facultative troglobite. Only five other described species of the genus have reduced eyes: *A. cavicola* (Australia) and *A. iguazuensis* Vitali-di Castri (Brazil) are completely blind, and *A. paraguayensis* Vitali-di Castri (Paraguay), *A. persimilis* Beier (Chile) and *A. tullgreni* (Beier) (South Africa) possess only two eyes. *Austrochthonius easti* is larger than those species of *Austrochthonius* with two eyes, and possesses a different tergal chaetotaxy.

Genus *Tyrannochthonius* Chamberlin

Remarks

This genus is common in tropical and subtropical regions, and extends into temperate zones such as Tasmania. Two cave-dwelling species have been previously described from mainland Australia: *T. cavicola* (Beier) from New South Wales (Beier, 1967) and *T. rex* Harvey from northern Queensland (Harvey, 1989).

Tyrannochthonius butleri, sp. nov.

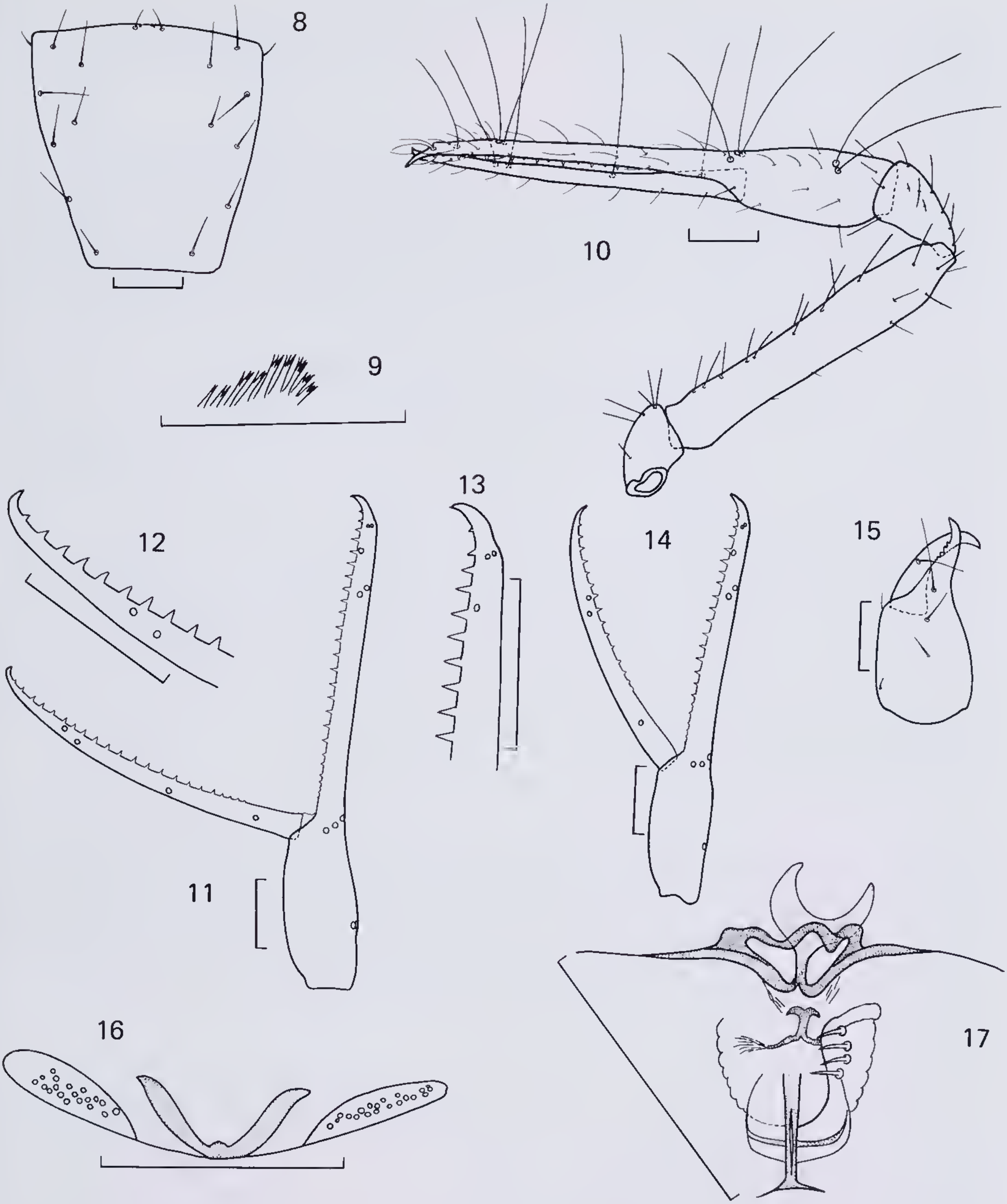
(Figures 8-17)

Holotype

♂, unnamed cave, C-167, Cape Range, Western Australia, 22°09′09″S, 113°59′39″E, under rock in dark zone, 20 June 1989, M.S. Harvey (WAM 91/275, slide).

Paratypes

Western Australia, Cape Range: 1 deutonymph, collected with holotype (WAM 91/276, slide); 1 tritonymph, unnamed cave, C-167 [22°09′09″S, 113°59′39″E], litter, September 1988, M.R. Gray (WAM 91/279); 1 ♀, unnamed cave, C-291, 22°16′01″S, 113°57′53″E, 16 August 1989, D. Brooks (WAM 91/277, slide); 1 ♀, Papillon Cave, C-15, 22°12′48″S, 113°58′32″E, 25 June 1989, M.S. Harvey (WAM 91/278); 1 ♂, 1 ♀ Papillon Cave, C-15, 22°12′48″S, 113°58′32″E, 29 March 1991, D. Brooks (WAM 91/1052-3).



Figures 8-17. *Tyrannochthonius butleri*, sp. nov., holotype ♂ unless otherwise stated: 8, carapace. 9, coxal spines. 10, right pedipalp, dorsal. 11, left chela, lateral. 12, tip of movable chelal finger. 13, tip of movable chelal finger. 14, left chela, lateral, paratype tritonymph. 15, left chelicera, dorsal. 16, ♀ genitalia, ventral. 17, ♂ genitalia, ventral. Scale lines = 0.1 mm.

Diagnosis

Eyes absent. Epistome very small. Chelal teeth homodentate and erect.

Description

Adults

Colour very pale yellow. Setae long, straight and acicular. Pedipalp (Figure 10): trochanter 1.75 (♂), 1.80 (♀), femur 5.88 (♂), 5.70 (♀), tibia 1.67 (♂), 1.90 (♀), chela 6.90 (♂), 6.15 (♀), hand 2.10 (♂), 1.30 (♀) times longer than broad, movable finger 2.19 (♂), 1.96 (♀) times longer than hand. Fixed chelal finger and hand with 8 trichobothria, movable chelal finger with 4 trichobothria (Figure 11); *ib* and *isb* situated on dorsum of hand; *sb* midway between *st* and *b*. Hand with 1 small, medial acuminate spine-like seta at level of *esb*. Venom apparatus absent. Chelal teeth erect, homodentate (Figures 12, 13): fixed finger with 27 (♂), 26 (♀) teeth; movable finger with 24 (♂), 24 (♀) teeth. Chelicera (Figure 15): with 5 setae on hand; movable finger with 1 seta; galea absent; fixed finger with 9 (♂), 11 (♀) teeth; movable finger with 9 (♂), 10 (♀) teeth; flagellum composed of *ca.* 7 blades, all except anterior blade bipinnate, anterior blade finely denticulate. Carapace (Figure 8) 1.06 (♂), 1.21 (♀) times longer than broad; lateral margins constricted posteriorly; eyes absent; epistome very small; with 18 setae arranged 6: 4: 4: 2: 2; without furrows. Tergites and sternites undivided. Tergal chaetotaxy: ♂, 2: 2: 4: 4: 4: 4: 4: 4: 4: 2: 0: 0; ♀ 2: 2: 4: 4: 4: 4: 4: 4: 4: 2: 0: 0. Sternal chaetotaxy: ♂, 9: (3)20[4](3): (2)6(2): 7: 7: 7: 7: 7: 6: 4: 2; ♀ 8: (2)7(2): (2)6(2): 6: 7: 7: 6: 6: 6: 6: 2. Coxal chaetotaxy: ♂, 3: 3+cs: 5: 5; ♀, 3: 3+cs: 5: 5; coxa II with 9-11 (♂), 8-9 (♀) terminally incised coxal spines set in an oblique row; pedipalpal coxa with 2 apical setae. Male genitalia as in Figure 17. Female genitalia (Figure 16) with incomplete lateral apodeme frame, lateral diverticulum sparsely cribrate. Legs: femur IV 2.93 (♂), 2.94 (♀) times longer than broad; heterotarsate; arolium slightly shorter than claws; claws simple.

Dimensions (mm): ♂ (♀): Body length 1.07 (1.22). Pedipalps: trochanter 0.14/0.08 (0.18/0.10), femur 0.47/0.08 (0.57/0.10), tibia 0.15/0.09 (0.19/0.10), chela 0.69/0.10 (0.80/0.13), hand length 0.21 (0.26), movable finger length 0.46 (0.51). Chelicera 0.30/0.13 (0.39/0.18), movable finger length 0.15 (0.21). Carapace 0.34/0.32 (0.41/0.34). Leg I: basifemur 0.25/0.04 (0.27/0.05), telofemur 0.16/0.04 (0.19/0.05), tibia 0.13/0.03 (0.16/0.04), tarsus 0.28/0.03 (0.32/0.03). Leg IV: entire femur 0.41/0.14 (0.50/0.17), tibia 0.28/0.06 (0.33/0.06), basitarsus 0.11/0.04 (0.14/0.05), telotarsus 0.32/0.03 (0.36/0.03).

Tritonymph

Pedipalps: trochanter 1.71, femur 5.71, tibia 1.71, chela 6.11, hand 2.11 times longer than broad, movable finger 1.95 times longer than hand. Fixed chelal finger with 7 trichobothria, movable chelal finger with three trichobothria (Figure 14); *isb* and *sb* absent. Chelicera with 4 setae on hand; 1 on movable finger; galea absent. Carapace 1.08 times longer than broad; eyes absent.

Dimensions (mm): Body length 0.70. Pedipalps: trochanter 0.12/0.07, femur 0.40/0.07, tibia 0.12/0.07, chela 0.55/0.09, hand length 0.19, movable finger length 0.37. Carapace 0.26/0.24. Chelicera 0.25/0.11, movable finger length 0.13.

Etymology

This species is named for W.H. Butler, who provided funds for field work in Cape Range.

Remarks

Tyrannochthonius butleri is quite similar to *T. brooksi* based on the homodentate chelal teeth and the small epistome, unusual character states amongst *Tyrannochthonius* species. The two species differ in the dentition of the movable chelal finger (erect in *T. butleri,* retrorse in *T. brooksi*), the absence (*T. butleri*) or presence (*T. brooksi*) of eyes, the tergal setation (2: 2: 4: 4: 4: in *T. butleri,* 4: 4: 4: 4: 6: in *T. brooksi*), and the colour of the cuticle (very pale in *T. butleri,* darker in *T. brooksi*).

Tyrannochthonius brooksi, sp. nov.

(Figures 18-26)

Holotype

♂, Monajee Cave, C-21, 22°14′00″S, 113°58′18″E, Cape Range, Western Australia, 20 July 1989, D. Brooks (WAM 91/280, slide).

Paratypes

Western Australia, Cape Range: 1 ♂, collected with holotype (WAM 91/281, slide); 1 ♀, unnamed cave, C-107, 22°07′00″S, 113°59′54″E, 2 July 1989, D. Brooks (WAM 91/283, slide); 1 ♂, unnamed cave, C-107, 22°07′00″S, 113°59′54″E, 30 June 1989, B. Vine, E. Bowra (WAM 91/285); 1 ♀, Breakdown Maze, C-111, 22°55′08″S, 114°00′17″E, 28 August 1989, B. Vine (WAM 91/282, slide).

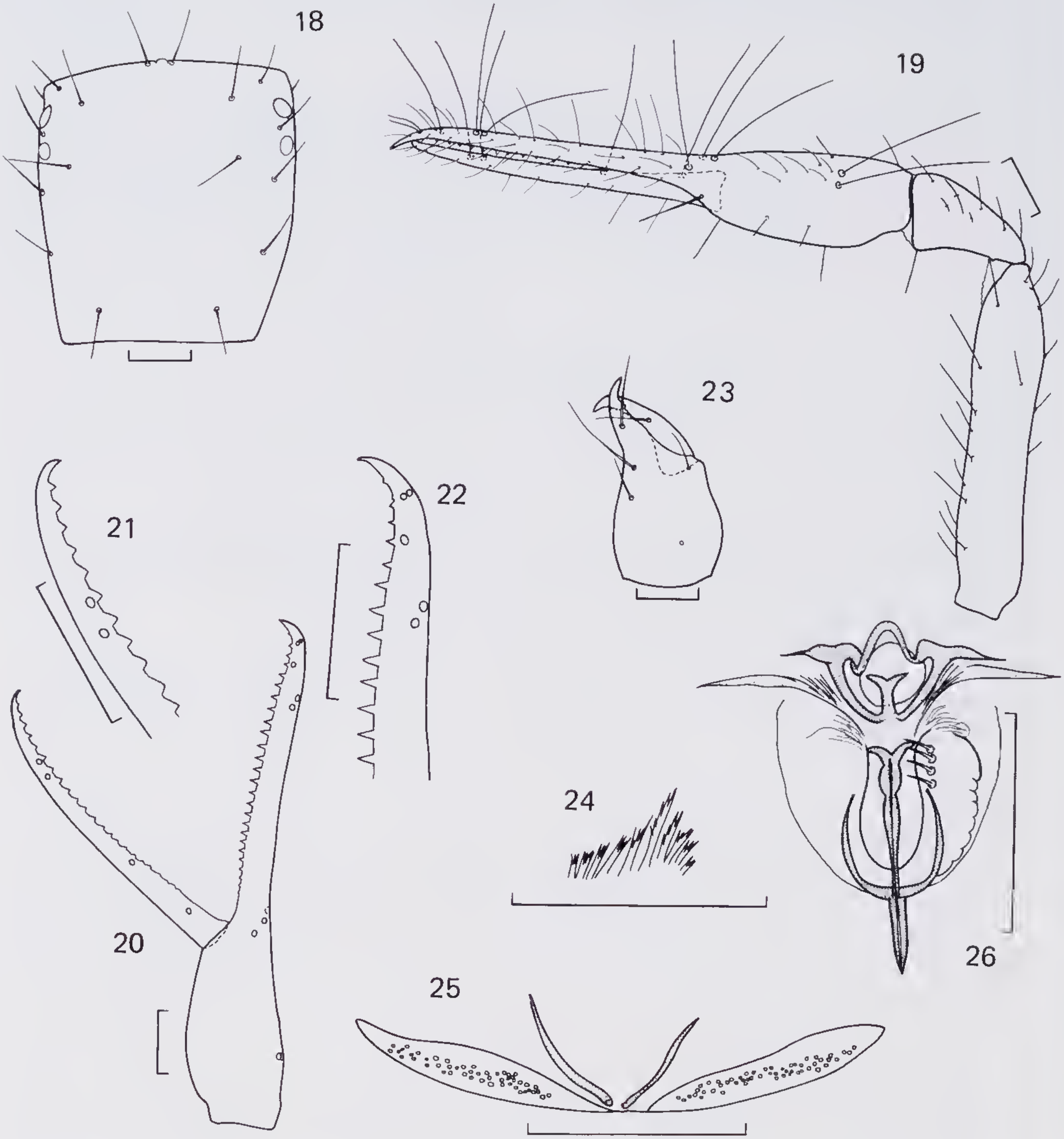
Diagnosis

Eyes present: anterior eyes corneate; posterior eyes reduced to eye-spots. Epistome very small. Chelal teeth homodentate, erect on fixed finger, retrorse on movable finger.

Description

Adults

Colour light yellow-brown. Setae long, straight and acicular. Pedipalp (Figure 19): trochanter 1.60-1.78 (♂), 1.67-1.77 (♀), femur 5.00-5.10 (♂), 4.46-5.00 (♀), tibia 1.82-1.83 (♂), 1.71-1.80 (♀), chela 5.64-5.69 (♂), 5.15-5.29 (♀), hand 1.92-2.00 (♂), 1.80-1.88 (♀) times longer than broad, movable finger 1.73-1.85 (♂), 1.78 (♀) times longer than hand. Fixed chelal finger and hand with eight trichobothria, movable chelal finger with four trichobothria (Figure 20); *ib* and *isb* situated on dorsum of hand; *sb* closer to *b* than to *st*. Hand with one large, medial acuminate spine-like seta at level of *esb*. Venom apparatus absent. Chelal teeth homodentate (Figures 21-22): fixed finger with 25-27 erect teeth; movable finger with 27-29 retrorse teeth. Chelicera (Figure 23): with five setae on hand; movable finger with one seta; galea represented by small mound; fixed finger with seven teeth; movable finger with 10 teeth; flagellum composed of *ca.* five blades, all except anterior blade bipinnate, anterior blade finely denticulate. Carapace (Figure 18) 0.95-1.00 (♂), 0.94-1.02 (♀) times longer than broad; lateral margins subparallel; with four eyes, anterior pair corneate, posterior pair represented by eye-spots; epistome very small; with 18 setae arranged 6: 4: 4: 2: 2; without furrows. Tergites and sternites undivided. Tergal chaetotaxy: ♂, 4: 4: 3-4: 4: 6: 6: 6: 6: 6: 4-5: 0: 0; ♀, 4: 4: 4: 4: 6: 6: 6: 6: 6: 4: 0: 0.



Figures 18-26. *Tyrannochthonius brooksi,* sp. nov., holotype ♂ unless otherwise stated: 18, carapace. 19, right pedipalp (without trochanter), dorsal. 20, left chela, lateral. 21, tip of movable chelal finger. 22, tip of fixed chelal finger. 23, left chelicera, dorsal. 24, coxal spines. 25, ♀ genitalia, ventral. 26, ♂ genitalia, ventral. Scale lines = 0.1 mm.

Sternal chaetotaxy: ♂, 10: (3)24-28[8](3): (3)9-10(3): 10: 9-10: 9: 7-9: 9: 6-7: 4: 2; ♀, 8: (3)10(3): (3)9(3): 9-10: 7-10: 7-8: 8-9: 8-9: 7-9: 4: 2. Coxal chaetotaxy: ♂, ♀, 3: 3+cs: 6: 5; coxa II with 9-10 (♂), 8-10 (♀) terminally incised coxal spines set in an oblique row; pedipalpal coxa with two apical setae. Male genitalia as in Figure 26. Female genitalia (Figure 25) with incomplete lateral apodeme frame, lateral diverticulum sparsely cribrate. Legs: femur IV 2.38-2.42 (), 2.52-2.86 () times longer than broad; heterotarsate; arolium slightly shorter than claws; claws simple.

Dimensions (mm): ♂ (♀): Body length 1.34-1.35 (1.58-1.60). Pedipalps: trochanter 0.16/0.09-0.10 (0.20-0.23/0.12-0.13), femur 0.51-0.55/0.10-0.11 (0.58-0.70/0.13-0.14), tibia 0.20-0.22/0.11-0.12 (0.24-0.27/0.14-0.15), chela 0.74-0.79/0.13-0.14 (0.90-1.03/0.17-0.20), hand length 0.26-0.27 (0.32-0.36), movable finger length 0.45-0.50 (0.57-0.64). Chelicera 0.34/0.17 (0.38-0.41/0.19-0.20), movable finger length 0.18 (0.21-0.23). Carapace 0.36-0.38/0.36-0.40 (0.42-0.45/0.41-0.48). Anterior eye diameter 0.04 (0.04), posterior eye diameter 0.03 (0.03-0.04). Leg I: basifemur 0.27-0.30/0.06 (0.32-0.38/0.07), telofemur 0.16-0.17/0.05-0.06 (0.190.20/0.06-0.07), tibia 0.15-0.16/0.04 (0.18-0.20/0.04-0.05), tarsus 0.270.30/0.03-0.04 (0.34-0.38/0.04). Leg IV: entire femur 0.46-0.50/0.19-0.21 (0.53-0.63/0.21-0.22), tibia 0.32-0.35/0.07-0.08 (0.37-0.44/0.08-0.09), basitarsus 0.16/0.05-0.06 (0.18-0.21/0.06-0.07), telotarsus 0.28-0.32/0.03 (0.34-0.42/0.04).

Etymology

This species is named for Darren Brooks, collector of some of the type specimens.

Remarks

The female from Breakdown Maze (C-111) is slightly larger than the female from C-107. However, significant differences in setation and chelal teeth morphology could not be found, and the C-111 population is considered conspecific with *T. brooksi*.

Family Syarinidae Chamberlin

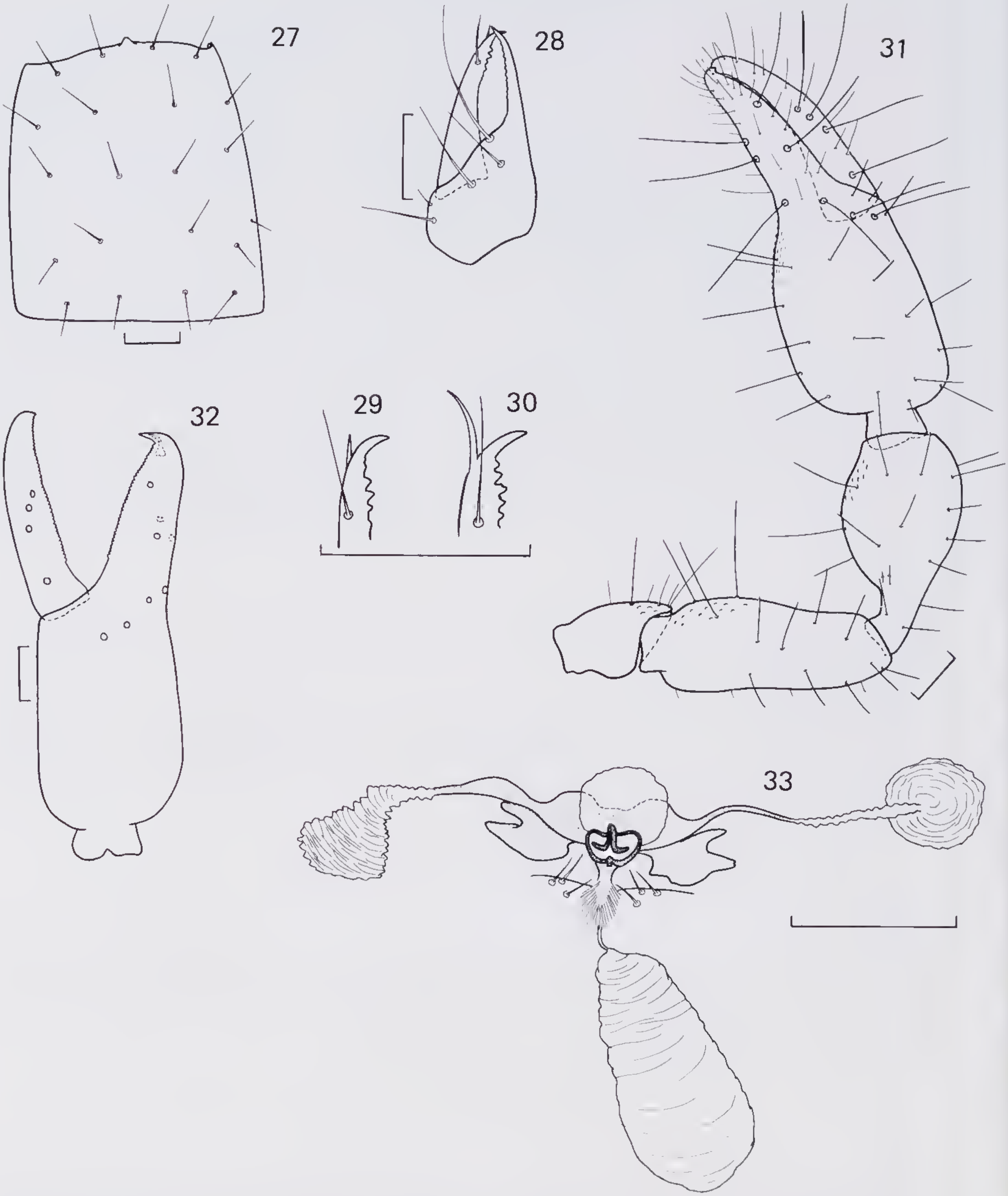
Remarks

Syarinids have not previously been described from Australia, although representatives of *Ideoblothrus* Balzan and *Ideobisium* Balzan are not uncommon in the rainforests of eastern Queensland. An undescribed genus of Syarinidae is present in Tasmanian temperate rainforests (Harvey, unpubl. data).

Genus *Ideoblothrus* Balzan

Remarks

The generic diagnosis provided by Muchmore (1982a) must be altered slightly with the discovery of the two species described below. The pedipalpal femur of *I. papillon* is greater than 3.0 times longer than broad, and the diagnosis (p. 208) should now read "... none of the segments more than 3.2 times as long as broad".



Figures 27-33. *Ideoblothrus woodi,* sp. nov., holotype ♂ unless otherwise stated: 27, carapace. 28, left chelicera, dorsal. 29, detail of left chelicera, movable finger. 30, detail of left chelicera, movable finger, paratype ♀. 31, right pedipalp, dorsal. 32, left chela, lateral. 33, ♂ genitalia, ventral. Scale lines = 0.1 mm.

Ideoblothrus woodi, sp. nov.

(Figures 27-33, 40-41)

Holotype

♂, unnamed cave, C-167, Cape Range, Western Australia, 22°09′09″S, 113°59′39″E, under stone in dark zone, 20 June 1989, M.S. Harvey (WAM 91/286, slide).

Paratype

Western Australia, Cape Range: 1 ♀, collected with holotype (WAM 91/287, slide).

Diagnosis

Male galea short. Chelal hand 1.33 (♂), 1.40 (♀) times longer than broad; pedipalpal femur length 0.45 mm (♂), 0.49 mm (♀).

Description

Adults

Colour light red-brown. Setae long, straight and acicular. Pedipalp (Figure 31): trochanter 1.85 (♂), 1.86 (♀), femur 2.81 (♂), 2.88 (♀), tibia 1.95 (♂), 2.00 (♀), chela (with pedicel) 2.81 (♂), 2.82 (♀), chela (without pedicel) 2.67 (♂), 2.63 (♀), hand 1.33 (♂), 1.40 (♀) times longer than broad, movable finger 0.97 (♂), 0.88 (♀) times as long as hand. Flexor margins of chela, tibia, femur and trochanter sparsely granulate. Fixed chelal finger and hand with 8 trichobothria, movable chelal finger with four trichobothria (Figure 32); *eb, esb, isb* and *ib* in oblique row on distolateral margin of hand; *t* barely lanceolate. Venom apparatus present only in fixed chelal finger, venom duct very short, terminating in nodus ramosus near distal end of finger. Chelal teeth: fixed finger with 37 (♂), 39 (♀) teeth; movable finger with 46 (♂, ♀) teeth. Chelicera (Figure 28): with five setae on hand; movable finger with 1 seta; galea very slender, not extending past tip of finger in ♂ (Figure 29), extending slightly past tip of finger in ♀ (Figure 30); fixed finger with 7-8 teeth; movable finger with 10-11 teeth; flagellum of 5 blades, distal blade finely denticulate. Carapace (Figure 27) 1.16 (♂) times longer than broad; lateral margins subparallel; epistome present; without eyes; with 21 (♂) setae arranged 4: 4: 4: 5: 4; without furrows. Tergites and sternites undivided, except for sternite IV which is incompletely divided. Tergal chaetotaxy: ♂, 5: 6: 7: 8: 9: 9: 9: 9: 8: 7: 6: 2; ♀, 5: 6: 6: 9: remainder crumpled. Sternal chaetotaxy: ♂, 9: (3)11[6](3): (2)8(2): 10: 10: 11: 11: 11: 11: 8: 2; ♀, 7: (3)8(3): (2)8(2): remainder crumpled; internal genital setae of ♂ arranged in two triads. Coxal chaetotaxy: ♂, ♀, 6: 4: 3: 5; pedipalpal coxa with 2 apical setae. Male genitalia as in Figure 33. Female genitalia not unusual. Legs: femur IV 3.00 (♂), 3.14 (♀) times longer than broad; dorsal surface of femur IV smooth; diplotarsate; subterminal tarsal seta denticulate; arolium slightly shorter than claws; claws simple.

Dimensions (mm): ♂ (♀): Body length 1.69 (?). Pedipalps: trochanter 0.24/0.13 (0.26/0.14), femur 0.45/0.16 (0.49/0.17), tibia 0.41/0.21 (0.46/0.23), chela (with pedicel) 0.76/0.21 (0.85/0.30), chela (without pedicel) 0.72 (0.79), hand length 0.36 (0.42), movable finger length 0.37 (0.37). Chelicera 0.27/0.13 (0.30/0.14), movable finger length 0.20 (0.24). Carapace 0.50/0.43 (?). Leg I: basifemur 0.19/0.09 (0.20/0.10), telofemur 0.16/0.08 (0.17/0.10), tibia 0.23/0.06 (0.25/0.06), basitarsus 0.08/0.04 (0.09/0.04), telotarsus 0.14/0.03 (0.15/0.04). Leg IV: entire femur 0.42/0.14 (0.44/0.14), tibia 0.34/0.07 (0.34/0.07), basitarsus 0.10/0.06 (0.11/0.06), telotarsus 0.18/0.05 (0.19/0.05).

Etymology

This species is named for Ray Wood.

Remarks

This species is extremely similar to *I. papillon,* but they differ in the size and shape of the pedipalpal segments (Figures 40, 41), and in the form of the male galea (short in *I. woodi,* long in *I. papillon*).

Ideoblothrus papillon, sp. nov.

(Figures 34-41)

Holotype

♂, Papillon Cave, C-15, Cape Range, Western Australia, 22°12′48″S, 113°58′32″E, under stone in dark zone, 25 June 1989, M.S. Harvey (WAM 91/288, slide).

Paratype

Western Australia, Cape Range: 1 ♀, Papillon Cave, C-15, 22°12′48″S, 113°58′32″E, 16 July 1989, W.F. Humphreys (WAM 91/289, slide).

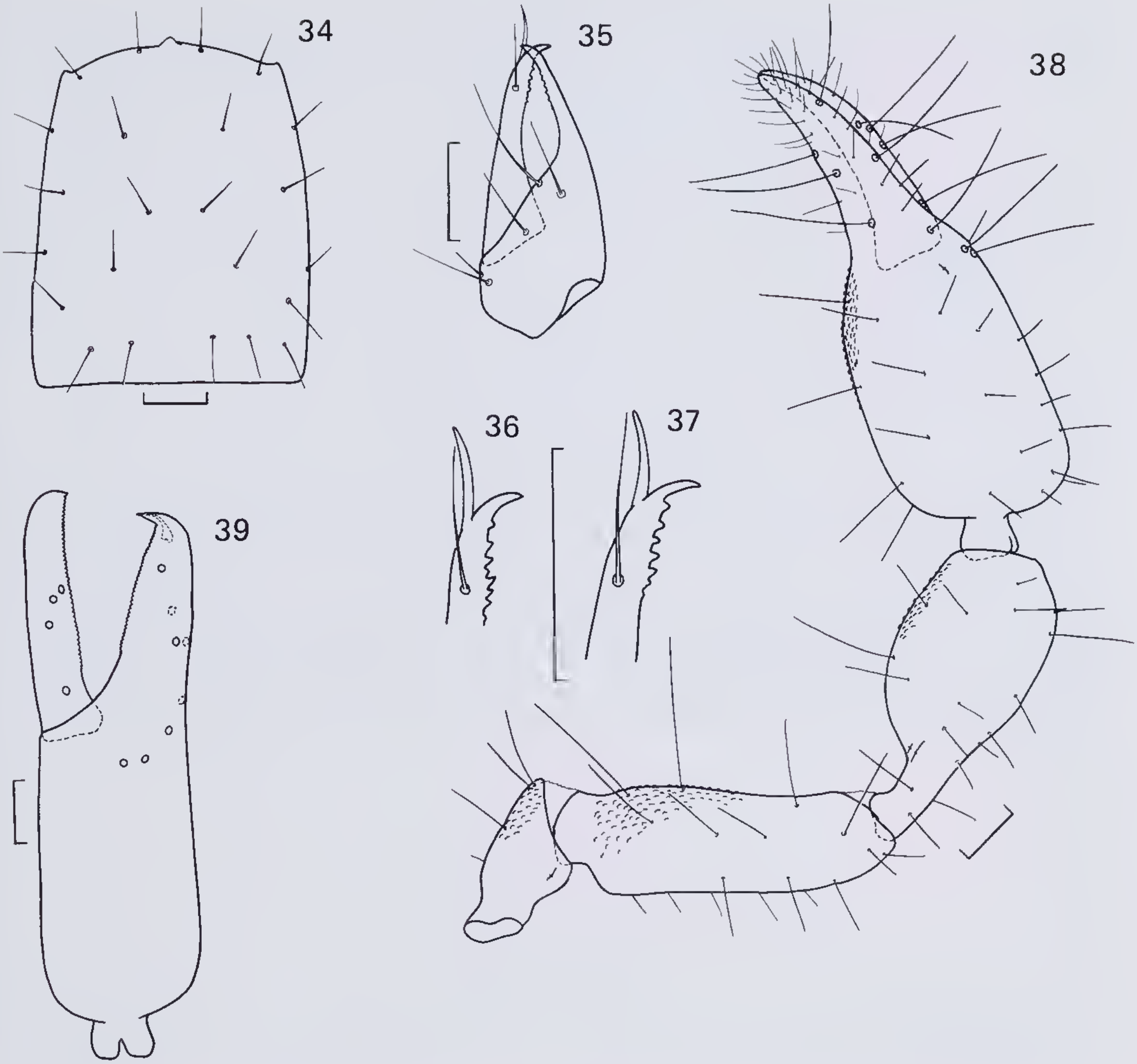
Diagnosis

Male galea long. Chelal hand 1.52 (♂), 1.58 (♀) times longer than broad; pedipalpal femur length 0.53 mm (♂), 0.55 mm (♀).

Description

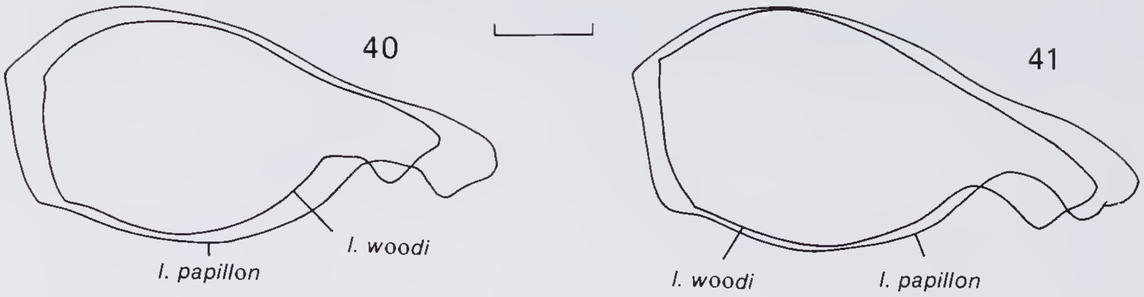
Adults

Colour light red-brown. Setae long, straight and acicular. Pedipalp (Figure 38): trochanter 2.23 (♂), 2.00 (♀), femur 3.12 (♂), 3.05 (♀), tibia 2.22 (♂), 2.17 (♀), chela (with pedicel) 3.00 (♂), 3.00 (♀), chela (without pedicel) 2.83 (♂), 2.74 (♀), hand 1.52 (♂), 1.58 (♀) times longer than broad, movable finger 0.86 (♂), 0.78 (♀) times as long as hand. Flexor margins of chela, tibia, femur and trochanter coarsely granulate. Fixed chelal finger and hand with eight trichobothria, movable chelal finger with four trichobothria (Figure 39); *eb, esb, isb* and *ib* in oblique row on disto-lateral margin of hand; *t* barely lanceolate. Venom apparatus present only in fixed chelal finger, venom duct very short, terminating in nodus ramosus near distal end of finger. Chelal teeth: fixed finger with 36 (♂), 35 (♀) teeth; movable finger with 46 (♂, ♀) teeth. Chelicera (Figure 35): with five setae on hand; movable finger with one seta; galea of and very slender, extending well beyond tip of finger (Figures 36, 37); fixed finger with nine teeth; movable finger with eight teeth; flagellum of five blades, distal blade finely denticulate. Carapace (Figure 34) 1.31 (♂), 1.23 (♀) times longer than broad; lateral margins subparallel; epistome present; without eyes; with 23 (♂, ♀) setae arranged 4: 4: 4: 4: 2: 5 (♂, ♀); without furrows. Tergites and sternites undivided, except for sternite IV which is incompletely divided. Tergal chaetotaxy: ♂, 6: 6: 7: 7: 7: 8: 8: 9: 10: 9: 8: 2; ♀, 6: 6: 7: 7: 8: 9: 9: 9: 9: 8: 2: 2. Sternal



Figures 34-40. *Ideoblothrus papillon,* sp. nov., holotype ♂ unless otherwise stated: 34, carapace. 35, left chelicera, dorsal. 36, detail of left chelicera, movable finger. 37, detail of left chelicera, movable finger, paratype ♀. 38, right pedipalp, dorsal. 39, left chela, lateral. Scale lines = 0.1 mm.

chaetotaxy: ♂, 11: (3)11[6](3): (2)9(2): 10: 12: 11: 11: 11: 11: 11: 2; ♀, 8: (3)6(3): (3)6(3): 11: 11: 11: 11: 11: 11: 6: 2; internal genital setae of ♂ arranged in two triads. Coxal chaetotaxy: ♂, 5: 5: 4: 7; ♀, 5: 6: 4: 6; pedipalpal coxa with two apical setae. Male genitalia as in *I. woodi.* Female genitalia not unusual. Legs: femur IV 2.93 (♂), 3.00 (♀) times longer than broad; dorsal surface of femur IV smooth; diplotarsate; subterminal tarsal seta denticulate; arolium slightly shorter than claws; claws simple.



Figures 40-41. *Ideoblothrus woodi* and *I. papillon,* right pedipalpal tibia, dorsal, superimposed for comparison: 40, males. 41, females. Scale lines = 0.1 mm.

Dimensions (mm): ♂ (♀): Body length 2.32 (2.67). Pedipalps: trochanter 0.29/0.13 (0.30/0.15), femur 0.53/0.17 (0.55/0.18), tibia 0.51/0.23 (0.52/0.24), chela (with pedicel) 0.87/0.29 (0.93/0.31), chela (without pedicel) 0.82 (0.85), hand length 0.44 (0.49), movable finger length 0.38 (0.38). Chelicera 0.30/0.13 (0.32/0.14), movable finger length 0.23 (0.24). Carapace 0.55/0.42 (0.58/0.47). Leg I: basifemur 0.19/0.10 (0.21/0.10), telofemur 0.16/0.09 (0.18/0.10), tibia 0.25/0.06 (0.26/0.06), basitarsus 0.09/0.04 (0.09/0.04), telotarsus 0.15/0.03 (0.16/0.03). Leg IV: entire femur 0.44/0.15 (0.45/0.15), tibia 0.37/0.08 (0.36/0.09), basitarsus 0.11/0.05 (0.11/0.06), telotarsus 0.18/0.05 (0.18/0.05).

Etymology

The specific epithet is a noun in apposition taken from the type locality, Papillon Cave.

Family Hyidae Chamberlin

Gen. et sp. nov.

Material examined

Western Australia, Cape Range: 1 ♀, Papillon Cave, C-15, under stone in dark zone, 22°13′S 113°59′E, 28 June 1989, M.S. Harvey, W.F. Humphreys (WAM 90/726); 1 tritonymph, Papillon Cave, C-15, 22°12′48″S, 113°58′32″E, 29 March 1991, D. Brooks (WAM 91/1054); 1 tritonymph, Trionomo Cave, C-103, 22°07′S 113°59′E, 15 August 1988, D. Brooks (WAM, 90/727).

Remarks

This unusual species will be described in a complete revision of the family (Harvey, in preparation).

Discussion

The affinities of the Cape Range pseudoscorpion fauna are diverse. The new hyid genus and *Ideoblothrus* spp. are clearly related to tropical elements. The hyid belongs to a subfamily that is elsewhere known only from rainforest patches in north-western Australia (Kimberley), India and Madagascar (Harvey, in preparation). *Ideoblothrus* spp. are found in tropical rainforests in Africa, Asia, the Americas, and eastern Australia (Muchmore, 1982a; Harvey, unpublished data). Members of this genus were not found in the Kimberley rainforests. Like all other members of the genus (Muchmore, 1982a), the Cape Range *Ideoblothrus* spp. are completely blind.

The affinities of the chthoniids are more difficult to ascertain. *Austrochthonius* spp. are restricted to gondwanan elements [Australia, New Zealand, South America and South Africa (Harvey, 1991a)], and it appears likely that *A. easti* may be a southern relic. However, the presence of an undescribed species from the Kimberley indicates that the genus may have once had a much wider distribution. Detailed analyses of relationships within the genus are needed before the affinities of *A. easti* are known.

Tyrannochthonius species are found in many different regions of Australia and other tropical and temperate zones around the world, and a large number of new species await description. The relationships of the two Cape Range species, *T. butleri* and *T. brooksi,* will depend on a full revision of the vast Australian fauna. Neither species appears to be closely related to the other cavernicolous members of *Tyrannochthonius* known from Australia, *T. cavicola* and *T. rex.*

The surface fauna

Although little collecting for epigean forms was conducted during the expeditions, four species of Olpiidae were found (*Xenolpium* sp., *Austrohorus* sp., Genus A and Genus B). One specimen of *Xenolpium* sp. was found under a rock in the fully lit entrance of a cave (C-64), and this species is not considered a cavernicole. A single *Tyrannochthonius* specimen was taken from under a rock amongst leaf litter on the surface. It is unclear whether this species is very closely related to *T. brooksi.*

Acknowledgements

Bill Humphreys' interest in the ecology of Cape Range provided the impetus to visit the region, which was made possible by a grant from the W.H. Butler Fund. Field work was partly funded under the National Estate Programme. The caving enthusiasm of Darren Brooks, Ray Wood, Brian Vine and Malcolm East convinced me to enter small crevices and to descend on long ropes, and their encouragement was much appreciated.

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Devonian fish remains from the Munabia Sandstone, Carnarvon Basin, Western Australia

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Abstract

Fish fossils have been recovered from two horizons at the base of the Munabia Sandstone, near the type section of Williambury Station. The fauna contains the antiarch *Bothriolepis* sp., the arthrodire *Holonema* sp., and an indeterminate osteolepidid crossopterygian. The presence of *Holonema* (Eifelian-Frasnian) with *Bothriolepis* (Givetian-Famennian), as well as microfossil dates from the underlying conformable Gneudna Formation (Early Frasnian), suggests a Frasnian age for the base of the Munabia Sandstone. Conodonts suggest that the top of the Munabia Sandstone is of Lower Famennian age.

Introduction

The Munabia Sandstone outcrops over a distance of almost 90 km from Mt. Sandiman homestead in the south to just north of Williambury Station as part of a linear belt of Devonian rocks at the base of the Carnarvon Basin sedimentary succession (Figure 1). The type section occurs about 8 km southeast of Williambury Station where it conformably overlies the lower Frasnian carbonates of the Gneudna Formation and underlies the coarser conglomerates of the Willaradie Formation (Condon 1954, 1965, Hocking *et al.* 1987). Although Condon (1965) favoured a marine depositional environment for the Munabia Sandstone and Willaradie Formation, Moors (1981) reported that only the base of the Munabia Sandstone was marine, the majority of the sequence representing distal fan to braided stream deposits, with minor marine incursions. The overlying Willaradie Formation is part of this depositional event, representing proximal alluvial fan deposits. None of the previous field studies of the Munabia Sandstone had found any body fossils, although trace fossils are common in the lower (marine) horizons, and the age of the unit was based entirely on extrapolation from the underlying Gneudna Formation, itself well-dated from marine invertebrates and palynomorphs (Seddon 1969, Dring 1980, Playford and Dring 1981). The Gneudna Formation has also yielded the world's youngest turiniid thelodont scales (Turner and Dring 1981). Recent studies of Gneudna Formation microfossils confirm the earlier age assessment of lower Frasnian (Balme 1988). Age determination of the top of the Munabia Sandstone from conodonts in a thin limestone intercalation gives a probable lower Famennian age (Dr. R. Nicoll, pers. comm.), indicating the unit straddles the Frasnian-Famennian boundary.

In August 1988 a field party from the Museum of Western Australia and the Geology Department, University of Western Australia, discovered remains of fossil fishes in two horizons near the base of the Munabia Sandstone (Figure 2), as well as many fish fossils

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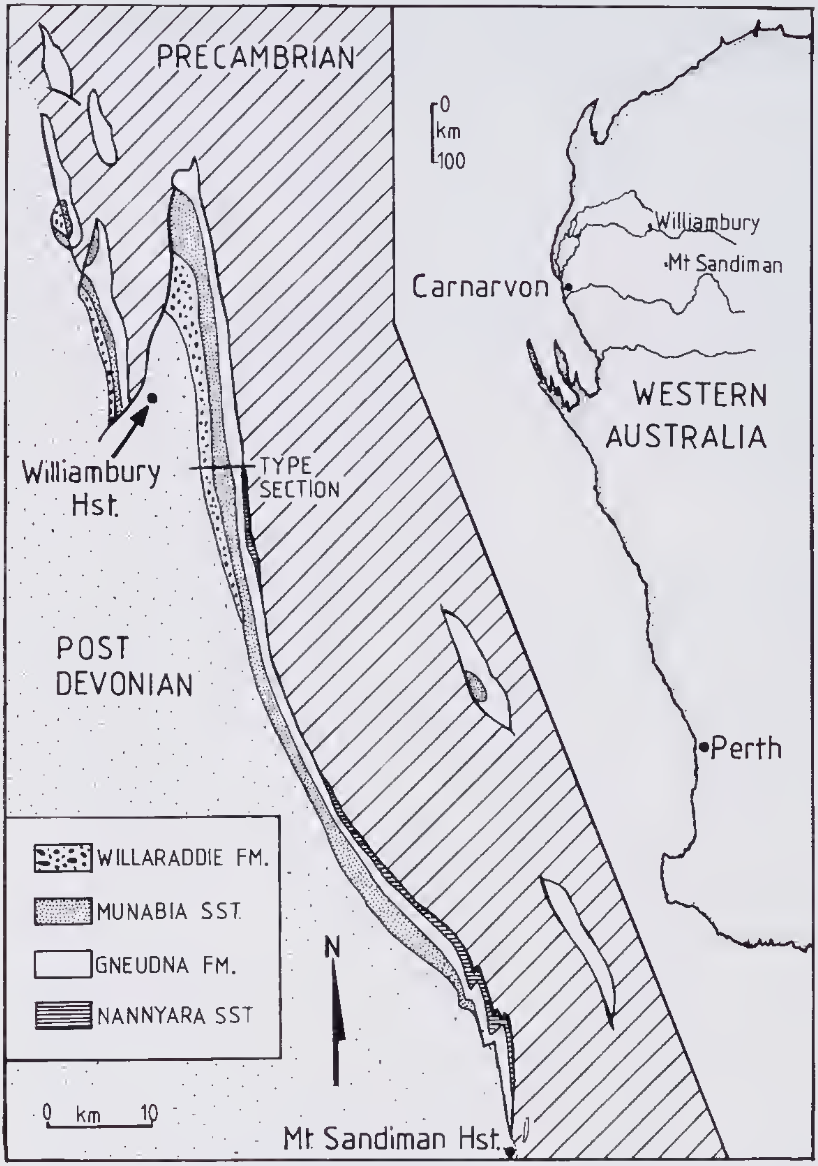

Figure 1. Locality map showing the Devonian formations of the Carnarvon Basin and location of type sections for the Gneudna Formation and Munabia Sandstone, where the fossils were found.

from the Gneudna Formation. The Munabia Sandstone fishes are preserved as natural moulds with no traces of bone preserved. The material is studied by latex casts. For convenience, and in convention with other workers (e.g. Young 1988) plate names are abbreviated in the text, and all abbreviations are listed at the end of the paper. Similarly the words "length, breadth and height" are abbreviated in the text as L, B and H respectively. Measurements taken are from points designated in Miles (1968). Indices are

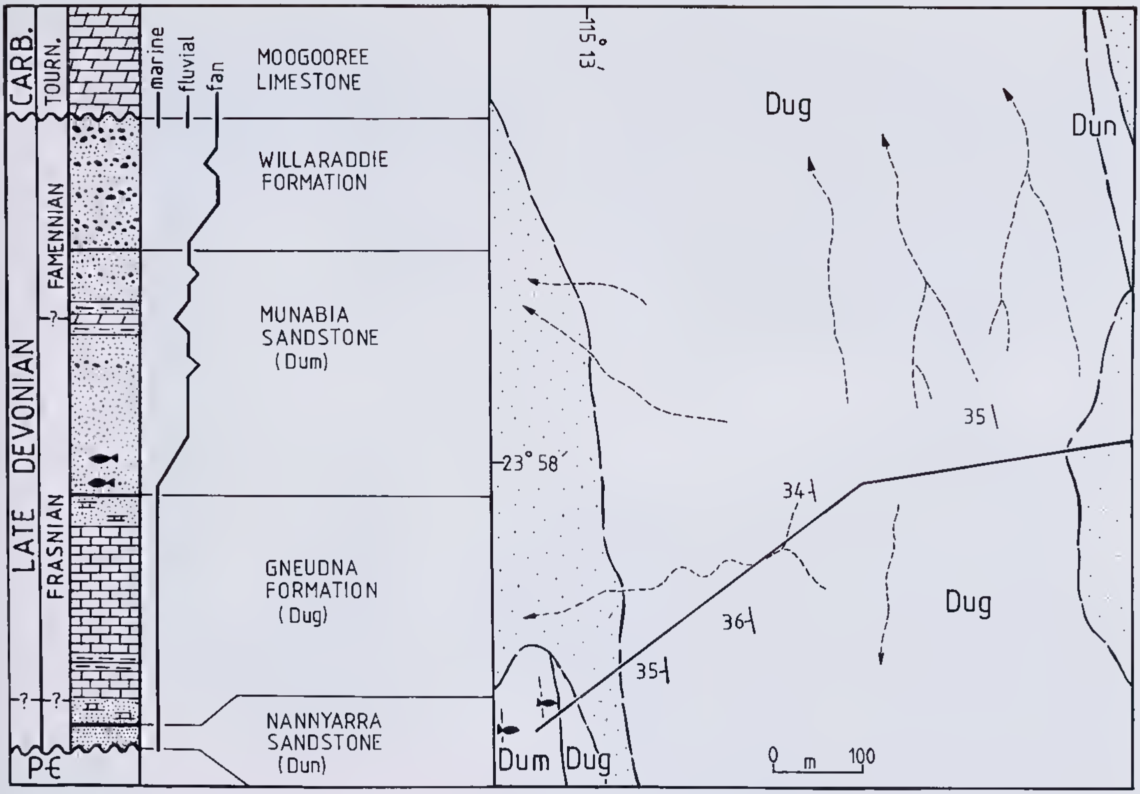

Figure 2. Detailed locality map showing the position of the two fish-bearing horizons in plan view, in the type section area and in the generalized stratographic column (as fish symbols). Geology after Dring (1980) and Moors (1981).

expressed as the ratio of two linear measurements multiplied by 100 (e.g. L/B index = L/B x 100). The specimens are housed in the palaeontological collections of the Western Australian Museum (prefix WAM).

Stratigraphic position of the fish fossils

The fossils were discovered about 1 km north of the type section of the Munabia Sandstone, immediately above the type section for the Gneudna Formation (Figures 1, 2). The lowermost fossil horizon, about 30 metres from the base of the unit, represents a lag accumulation of claygall pebbles with broken fish plates. The abundance of trace fossils from near this horizon is suggestive of marine deposition (Moors 1981). The fish plates from this lag horizon are all broken fragments, dominantly of *Bothriolepis* sp., indicative of high energy deposition. A single osteolepidid scale was also found in this horizon. Both *Bothriolepis* and osteolepidids are known from marine and continental deposits (Gardiner and Miles 1975).

The second fossiliferous horizon is about 90-100 metres from the base of the unit. The fossils come from clean white-reddish sandstones and brownish-silty sandstones, which according to the criteria of Moors (1981) could represent either marine or continental deposition. The fauna contains *Bothriolepis* sp. and the arthrodire *Holonema* sp., a fish known predominantly from marine deposits (Miles 1971; Denison 1978). The fish material from this horizon was deposited as complete isolated plates indicating a lower energy of deposition than for the lower fossil horizon.

Systematics

Class Placodermi

Order Antiarcha

Family Bothriolepididae

Genus *Bothriolepis* Eichwald 1840

Type species

Bothriolepis ornata Eichwald 1840. Upper Devonian of the Leningrad region, U.S.S.R.

***Bothriolepis* sp.**

Figures 3 A-D, F, 4

Material

WAM 87.8.1, a complete external mould of the left ADL plate; WAM 87.8.2, imperfect external mould of a PVL plate; WAM 87.8.3, external mould of proximal bone of pectoral appendage; WAM 87.8.4, internal mould of an AMD plate; 87.8.5, internal mould of a L plate.

Description

The material is assumed to belong to one species, because the external ornament on plate fragments in the lower horizon is similar to that of more complete plates from the upper horizon.

The headshield is represented by a single L plate in visceral view (Figure 3B). It is almost complete save for damaged rostral (rm) and posterior margins, but can easily be restored to full shape (Figure 4B). It has a B/L index of 82, and is of regular bothriolepidoid morphology showing clearly the large orbital notch (orb), depression for the anterior postorbital process of the endocranium (pr. apo), the transverse lateral groove (tig) bound by two cristae (cr 1, cr 2) and a moderately large lateral pit (p). The latter feature is characteristic of certain *Bothriolepis* species from Victoria and Antarctica, although in those species it is much larger (Long 1983, Long and Werdelin 1986; Young 1988). The preorbital recess (prh) is of the simple semilunar type. The anterior (a.ar.SM) and posterior (p.ar.SM) articulations for the submarginal plate are normally developed (Young 1984)

The trunkshield is represented by an almost complete ADL plate, an imperfect PVL plate and an imperfect AMD plate. These all suggest that the armour was deeper than in *B. canadensis* (Stensiö 1948), being low-vaulted with an estimated trunkshield breadth comparable to *B. canadensis* relative to its length.

The left ADL plate (Figures 3C, 4A) lacks only the dorsal overlap area and the posterior margin. It is 48 mm long and 30 mm deep. The dorsal lamina (dlam) has a weakly concave external dorsal margin (dem) and an apparently strongly convex

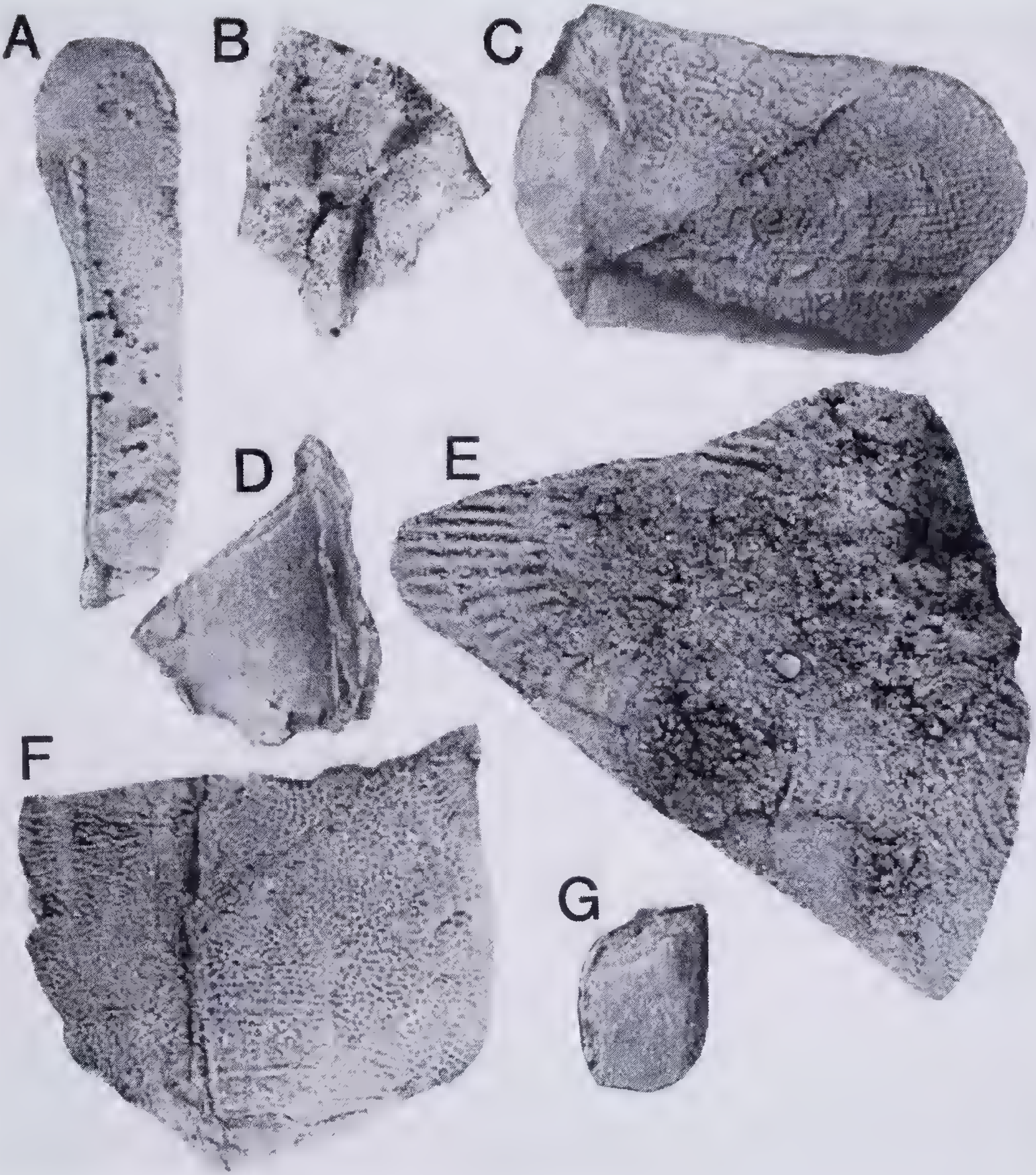

Figure 3. Fish fossils from the Munabia Sandstone. All are latex casts whitened with ammonium chloride. A-D, F. *Bothriolepis* sp. A, part of proximal segment of the right pectoral appendage, WAM 87.8.3. (x2). B, left L plate in visceral view. WAM 87.8.5. (x2). C, left ADL plate in dorsolateral view, WAM 87.8.1. (x1.5). D, visceral view of imperfect AMD plate, WAM 87.8.4. (x2). F, imperfect left PVL plate in ventrolateral view, WAM 87.8.2. (x1.5). E, *Holonema* sp., part of AMV plate in ventral view. WAM 87.8.6. (x1.5). G, osteolepidid scale in external view, WAM 87.8.7. (x3).

posterior margin (pm), although the dorsal division is not complete. The postnuchal ornamental angle (pnoa) is not accentuated as in some species (e.g. *B. maxima,* Gross 1948, in Stensiö 1948). The dorsal lamina is deepest anteriorly and is just over twice as long as its midline breadth. The dorsolateral ridge (dlr) is weakly defined, not developed as a prominent keel, and is gently curved throughout its length. The lateral lamina (llam) is almost triangular in form, being very deep posteriorly and narrow anteriorly. It is 17 mm deep at the posterior margin and 40 mm long. The external ventral margin (vem), and the ventral margin (vm) are quite straight. The processus obstans (pro) is quite short and blunt, not projecting far anteriorly. The articular area of the plate is developed as normal for the genus except that the *crista transversalis interna anterior* (cit) has an additional small transverse ventral ridge (tvr) ventral to its junction with the overlap area for the AVL (l.oa.AVL). The articular fossa (arf) is bounded dorsally by a thick supra-articular crista (crs) and ventrally by a narrower infra-articular crista (cri). A weak transverse ridge (ri) is developed in the lower half of the *crista transversalis interna anterior.*

The PVL plate (Figures 3F, 4C) is imperfectly preserved showing the external surface of its anterior half. The ventral lamina (v. lam) is 22.5 mm at its widest, meeting the lateral lamina (l.lam) along a well-defined ventrolateral ridge (vlr). The lateral lamina has a maximum breadth of 15 mm, although the dorsal margin is poorly preserved. The overlap surfaces for the AVL plate (v.ao.AVL, l.oa.AVL) are developed as normal for the genus.

The AMD plate (Figure 3D) is represented only by a fragment showing part of the visceral surface, with a very small portion of the external surface visible on the latex cast. It indicates that the AMD was of regular proportions. The dorsal surface shows the median dorsal ridge developed as a sharp keel, although, because of the small size of the plate, this character may be a juvenile feature, as recorded for other species (Stensiö 1948, Werdelin and Long 1986, Long 1990). The visceral surface shows a well-developed median ventral ridge, but the region of the ventral pit is not sufficiently preserved for description.

The pectoral fin is represented by an imperfect proximal segment (Figures 3A, 4D) which shows a mesial ridge (cr. dm) on the CD1 plate that is abraded and lacking denticulations, a weak mesial thickening (mt) and the anconeal area at the proximal end of the bone (ard), all of which are developed as normal for the genus. Sutures dividing individual plates of the pectoral appendage are not seen, but its overall length suggests that part of the MM2 plate (Figure 4D, MM2?) is also preserved.

The dermal ornament of the dorsal and lateral laminae is best known on the ADL plate, and the PVL plate shows that of the ventral lamina. The dorsal lamina has closely packed tubercles, some with weakly interconnecting ridges, and is quite similar to that of mature *Bothriolepis gippslandiensis* from Victoria (Long and Werdelin 1986, figure 4A, B). On the lateral lamina the tubercles have a more rectangular disposition, forming almost transverse alignments between the dorsolateral ridge and the lateral line canal groove. Close to the ventral margin of the ADL plate the tubercles are more widely

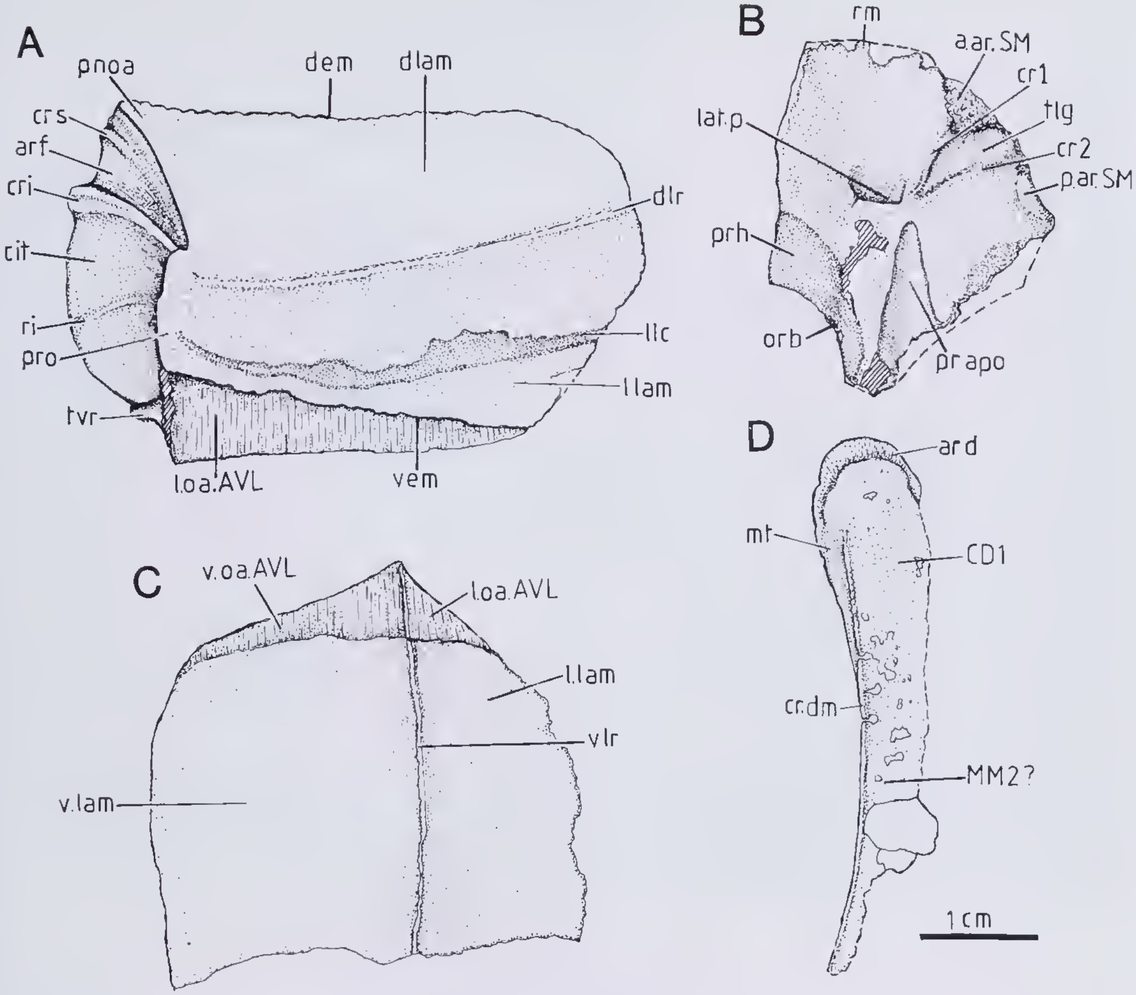

Figure 4. *Bothriolepis* sp. from the Munabia Sandstone. A, left ADL plate in dorsolateral view, WAM 87.8.1. B, left lateral plate in visceral view. WAM 87.8.5. C, imperfect left PVL plate in ventrolateral view, WAM 87.8.2. D, part of proximal segment of pectoral fin in dorsal view, WAM 87.8.3.

spaced and the ornament gives way to a reticulate network of thick ridges. The ventral lamina has an ornament almost entirely of thin reticulated ridges forming a pattern of small equally-sized enclosures, with some ridges developed parrallel to and near the plate margins.

Order Arthrodira

Family Holonematidae

Genus *Holonema* Newberry 1889

Type species

Holonema rugosum (Claypole 1883), Middle-Upper Devonian of North America.

Holonema sp.
(Figures 3E, 5A)

Material

WAM 87.8.6, an impression of the external surface of the right half of the AMV plate.

Description

The specimen is identified as *Holonema* by the ornamentation of bony ridges bearing small tubercles (as distinct from *Deirosteus* and other genera allied to *Holonema*, Miles 1971; Denison 1978), and by the shape of the AMV plate which is characteristic for holonematids (Figure 5). Aside from ornament, the presence of a ventral sensory-line canal on the AMV distinguishes it from that of *Groenlandaspis* (Ritchie 1975). The plate is comparable in size with that of *H. westolli* from the Frasnian Gogo Formation, if restored to full size it would be approximately 10 cm in breadth (Figure 5A). It shows conspicuous overlap surfaces for the AVL plates (Figure 5, oa.AVL) and a posterior overlap surface presumably for the PMV plate (oa. PMV). Although the PMV is overlapped by the AMV in *Holonema westolli* and most other arthrodires, the reverse condition may occur occcasionally (e.g. *Dicksonosteus*, Goujet 1984, figure 64), and there is generally much variation exhibited in the extent of contact between median ventral plates in the sample of arthrodires from the Gogo Formation in the collections of the Western Australian Museum. The overlap area for the interolateral plate is not seen in ventral view on *H. westolli* (WAM 90.12.137), and similarly there is no trace of this on the Munabia Sandstone plate. The ossification centre of the plate is not clearly defined. A short sensory-line canal groove runs towards the centre of the plate (vsl) just anterior to an indentation (ind) in the external lateral margin. The posteroventral corner (plc) is sharply pointed, unlike the anterolateral corner (alc) which is rounded. In all of these features the plate closely agrees with that in *Holonema westolli*.

Subclass Osteichthyes
Order Osteolepiformes
Family Osteolepididae
osteolepidid gen. indet.
(Figure 3G)

Material

One scale, preserved as an impression in external view, WAM 87.8.7.

Description

The scale is a typical osteolepidid type, distinguished from the rhombic scales of porolepiforms by the lack of pores. It is rectangular with a well-marked groove around the external, presumably cosmine-covered surface. It is thick, and the overlap area for neighbouring dorsal and anterior scales are short. There is no large dorsal peg as in some Australian forms like *Beelarongia* (Long 1987).

Such scales are commonly found in deposits of both marine and continental facies, especially during the Middle and early Late Devonian (Jarvik 1950, 1985; Janvier and

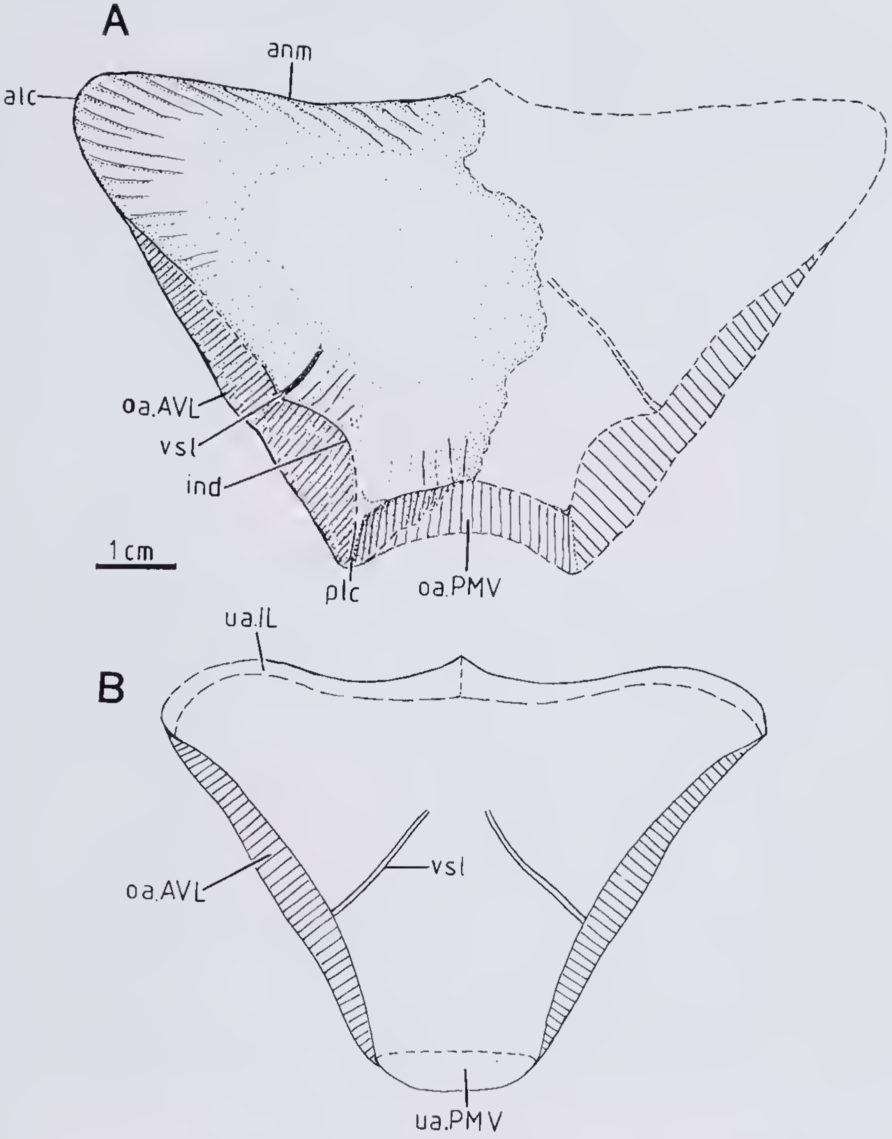

Figure 5. A, *Holonema* sp., AMV plate in ventral view, with missing areas restored (WAM 87.8.6; see Figure 3E for scale). B, the AMV plate of *Holonema westolli* from the Frasnian Gogo Formation (after Miles 1971, Figure 65 and WAM 90.12.137).

Martin 1979). By the Famennian most osteolepiforms had developed cycloid scales, except for the megalichthyids, but these have relatively thinner scales than in more primitive osteolepidids. The Munabia Sandstone osteolepidid scale is indistinguishable from those of the Gogo Formation osteolepiform *Gogonasus,* (based on WAM 86.9.661) but confident identifications cannot be made from scales alone.

The age of the Munabia Sandstone

The most age-diagnostic fish taxa identified from this assemblage are *Bothriolepis* and *Holonema*. *Bothriolepis* is restricted to the late Middle Devonian (Givetian) and Late Devonian in Europe, North America and the eastern U.S.S.R. (henceforth collectively referred to the Palaeozoic province of Euramerica, *sensu* Young 1981), but occurs in the Middle Devonian of China (P'an Jiang 1981), Antarctica and probably Australia (Young 1974, 1988). "*Bothriolepis*" from the Middle Devonian (?Eifelian) Hatchery Creek Conglomerate in New South Wales (Young and Gorter 1981) has since been referred to the new genus *Monarolepis* (Young 1988), but is a closely related form to *Bothriolepis* and *Briagalepis* (Long *et al.* 1990). Perhaps the oldest occurrences of *Bothriolepis* in Australia are now placed as possibly Late Givetian (Tatong, Victoria; Long and Werdelin 1986; Amadeus Basin, Young 1985).

Holonema has an age range of Middle Devonian -Frasnian in Euramerica and has been reported in association with *Bothriolepis* from several localities (e.g. Antalya Nappe, Turkey, Janvier 1983). However it is known from only one other site in Australia — the early Frasnian Gogo Formation. The occurrence of these two forms together in Western Australia is consistent with an early Frasnian age, indicated by the invertebrate and microfossil ages given for the underlying Gneudna Formation (late Givetian to earliest Frasnian). The base of the unit interfingers with the marine Gneudna Formation and there is no field evidence for assuming that the Munabia Sandstone is not conformable with the Gneuda Formation.

The uppermost section of the Munabia Sandstone has yielded some conodonts from a limy horizon within the sandstone (interval 24 of section CB93, Bureau of Mineral Resources unpublished report GEOL 79:034, by R.S. Nicoll). Nicoll identified *Polygnathus communis communis* and *Icriodus cornutus,* indicating the upper horizons of the unit may be of early Famennian age. Thus from both contact relationships with the Gneudna Formation and biostratigraphic assessment of fish and conodonts, the Munabia Sandstone is most likely to be early-middle Frasnian at the base, ranging into early Famennian in its youngest horizons. The maximum thickness for the unit is 555 metres at the type section (Hocking *et al.* 1987) and near where both the fish and conodonts were found. It would seem therefore that the Munabia Sandstone was deposited continuously over a time range of approximately 7-10 million years.

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Abbreviations used in text and figures

a.ar.SM	anterior articulation area for submarginal plate
ADL	anterior dorsolateral plate
alc	anterolateral corner
AMD	anterior median dorsal plate
anm	anterior margin of plate
ard	anconeal area of central dorsal plate 1
arf	articular fossa of anterior dorsolateral plate
AVL	anterior ventrolateral plate
CD1	central dorsal plate 1 of pectoral appendage
cit	crista transversalis interna anterior
cr1,2	cristae defining transverse lateral groove
cr.dm	mesial ridge on dorsal margin of pectoral appendage
cri	infra-articular crista of anterior dorsolateral plate
crs	supra-articular crista of anterior dorsolateral plate
dem	dorsal external margin of plate
dlam	dorsal lamina of plate
dlr	dorsolateral ridge of trunkshield
ind	indentation in plate margin
L	lateral plate
lat.p	lateral pit of lateral plate
llam	lateral lamina of plate
l.oa.AVL	overlap area for anterior ventrolateral plate
MM2?	suggested mesial marginal 2 plate
mt	mesial thickening on pectoral appendage
oa.AVL	overlap surface for anterior ventrolateral plate
oa.PMV	overlap surface for posterior median ventral plate
orb	orbital notch
p.ar.SM	posterior overlap area for submarginal plate
plc	posterolateral corner of plate
pnoa	postnuchal ornamental angle
pr.apo	groove for anterior postorbital process of endocranium
prh	preorbital recess
pro	processus obstans
PVL	posterior ventrolateral plate
ri	ridge
rm	rostral margin
tvr	transverse ventral ridge on anterior dorsolateral plate
ua.IL	area underlapped by interolateral plate
ua.PMV	area underlapped by posterior median ventral plate
v.lam	ventral lamina of plate
vlr	ventrolateral ridge of trunkshield
v.oa.AVL	ventral overlap surface for anterior ventrolateral plate
vsl	ventral sensory-line canal groove.

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Larval development of the oral brooding cardinalfish *Apogon rueppellii* (Teleostei: Apogonidae) in Western Australia

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Abstract

Late stage eggs and the development of the planktonic larvae of the oral brooding apogonid, *Apogon rueppellii*, are described and illustrated using material collected in the Swan Estuary, in south-western Australia. The eggs (2.2-2.5 mm) are nearly spherical and contain the embryos coiled with the tail covering the right eye. The larvae examined (5.5-16.3 mm) are pelagic, lightly pigmented, have a moderately deep body, a compact, coiled gut which extends to about midbody, a large, conspicuous gas bladder and 24 myomeres. *Apogon rueppellii* larvae are unique among previously described apogonid larvae in that they hatch in an advanced postflexion stage, possessing a yolk sac, functional mouth, developed eye and completely formed second dorsal, anal and caudal fins. The first dorsal and pelvic fins form during their short planktonic life and individuals settle at about 16 mm. It is suggested that both the advanced stage of development at hatching and short planktonic life contribute to maximize their survival and retention within the estuary. Comparisons with similar taxa and the early life history of other oral brooding apogonids are also presented.

Introduction

Most representatives of the perciform family Apogonidae are known to incubate their eggs orally (Breder and Rosen 1966, Leis and Rennis 1983, Thresher 1984). This type of incubation has been reported to be carried out predominantly by males and, in some instances, both sexes, after which the parent(s) may or not temporarily guard the newly-hatched larvae in their mouths (Ebina 1932, Smith *et al.* 1971, Chrystal *et al.* 1985). While most published accounts on oral brooding in this family have been restricted to reports of the occurrence of this reproductive specialization in several species (e.g. Hale 1947, Garnaud 1950, Fishelson 1970, Charney 1976, Omori and Takahashi 1980, Kuwamura 1983), only a few have also included a description of the eggs and larvae (Ebina 1932, Allen 1975).

The cardinalfish *Apogon rueppellii* is very abundant in marine coastal embayments and estuaries of the west coast of Australia. Its distribution extends from Albany in south-western Australia to Arnhem Land in the Northern Territory (Hutchins and Thompson 1983; Hutchins and Swainston 1986). The members of the large population of this species found in the Swan Estuary typically have a one year life cycle and breed within the middle and upper regions of this estuary between December and March (Chubb *et al.* 1979, Chrystal *et al.* 1985, Neira *et al.* in press). Individuals are sexually mature between 45 and 49 mm and the males brood from 50 to 230 fertilized eggs for about two weeks until the hatching of the larvae (Chrystal *et al.* 1985).

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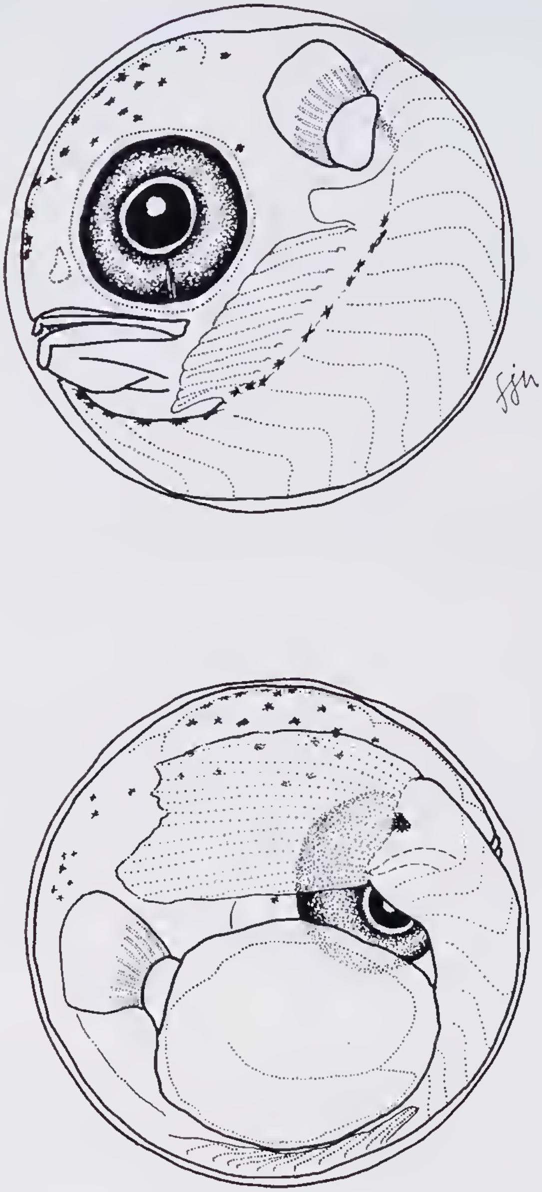

Figure 1. Lateral views of a 2.3 mm diameter late stage egg of *Apogon rueppellii* removed from the mouth of a 45.9 mm male.

This paper describes the planktonic larval stages of *A. rueppellii* from material collected in the Swan Estuary, in south-western Australia. It also compares some aspects of the oral brooding of *A. rueppellii* with those of other apogonids and discusses the significance of this reproductive specialization in an estuarine embayment.

Materials and Methods

Collection of larvae

Larvae of *Apogon rueppellii* were obtained from surface plankton samples collected between January 1986 and April 1987 in the middle and upper Swan Estuary (Lat 32°04′S; Long 115°44′E), in south-western Australia (see Neira and Gaughan 1989 for details of collection methods).

Material examined

A total of 81 larvae, ranging in body length (BL) from 5.5 to 16.3 mm, were examined to describe the changes in pigmentation, morphometrics and meristics. Ten larvae were deposited in the Australian Museum, Sydney, under the catalogue number I.27027-001.

Measurements and counts

Larvae of *A. rueppellii* were measured to the nearest 0.01 mm using a dissecting microscope fitted with an eyepiece micrometer. Terminology and body measurements of larvae follow Leis and Rennis (1983). All measurements except body length (BL, mm), i.e. the standard length in all specimens, are expressed as a percentage of body length. Myomere counts and ray counts of paired fins were made on the left side of the body. Pigment refers to melanin. Drawings were done with the aid of a drawing tube fitted to the dissecting microscope.

Thirty specimens were cleared and double-stained following the technique of Potthoff (1984), to count fin rays and vertebrae and to determine the sequence of bone ossification. The term "ossified" refers to structures stained positively for bone.

Results

Identification

Larvae were identified as belonging to the family Apogonidae by the presence of two separate dorsal fins, the presence of 24 myomeres and a prominent swim bladder (Miller *et al.* 1979, Leis and Rennis 1983). Larger specimens were identified as those of *Apogon rueppellii* by the dorsal and anal fin counts of VII+I,9 and II,9-10 respectively (Munro 1960). Embryos close to hatching, obtained from late stage eggs removed from the mouth of a 45.9 mm male captured in the upper Swan Estuary, were used in the initial assemblage with the early planktonic larvae. More advanced larvae were linked in a series using pigmentation and fin development.

Description of late stage eggs

Eggs of *A. rueppellii* prior to hatching are spherical and slightly ovoid and measure between 2.2 and 2.5 mm in diameter (mean = 2.3 mm; SD = 0.08; n = 20). Embryos possess a yolk sac, developed eye and developed anal, second dorsal and caudal fins. All eggs examined had the embryos coiled, with their tails covering the right eye (Figure 1).

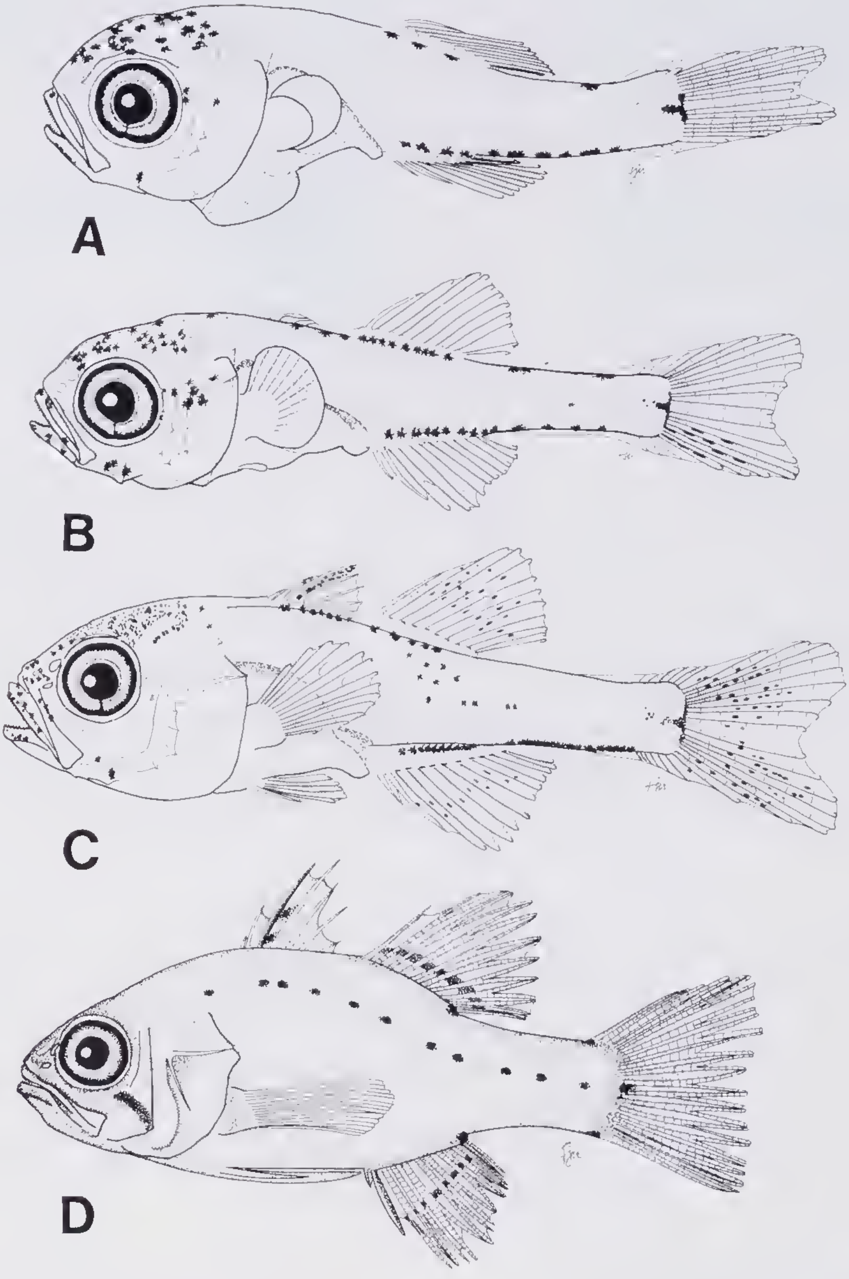

Figure 2. Larvae and juvenile of *Apogon rueppellii* from the Swan Estuary. (A) newly-hatched 6.0 mm larva with yolk sac. (B) 7.3 mm larva with developing pelvic fins. (C) 11.3 mm larva. (D) 30.0 mm juvenile. Larva illustrated in A and those in B and C were collected in the upper estuary in February 1986 and January 1987, respectively. Juvenile illustrated in D was caught in the middle estuary in October 1986.

Description of the planktonic larvae

Apogon rueppellii larvae (Figure 2) are moderately deep bodied and have a compact, coiled gut which extends to about midbody, a large, conspicuous gas bladder and 24 myomeres (range = 23-25, mean = 24, SD = 0.46, n = 25). Larvae hatch from orally brooded eggs at sizes between 5.5 and 6.4 mm with a yolk sac and the notochord already flexioned (Figure 2A). Remnants of the yolk sac are reabsorbed by 6.8 mm (Figure 2B). The mouth is functional in the newly-hatched larvae and presents canine-like teeth along the premaxilla and dentary. The head length and body depth remain about one third of the body length during development, whereas the preanal length increases from about 50.0% in newly-hatched larvae to around 59% in older larvae (Table 1). There is no gap between the anus and the origin of the anal fin. Scales appear by 12.0 mm and settlement occurs at sizes over 16.0 mm.

At hatching, the maxilla and premaxilla are the only bony structures which are ossified. The vertebral elements and the haemal and neural spines start to ossify shortly after hatching and are completely ossified by 8.0 mm.

Development of fins

Fin development is summarised in Table 2. At hatching, larvae possess the complete set of elements on the second dorsal, anal and caudal fins (Figure 2A). The rays of the pectoral fin start to form sequentially from dorsal to ventral by 6.9 mm and all (15-17) rays are present by 10.2 mm. The buds of the pelvic fins appear by 6.9 mm and all (I,5) elements are formed by 7.7 mm. The first dorsal fin start to appear at about 6.8 mm and the seven spines are present by 8.5 mm (Table 2).

Development of head spines

Spines on the head develop along the preoperculum and on the operculum and supracleithrum. Larvae hatch with two and three small spines along the anterior and posterior preopercular margins respectively. The posterior preopercular spines remain the same in length but increase in number throughout development. These spines merge into fine serrations along the preoprecular border in larvae over 15 mm. The anterior preopercular spines disappear by 11.5 mm. A small supracleithral spine is visible by 7.0 mm and disappears by 12.0 mm. The single opercular spine appears by 7.5 mm and remains in juveniles (Figure 2D).

Pigmentation

Larvae of *A. rueppellii* are lightly pigmented and do not undergo significant changes in pigmentation after hatching (Figure 2). Internal pigment is visible on the dorsal surface of the swim bladder and gut in all planktonic larval stages prior to settlement. The head of newly-hatched larvae possesses scattered melanophores on the midbrain and snout. Pigment increases in these areas during growth and becomes particularly intense on the midbrain at the settlement stage. A melanophore at the angle of the lower jaw is present in individuals during development and remains in adults. The preopercular area remains relatively unpigmented during development until a dark pigmented patch develops underneath the eye in juveniles (Figure 2D).

Table 1. Morphometric measurements for larval *Apogon rueppellii*. Body intervals are expressed as a percentage of body length. n, number of individuals. Means and standard deviations (in parentheses) are given when n>1. Blanks indicate character is absent. Values with additional n (when n>1) indicate number of specimens in which character was observed and measured.

Body Length (mm)	n	Head Length	Eye Diameter	Body depth At P_1 Base	Preanal Length	Pre-second Dorsal Fin Length	Pre-first Dorsal Fin Length
5.5	1	36.3	13.6	29.0	49.0	52.7	
6.0	3	32.8 (3.14)	14.2 (0.68)	29.4 (5.15)	51.6 (1.36)	51.6 (2.35)	
6.1	3	31.7 (2.05)	14.2 (0.77)	36.0 (0.00)	50.3 (1.54)	50.3 (0.77)	
6.2	4	31.8 (2.09)	14.3 (0.35)	34.6 (3.32)	50.4 (0.69)	50.0 (1.97)	
6.3	6	33.3 (2.24)	14.0 (0.59)	31.7 (4.49)	51.3 (2.37)	50.8 (3.04)	
6.4	1	31.2	14.0	37.5	50.0	46.8	
6.5	2	32.3 (1.54)	14.2 (0.38)	30.7 (3.07)	51.5 (2.30)	50.7 (1.54)	38.5
6.6	8	30.5 (0.50)	13.7 (0.25)	32.4 (0.73)	49.6 (1.00)	47.5 (0.73)	
6.7	7	30.9 (1.31)	13.7 (0.37)	31.6 (0.52)	49.5 (0.95)	48.2 (1.73)	34.3
6.8	7	30.2 (1.07)	13.5 (0.75)	29.6 (2.77)	49.8 (1.22)	50.6 (0.72)	36.7 (1.20) (n = 3)
6.9	7	30.6 (1.63)	13.2 (0.74)	29.6 (2.30)	49.7 (1.27)	49.9 (0.71)	36.8 (0.71) (n = 5)
7.0	4	29.6 (0.62)	13.5 (0.18)	31.4 (0.00)	49.3 (0.71)	49.3 (0.71)	35.7 (1.16) (n = 3)
7.1	1	30.9	11.3	25.3	50.7	47.9	35.2
7.2	2	34.0 (0.69)	12.5 (0.00)	27.0 (0.69)	53.5 (0.69)	52.7 (0.00)	40.3 (0.00)
7.4	1	33.8	12.2	25.7	55.4	52.7	39.2
7.8	1	33.3	12.8	25.6	53.8	52.5	38.4
7.9	1	31.6	12.6	25.3	53.1	51.9	36.7
8.3	1	34.9	10.8	25.3	55.4	50.6	37.4
8.4	1	33.3	10.7	27.4	54.7	52.4	40.5
8.5	1	34.1	11.7	28.2	60.0	55.3	41.2
9.4	1	36.2	11.7	27.6	55.3	53.2	38.3
9.5	1	33.7	10.5	25.2	55.8	52.6	35.8
9.7	1	35.0	11.8	24.7	54.6	53.6	42.3
10.3	1	33.0	11.6	28.1	54.7	50.5	40.7
11.0	1	32.7	12.7	27.3	52.7	55.4	42.7
11.2	2	32.1 (0.89)	12.7 (0.22)	30.4 (1.78)	57.6 (1.31)	56.2 (1.78)	41.1 (0.89)
11.3	1	33.6	12.4	29.2	53.1	56.6	43.4
12.0	3	35.6 (1.04)	12.5 (0.34)	29.7 (1.96)	56.9 (1.04)	54.7 (0.39)	39.7 (1.71)
12.1	1	35.5	12.4	30.6	56.2	52.9	38.8
13.0	1	30.0	12.3	34.6	59.2	56.1	40.0
13.2	1	34.1	12.5	30.3	58.3	56.8	39.4
13.5	1	34.8	12.9	33.3	59.3	58.5	40.7
13.9	1	33.1	12.2	32.3	53.9	55.4	39.5
14.5	1	34.5	12.4	31.0	57.9	59.3	42.0
16.3	2	36.5 (0.93)	12.2 (0.31)	31.2 (1.87)	57.5 (1.25)	57.5 (1.25)	40.0 (0.62)

The tail of newly-hatched larvae possesses melanophores on the ventral surface of the caudal peduncle and along the base of the anal fin. The melanophore at the centre of the caudal fin base is very conspicuous in all larvae and remains in juveniles (Figure 2). The melanophores which appear dorsally along the bases of the tail and second dorsal fin by 6.5 mm start to expand ventrally over the trunk and into the tail by 12.0 mm. A very distinct dark blotch forms at the base of the last soft ray of each of the second dorsal and anal fins by 15 mm and remains in juveniles. Shortly after, a series of small dark patches start to appear along the lateral line, finally becoming 9-11 in juveniles.

The second dorsal, anal and caudal fins are unpigmented in newly-hatched larvae. Scattered melanophores appear on the membranes of these fins by 6.5 mm and a distinct patch of melanophores form on the membrane which lies between the third and fourth spines of the first dorsal fin by 9.0 mm (Figure 2C). These patches and those on the base of the membranes of the dorsal and anal fins become very distinct in juveniles (Figure 2D).

Discussion

Larval development

Most of the larval development of *A. rueppellii* occurs inside the eggs which are incubated orally by adult males over a period of nearly two weeks (Chrystal *et al.* 1985). Unlike apogonid larvae previously described, those of *A. rueppellii* hatch in a stage which can be described as "late postflexion", i.e. with the notochord already flexioned and possessing remnants of a yolk sac, functional mouth, pectoral fin buds and the elements of the second dorsal, anal and caudal fins completely formed. The rays of the pectoral fins and the spines of the first dorsal fin form during their short planktonic life. Larvae of *A. rueppellii* show no apparent morphological specializations during their planktonic life and their exclusive features are consistent with the fact that most apogonid larvae are extremely variable not only in morphology but also in developmental patterns (Leis and Rennis 1983).

Similar taxa

Larval *A. rueppellii* are unique among other perciform larvae found in the Swan Estuary since they hatch possessing many adult characters. They can be easily identified by the short and light pigmented body, conspicuous, pigmented swim bladder, presence of two separate dorsal fins, fin ray counts, and the myomere number. Other characters include the dark pigmented patch at the centre of the base of the caudal fin and the absence of a gap between the anus and the origin of the anal fin.

Larvae of other representatives of Apogonidae occurring along the coast outside the Swan Estuary, namely the marine species *Siphamia cephalotes, Apogon victoriae* and *Vincentia punctata,* have not yet been described. With the exception of *S. cephalotes,* adults of the other two species have not yet been recorded in the Swan Estuary (Chubb *et al.* 1979, Loneragan *et al.* 1989). Adults *S. cephalotes* can be distinguished from those of *Apogon* and *Vincentia* by their possession of a luminous organ, a characteristic found only in the genus *Siphamia,* and the dorsal and anal fin counts of VI+I,8 and II,8 respectively (Munro 1960, Fraser 1972). In addition, the head spination of the larvae of a

Table 2. Fin ray development and vertebral counts in larval *Apogon rueppellii*. Vertebrate were counted only in cleared and double-stained specimens (denoted by *) in which vertebrae were clearly differentiated. Other blanks indicate character is absent. Pectoral and pelvic fin ray counts were made on the left side of the body. Procurrent rays are shown as dorsal/ventral elements.

Body Length (mm)	n	Dorsal Fin	Anal Fin	Pectoral Fin	Pelvic Fin	Caudal Fin Rays	Procurrent Rays	Vertebrae
6.3*	1	0+I,9	II,9	bud		9+8	2 / 2	24
6.5*	1	0+I,9	II,9	"		"	2 / 2	24
6.7*	1	0+I,9	II,9	"		"	2 / 1	24
6.7	1	0+I,9	II,9	"		"	2 / 2	
6.8*	1	II+I,9	II,9	"		"	2 / 1	24
6.9*	3	0-III+I,9	II,8-9	"	bud	"	3 / 1-3	24
6.9	1	II+I,9	II,10	3	"	"	3 / 3	
7.0*	2	III-V+I,9	II,9	4	"	"	2-3 / 3	24
7.0	1	VI+I,9	II,10	6	"	"	4 / 3	
7.1*	3	0-V+I,9	II,9-10	6-8	"	"	1-3 / 1-3	24
7.3*	1	II+I,9	II,9	6	"	"	3 / 2	24
7.5*	2	V-VI+I,9	II,9	8-10	"	"	3-5 / 4	24
7.7	1	VI+I,9	II,9	11	I,5	"	3 / 3	
7.8*	2	VI+I,9	II,9	10-12	"	"	4 / 3-4	24
8.0*	1	VI+I,9	II,10	13	"	"	5 / 5	24
8.1*	1	VI+I,9	II,9	13	"	"	4 / 4	24
8.1	1	VI+I,9	II,10	13	"	"	5 / 5	
8.2*	2	VI+I,9	II,9	9-11	"	"	4-5 / 3-5	24
8.5	1	VII+I,9	II,10	14	"	"	5 / 5	
9.0	1	VII+I,9	II,10	14	"	"	5 / 5	
9.4*	3	VII+I,9	II,9-10	13-15	"	"	6-7 / 6	24
9.5	1	VII+I,9	II,10	14	"	"	5 / 5	
9.6*	1	VII+I,9	II,9	13	"	"	6 / 5	24
10.2*	1	VII+I,9	II,9	15	"	"	7 / 7	24
10.2	1	VII+I,9	II,10	15	"	"	6 / 7	
11.0*	1	VII+I,9	II,9	15	"	"	7 / 7	24
11.3	1	VII+I,9	II,10	15	"	"	8 / 7	
11.4	1	VII+I,9	II,10	15	"	"	7 / 7	
11.5	1	VII+I,9	II,10	15	"	"	8 / 7	
11.7*	1	VII+I,9	II,10	15	"	"	8 / 7	24
12.0*	1	VII+I,9	II,10	15	"	"	7 / 6	24
16.3*	1	VII+I,9	II,10	17	"	"	7 / 7	24

species of *Siphamia* from eastern Australia (Leis and Bullock 1986), appear much more complex and developed than in any *Apogon* larvae.

Comparisons with other oral brooding apogonids

Apogon rueppellii is the only oral brooding teleost found in the Swan Estuary and the first apogonid which has been reported to exhibit such reproductive specialization within an estuarine embayment (Chrystal *et al.* 1985). G.R. Allen (Western Australian Museum, pers. comm), however, believe that other estuarine apogonids such as *Apogon ceramensis, A. hyalosoma* and *A. amboinensis,* which are found within the Indo-Australian Archipelago, may also incubate their eggs orally. Late stage eggs of *A. rueppellii* are spherical as in all apogonids for which eggs have been described except those of the northern Australian species *Apogon fusovatus* which produce spindle-shaped eggs (Allen 1985).

The number of eggs brooded by males *A. rueppellii* is considerably lower than that reported in most oral brooding apogonids (Table 3). This difference lies in the fact that fertilized eggs of *A. rueppellii* are much larger than most apogonid eggs previously described, a feature which, together with the volume of the buccal cavity of males, are the major factors limiting the maximum number of eggs they can incubate (Omori and Takahashi 1980, Chrystal *et al.* 1985). The largest eggs recorded to date in an apogonid (approximately 4.5 mm in diameter) were obtained from the mouth of a 95 mm specimen of *Vincentia conspersa* from southern Australia (Hale 1947).

Oral brooding has been reported in detail in the marine species *Apogon semilineatus* and *Sphaeramia orbicularis,* for which the eggs and larvae have also been described (Ebina 1932, Allen 1975). The sizes of the larvae of these species at hatching, i.e. 2.3 and 3.3 mm total length respectively, are significantly smaller than those of *A. rueppelli* (7.5-7.8 mm total length), a feature certainly associated with the smaller diameter of the eggs brooded by these marine apogonids (0.58 and 0.65 mm respectively; Ebina 1932, Allen 1975; Table 3). Moreover, in contrast to *A. rueppellii,* the larvae of these two marine apogonids hatch in a poorly-developed stage possessing a yolk sac and only the buds of the pectoral fins (Ebina 1932, Allen 1975). Newly-hatched larvae of *A. semilineatus* are retained in the mouth of the adult for some time after hatching (Ebina 1932). This parental care has never been reported in *A. rueppellii* and seems unlikely considering the large larval size and the advanced stage of development at hatching.

Oral brooding within an estuary

Most apogonids are strictly marine; only a few species inhabit brackish and fresh waters (Fraser 1972). In the case of *Apogon rueppellii,* which in Western Australia is represented by populations in coastal marine waters as well as estuaries (Chrystal *et al.* 1985), it is not known whether marine breeding habits differ from those reported here for an estuarine population. Oral brooding of eggs by male *A. rueppellii* within this estuary provides a high level of parental care and thereby compensates for the low fecundity of the females. Indeed, females of this species produce between 70 and 345 eggs, of which over 70% are retrieved by the males after their release (Chrystal *et al.* 1985). The chances

Table 3. Aspects of the reproductive biology of oral brooding apogonid species. Blanks indicate information not available. Size of brooders and that of larval size at hatching are assumed to be total length in those cases not stated in references. Sole figures in number of eggs carried are from only one specimen and those indicated by * were calculated from formulas. BL = body length.

Species	Location of Study	Brooders	Size of brooders (mm)	Number of eggs carried	Egg diameter (mm)	Larval size at hatching (mm)	Source
Apogon affinis	Venezuela	males and females	54.7-87.5	21,000	0.35-0.40	1.0	Smith *et al.* 1971
Apogon imberbis	Mediterranean	males		22,137	0.50		Garnaud 1950
Apogon lineatus	Yuya Bay, Japan	males	53.2-83.9	3,160-13,215*			Omori and Takahashi 1980
Apogon maculatus	Bahamas		56.5-60.5	75-100	0.16-0.34 (x = 0.24)		Charney 1976; Thresher 1984
Apogon rueppellii	Western Australia	males	45.0-85.0	70-280*	2.20-2.50 ($\bar{x}$ = 2.33)	7.5-7.8 (5.5-6.4BL)	Chrystal *et al.* 1985; this study
Apogon semilineatus	Tateyama Bay, Japan	males and females	70.0-100.0		0.58-0.60	2.3	Ebina 1932
Phaeoptyx conklini	Bahamas		34.8-42.4		0.19-0.31 ($\bar{x}$ = 0.24)		Charney 1976
Sphaeramia orbicularis	Palau Archipelago, USA	males	69.0-89.0	6,100-11,700	0.60-0.70	3.3	Allen 1975
Vincentia conspersa	Southern Australia		95.0	150	4.50		Hale 1947

of larval survival during their short planktonic phase are, on the other hand, enhanced by the fact that most of the larval development takes place within the egg. It thus seems probable that both the advanced stage of development of *A. rueppellii* at hatching and their short planktonic life contribute to maximize their survival and retention within estuaries, where conditions are much less stable than those at sea where apogonids are more abundant.

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Revision of *Lerista picturata* (Lacertilia: Scincidae) of southern Australia

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Abstract

The former subspecies of *Lerista picturata*, viz. *L. p. picturata*, *L. p. baynesi* and *L. p. edwardsae* are raised to full species. The first two are redescribed.

Introduction

For my revision of *Lerista* in 1972 only 10 *picturata* and 15 *baynesi* were available. The westernmost *baynesi*, in their relatively strong colour pattern, approached *picturata;* and as the 230 km that separated the two taxa left plenty of room for integradation, I treated them as conspecific.

Since then another 80 *picturata* and 106 *baynesi* have been accessed. Although the gap between them has been narrowed to 40 km, none of the additional material reveales gene-flow between the two taxa. Consequently they are now regarded as parapatric species. Because *edwardsae* of South Australia is not especially close to either *picturata* or *baynesi*, it too is treated as a full species. The three taxa comprise a subgroup of the *L. macropisthopus* species group characterized by two, rather than three, supraoculars.

This brings me to an error in my previous descriptions of thc three species: the first, very wide supraciliary was mistaken for a supraocular. The true nature of this scale is revealed by the odd specimens with four supraciliaries; here, as in many other *Lerista*, the high first and small second supraciliaries have not fused (see figure 1). It is also believed that the large anterior supraocular in the *L. picturata* subgroup is derived from the fusion of the original first and second supraoculars. In other members of the *macropisthopus* group the first supraocular never fuses with the second but commonly fused with anterior supraciliaries.

As this revision is based wholly on specimens in the Western Australian Museum, prefixes have been omitted from catalogue numbers.

Systematics

Lerista picturata (Fry)

Lygosoma (Rhodona) picturatum Fry (1914: 186). Boulder, W.A.

Diagnosis

A large *Lerista* with one finger (terminating in wide flat scale), two toes, movable eyelid, two supraoculars and strong colour pattern (four dark dorsal lines and wide sharp-edged upper lateral stripe).

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†Deceased 26/6/90.

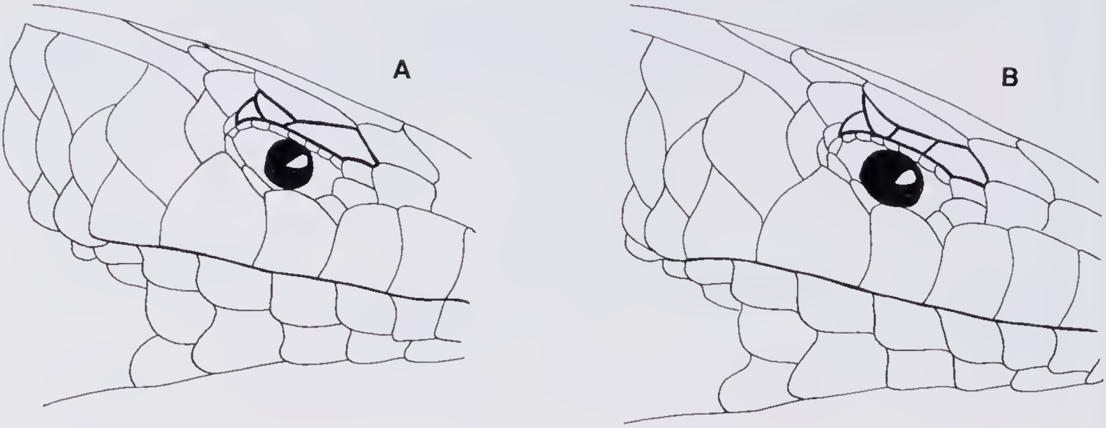

Figure 1. Head scalation in *Lerista picturata* showing (A) fusion of first and second supracillary scales, as seen in the majority of specimens of the *picturata* subgroup: and (B) lack of fusion of these scales, as occurs in a minority of specimens of the *picturata* subgroup but in many other *Lerista* species (supracillaries emphasised).

Description

Snout-vent length (mm): 40-92 (N 90, mean 73.4). Length of appendages etc. (% SVL): foreleg 1-2 (N 71, mean 1.4), hindleg 14-20 (N 84, mean 16.8), tail 76-109 (N 24, mean 94.1), snout to foreleg 22-29 (N 77, mean 25.4).

Nasals in contact (N 75). Prefrontals widely separated. Frontoparietals separated, very much smaller than interparietal (N 74). Nuchals 1-6 (N 51, mean 3.8). Supraoculars two, first in contact with frontal. Supraciliaries three with first much the largest (N 69) or four with first and third largest (5). Upper labials six (N 77). Midbody scale rows 20 (N58), 21 (4) or 22 (10). Lamellae under longer toe 10-16 (N 83, mean 12.8).

Upper surface pale brown, slightly tinged reddish and marked with dark brown or blackish brown: blotches on head, four lines on back and stripe from lore to tail (on which it becomes narrower and broken into spots), $1\frac{1}{2}$-2 scales wide on body. Lower lateral and ventral surfaces yellow in life.

Distribution

Semiarid south-eastern interior of Western Australia from Riverina and Comet Vale south to lat. 33°S, west to Woolgangie and McDermid Rock and east to Zanthus, Caiguna and Mardabilla Rock. See map, Figure 2.

Remarks

For colour photographs see Storr *et al.* (1981, pl. 15) and Wilson and Knowles (1988, pl. 566).

Material

Eastern Division (WA): Riverina (66287); 14 km ENE Comet Vale (65822-3); Grants Patch (10147); 3.5 km SW Black Flag (73241) and 5 km SW (78535) and 12.5 km WSW (73306, 73318); 16 km S Woolgangie (78714) and 31 km SSE (78752-3); 5 km SW Boulder (22513); 31 km W Randell (12229); Zanthus (12227);

Figure 2. Map of south-eastern Western Australia, showing location of specimens of *Lerista picturata* (spots) and *L. baynesi* (circles).

Buningonia Spring (65575) and 3.5 km SW (65651) and 6.5 km SE (65525, 65592, 65624); 90 km SE Karonie (17340); 20 km N Heartbreak Ridge (65397, 65404, 65475) and 18 km N (65378); 47 km N Balladonia Hotel (29473).

Eucla Division (WA): McDermid Rock (65263, 65270, 65273-6, 65294, 65345, 66172, 74250, 74278, 84221-3, 85109); Norseman (8152, 96172-3, 96258); Heartbreak Ridge (72373); 11 km E Kilidwerinia Granite Rock (92028); 2 km S Balladonia Hotel (70004-6) and 13 km S (94239-42); 37 km W Caiguna (66666, 66676); 20 km E Jyndabinbid Rocks (62276-8); 37 km NW Toolinna Rockhole (77795); Mardabilla Rock (93799-801, 93803-6); Coragina Rock (66834-8); 32 km ESE Mt Newmont (59816) and 30 km SE (59825); Deralyinya (93304-10, 93315-22).

Lerista baynesi Storr

Lerista picturata baynesi Storr 1972: 66. (Old) Eucla, W.A.

Diagnosis

A large *Lerista* with one finger (terminating in wide flat scale), two toes, movable eyelid, two supraoculars and very weak to moderately strong pattern (four dark dorsal lines or rows of spots present or absent, and upper lateral stripe narrow and either solid, hollow or diffuse). Further differing from *L. picturata* in its shorter appendages, fewer subdigital lamellae, more greyish upper surface and whitish rather than yellow lower surface; it is also slightly smaller and more elongate.

Description

Snout-vent length (mm): 36-91 (N 121, mean 69.7). Length of appendages etc. (% SVL): foreleg 0.5-1.5 (N 74, mean 1.0), hindleg 9.5-13.5 (N 71, mean 11.7), tail 70-98 (N 51, mean 82.0), snout to foreleg 20-27 (N 70, mean 23.9).

Nasals in contact (N 53) or very narrowly separated (1). Prefrontals widely separated. Frontoparietals separated, much smaller than interparietal (N 52). Nuchals 1-6 (N 51, mean 3.8). Supraoculars two, first in contact with frontal (N 53).

Supraoculars two, first in contact with frontal (N 53). Supraciliaries three with first much the largest (N 42), two with first much the largest (2) or four with first and third largest (7). Upper labials 6 (N 55). Midbody scale rows 18 (N 4), 20 (40), 21 (1) or 22 (1). Lamellae under longer toe 7-10 (N 53, mean 8.8).

Upper surface pale greyish brown to pale brownish grey, marked with reddish brown, dark brown or blackish brown: four rows of dots or short dashes on back, occasionally coalescing into lines, often faint or absent; upper lateral stripe from lore to tail, at best solid, ragged-edged and about a scale wide on body, at worst hollow or very diffuse.

Distribution

Semiarid far south-east of Western Australia (Roe Plains and extreme south of Hampton Tableland, west to Twilight Cove) and extreme west of South Australia; with an isolated population further west (Bilbunya Dunes). See map, Figure two.

Geographic variation

Colour pattern is weakest in the east. The single specimen from west of the Baxter Cliffs is dorsally pale grey with black markings (four lines and hollow upper lateral stripe); it alone has 22 midbody scale rows.

Remarks

For colour photographs see Storr *et al.* (1981, pl. 15) and Wilson and Knowles (1988, pl. 564).

Material

Eucla Division (WA): Bilbunya Dunes in 32°58′S, 124°19′E (93351); Twilight Cove (28705); Eyre (60814, 67304-5) and 13 km W (66930-42) and 2.5 km N (91964) and 6 km N (91439, 91445) and 7 km N (77861-2); 30 km SE Cocklebiddy (94109); Burnabbie (60813, 94217-23) and 11 km E (93780-8); top of Madura Pass (28128, 67292); 43 km S Madura (34445) and 48 km E (66848-51); 28 km NNW Middini Beach (91442) and 15 km NNW (91440, 91891); 6 km S Mundrabilla (91298); 8 km SW Yuwanyandi Rockhole (91297, 91437, 91444, 92000) and 19 km S (89966, 91303, 91436, 91441); Eucla Pass)18188, 66642-3) and 40 km WSW (66452-4, 77887, 77892, 77898-9) and 4 kms S (24609-17, 64495-6, 66506-34, 66597, 66606-8, 70011-5) and 10 km ENE (66861).

South Australia: 23 km ENE Eucla Pass (96542).

Lerista edwardsae Storr

Lerista picturata edwardsae Storr (1982: 1).

Diagnosis

A large *Lerista* with no finger (forelimb a tiny stump in groove), two toes, movable eyelid, two supraoculars and strong pattern (two, rarely four, dark dorsal lines and wide sharp-edged upper lateral stripe). Further differing from *L. picturata* and *L. baynesi* in fewer midbody scale rows (mode 18) and usually having no nuchals.

Description

See Storr (1982: 2), where the following corrections should be made: supraoculars two (first in contact with frontal) and supraciliaries usually three (first much the largest). Its strong colour pattern and yellow venter make *L. edwardsae* superficially similar to *L. picturata*, but it is best treated as a full species. It differs from *L. picturata* and *L. baynesi* in its pale silvery grey upper, two (rather than four) dorsal lines or rows of spots, greatly reduced foreleg, lack of nuchals and fewer midbody scale rows.

The known gap between *L. baynesi* and *L. edwardsae* in the far west of South Australia was reduced by Schwaner and Miller (1984) to less than 200 km.

For coloured photograph see Wilson and Knowles (1988, pl. 565).

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Ecology and behaviour of the bee *Amegilla (Asaropoda) dawsoni* (Rayment) with notes on a related species (Hymenoptera: Anthophoridae)

Terry F. Houston*

Abstract

Amegilla dawsoni, Australia's largest anthophorine bee, annually produces a single generation from July to September. Females nest solitarily or more often gregariously in flat, hard, bare clay, apparently using nectar to soften the soil during excavation. Each burrow is furnished with a mud turret which is demolished when the nest is complete. Nest structure is described in detail.

Larval provisions are liquid. After consuming their provisions, larvae eat the wax lining of their cells, defaecate and enter a diapause which may last for one or more years. They do not spin cocoons.

Mating occurs at nesting areas and at the forage plants. Males vary conspicuously in size and exhibit a bimodal size frequency distribution. Large size appears to be an advantage to males competing for access to newly emerging virgin females at the nesting sites. Small males predominate amongst the 'patrollers' at forage plants.

A miltogrammine fly and a mutillid wasp were observed to develop at the expense of the bees in their brood cells. The bees swarm about intruders (humans and corvids) at nesting aggregations but do not attack them.

Brief observations on the nests and behaviour of a second, undescribed species of *Asaropoda* are also recorded.

The biology of *Amegilla (Asaropoda)* is briefly discussed and compared with that of other Anthophorini.

Introduction

The world-wide tribe Anthophorini (sensu Brooks 1988) consists of the genera *Anthophora* and *Amegilla* and only the latter genus occurs in Australia where it is represented by three subgenera *Asaropoda, Notomegilla* and *Zonamegilla.* The biology of the tribe is very incompletely studied and most of the available information relates to *Anthophora.* What little information is recorded for *Amegilla* relates to the Australian subgenera *Asaropoda* and *Zonamegilla.*

The most detailed published information concerns two species studied in Brisbane: *A. (Zonamegilla) pulchra* (Smith) (Michener 1960, as *A. salteri* (Rayment); Cardale 1968a) and *A. (Asaropoda)* sp. (*?bombiformis,* Cardale 1968b). Minor observations of some other species were recorded by Rayment (1935, 1951).

The present study significantly extends our knowledge of *Asaropoda* revealing that while *A. dawsoni* may have much in common with its congeners, it is unique in several respects.

All specimens taken during the course of this study are lodged in the collection of the Western Australian Museum, Perth.

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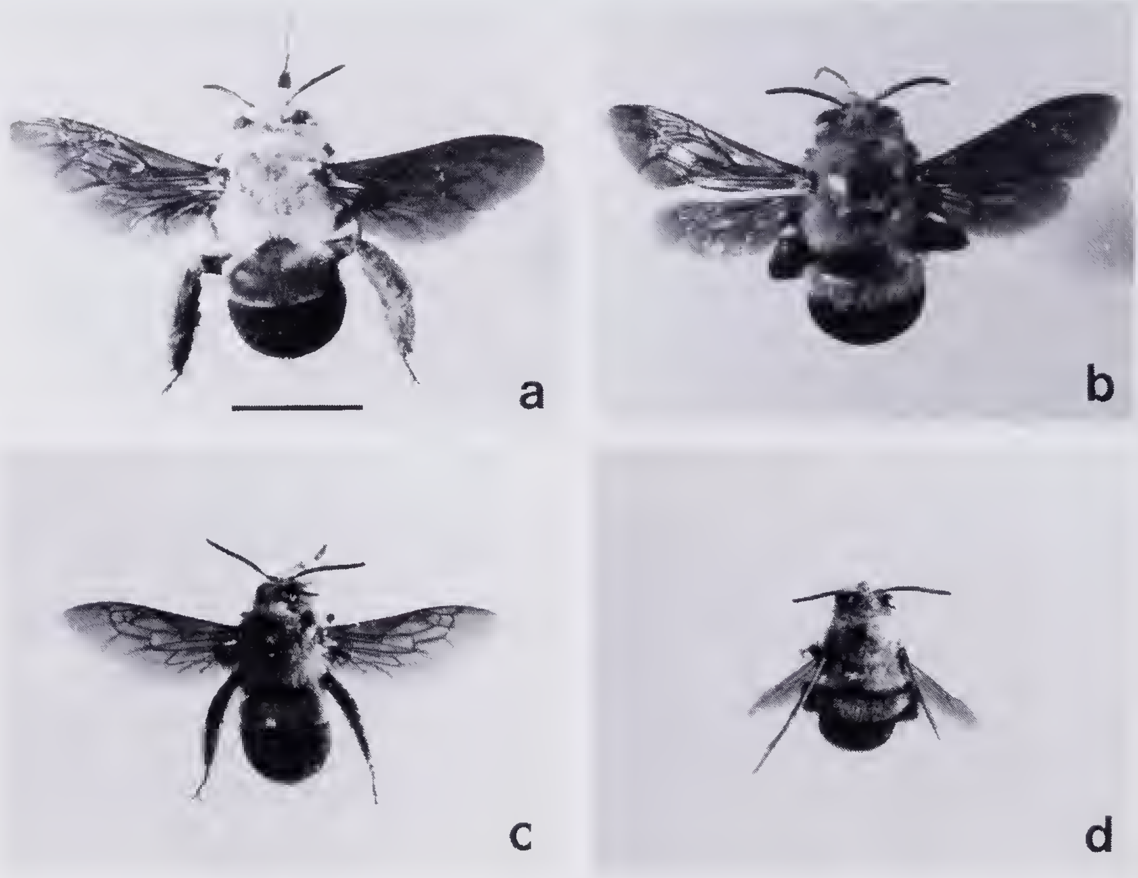


Figure 1 Pinned adults of *Amegilla (Asaropoda) dawsoni*: (a) female; (b-d) males showing size variation. All to same scale; scale line, 1 cm.

Methods and Materials

Most field observations of behaviour were recorded immediately on a mini-tape recorder and later transcribed into field note books.

Live specimens were marked for individual recognition in the field using various colours of "Liquid Paper" typing correction fluid, spots being placed on the mesoscutum.

Observations

Amegilla (Asaropoda) dawsoni (Rayment)

Amegilla dawsoni (Rayment) is a very large, robust, dark-winged bee resembling a *Xylocopa* (Figure 1) and is the largest of the Anthophorini in Australia.

It is endemic to north-western Australia, ranging from near Roebourne and Onslow south almost to Paynes Find and inland to the Great Sandy Desert (Figure 2). It is often locally abundant and its large size and gregarious nesting habits occasionally bring it to

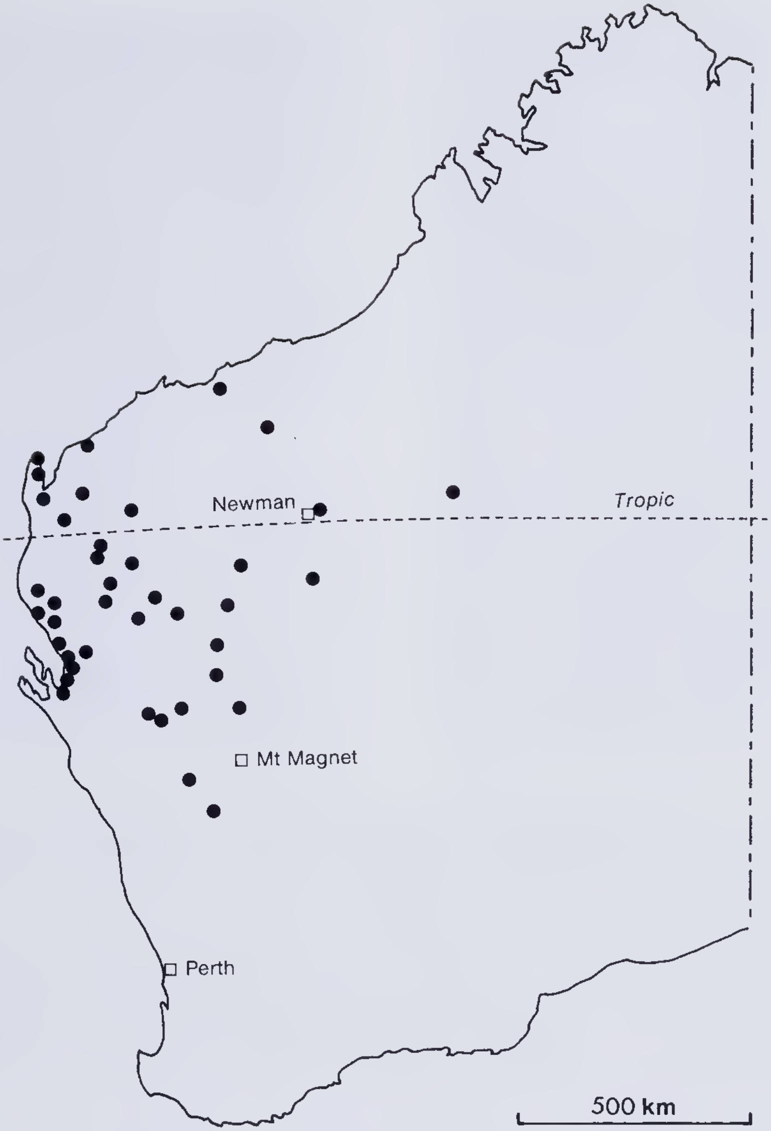


Figure 2 Map of Western Australia showing collection localities for *Amegilla (Asaropoda) dawsoni.*

public attention. It is surprising, therefore, that the species was not scientifically described until Rayment (1951) included it in his revision of *Asaropoda.* Nothing was recorded of its habits until Michener (1965) related a few notes from another observer on its nesting and behaviour in his comprehensive systematic study of Australian bees.

Phenology

Data accompanying 61 separate collection lots of adults in Australian museums and my own observations indicate that *A. dawsoni* is a univoltine species with a late-

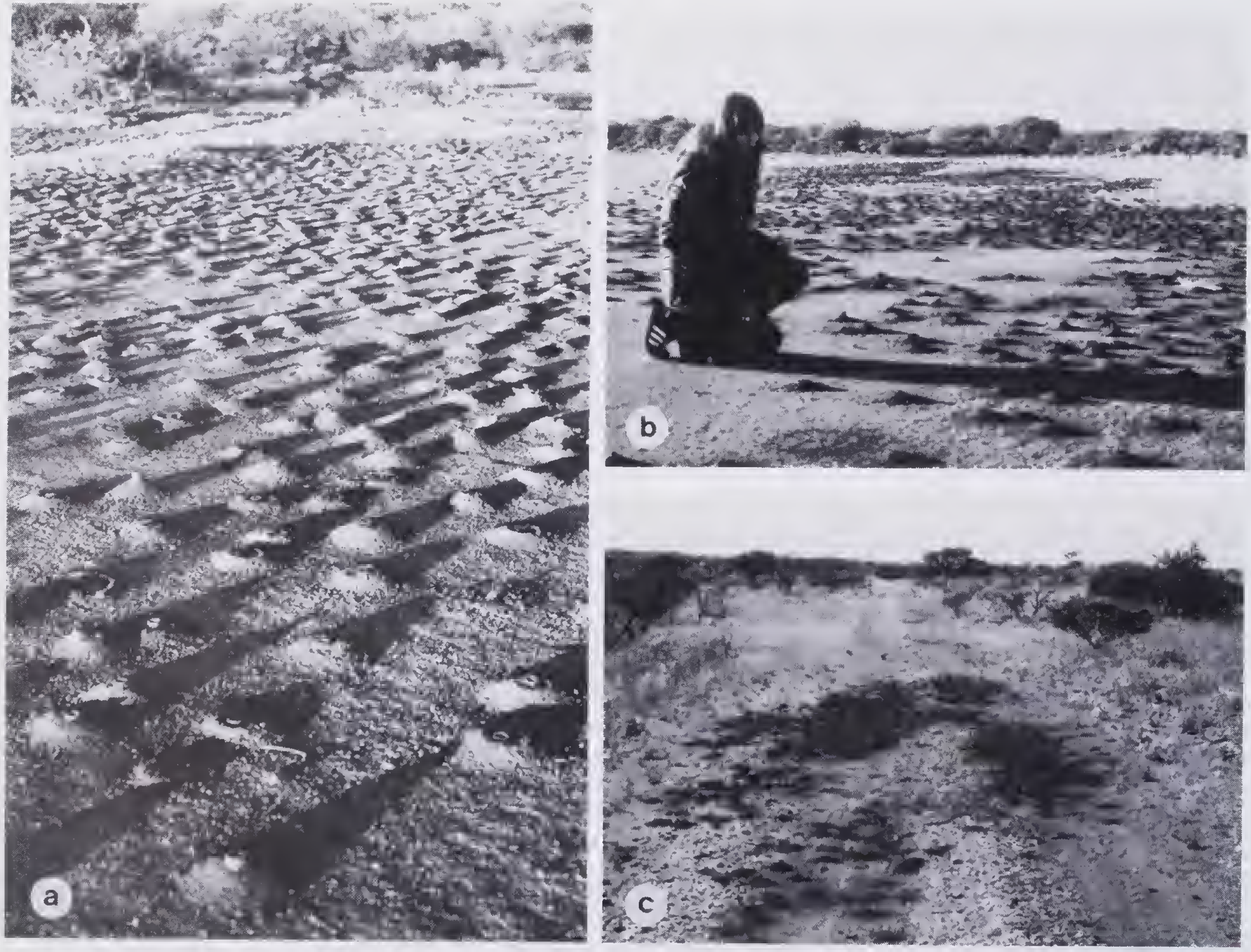


Figure 3 Active nesting areas of *Amegilla (Asaropoda) dawsoni*: (a,b) two views of a very large aggregation containing at least 10,000 nests on the margin of a playa on Meedo Station; (c) a smaller aggregation in a little used track on Gifford Creek Station.

winter/early-spring flight season. Adults of both sexes have been collected from mid July to mid September with most being taken in August. Two females purportedly collected in April and May were the only evidence of emergences at other times of the year. On examining the nesting aggregation on Meedo Station in May 1981, I found no evidence of recent nesting activity and about 50 viable cells excavated all contained dormant mature larvae (see Immature Stages for details of larval and pupal development).

Adult activity at any particular nesting site is likely to be limited to a few weeks. However, nesting populations at different localities were observed to be widely out of phase.

Nesting sites are perennial and the soil in which the bees nest is sometimes honeycombed with old cells and shafts.

Flower preferences

Females were observed to forage at flowers of only four plant genera — *Cassia* (Caesalpiniaceae), *Eremophila* (Myoporaceae), *Solanum* (Solanaceae) and *Trichodesma* (Boraginaceae) — despite the availability of a much wider selection of pollen and nectar sources at some localities. Pollen of *Cassia, Solanum* and *Trichodesma* species was obtained by very audible vibration of the anthers. *Eremophila* species, especially those with reddish or pink flowers (e.g. *E. longifolia* and *E. leucophylla*) provided nectar (and possibly pollen in a few cases). The females did not enter the tubular corollas and were able to extract nectar by inserting their long proboscides.

Pollen sampled from the scopae of 12 pinned females in the Western Australian Museum collection was examined microscopically and was consistent with that of *Trichodesma zeylanicum* (9 cases), a mixture of *Cassia* sp. and *T. zeylanicum* (2 cases) and possibly *Eremophila* sp. (1 case).

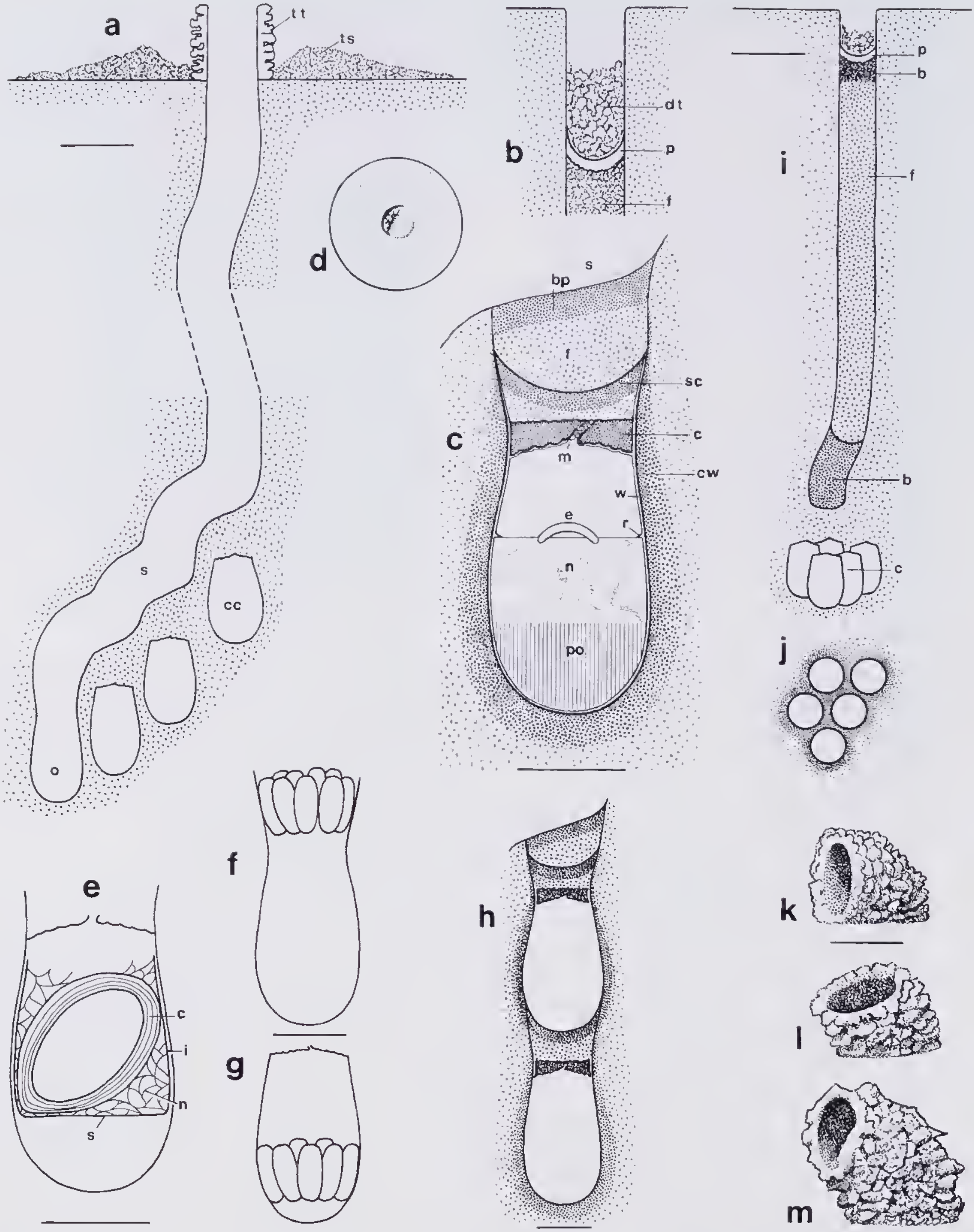
Male size variation

Males within any given population vary markedly in size while females tend to be rather uniform. In a total sample of 144 males, the head width range was 4.9-7.3 mm while in a sample of 81 females it was 6.4-7.4 mm (Figure 6a, b).

Males vary allometrically, large males exhibiting relatively longer mandibles and more robust bodies (relatively thicker genae and broader abdomens) than smaller males. The largest males approximate the females in size (Figure 1a, b).

Taking pinned specimens in the collection of the WAM as a sample, it appears that the size/frequency distribution of females is normal while that of males is distinctly bimodal (Figure 6). This bimodality could reflect the situation in natural populations or it could be an artefact produced by collectors tending to sample extremes of size.

That it is natural is supported by the distinctly bimodal weight/frequency distribution of a sample of mature dormant larvae taken at random from cells excavated in the field (Figure 7). The smallest larva weighed only 1/4 as much as the largest. Although the larvae could not be sexed, it may be assumed that those in the smaller weight classes (<0.8 gm) were males and it is interesting to note that these larvae made up 63% of the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sample. This suggests that small males greatly outnumber large males in natural populations (contradicting the pinned adult sample, Figure 6) and that males greatly outnumber females. A random sample of pupae is required to establish the sex ratio and size/frequency distributions of males and females in a natural population.

Nests and nesting behaviour

Nesting sites

Females nest in bare, flat, hard, clay soil, frequently in the vicinity of playas and sometimes in little-used roads or road margins (Figure 3). The soil is usually so hard that it can scarcely be chipped with a spade or pick.

Nests occur singly and widely scattered or, more usually, in aggregations of from 2 to about 10,000. The largest aggregation I examined extended for over 200 m around the periphery of a bare clay depression (Figure 3a, b) with up to 35 burrows per m^2.

Nest construction

In initiating a new nest, a female selects a site and begins to excavate a burrow by biting at the soil with her mandibles. The soil is periodically wet and softened with liquid from the mouth. Females interrupt their burrowing from time to time and depart on flights away from the nesting area presumably to recharge their crop with liquid. As I have never seen the bees at free water and free water is seldom available in the near vicinity of their nests, I assume they use nectar to wet the soil.

When a female has excavated a pit about 10 mm deep she begins constructing a turret. Wet soil brought up from the burrow is tamped into position around its rim with the apex of the abdomen used in conjunction with the hind legs, the female rotating in the burrow as she applies the soil. Successive loads of excavated soil are added to the rim of the turret which grows vertically to a height of usually no more than 15-20 mm although taller ones were occasionally noted including one 90 mm high. While being rough and granular externally the turrets were smooth internally with a bore of 13-14 mm (Figure 4a).

◄ **Figure 4** Details of nests of *Amegilla (Asaropoda) dawsoni* (a-h) and Species 2 (i-m): (a) diagrammatic profile of open incomplete nest (cc, closed brood cell; o, open brood cell; s, shaft; ts, tumulus; tt, turret); (b) profile of upper section of shaft of closed nest (dt, debris from demolished turret; f, unconsolidated soil fill; p, concave plug); (c) profile of freshly completed brood cell and its closure (bp, access burrow plug; c, cell cap; cw, cemented earthen wall; e, egg; f, unconsolidated soil fill; m, 'micropyle'; n, nectar with sparse suspended pollen; po, pollen sediment in nectar; r, ring of wax at edge of nectar surface; s, shaft; sc, supracap; w, wax lining); (d) inner view of cell cap showing faint spiral pattern and plugged 'micropyle'; (e) diagrammatic profile of brood cell containing mutillid wasp cocoon (c, multilayered inner cocoon; i, silken involucrum applied to cell wall; n, network of silk threads filling space; s, septum formed by involucrum); (f, g) profiles of open and closed brood cells, respectively, showing positions of puparia of the cleptoparasitic fly *Miltogramma rectangularis;* (h) profile of two brood cells constructed in series; (i) diagrammatic profile of completed nest with five brood cells (b, barricade of consolidated soil; c, cells; f, unconsolidated soil fill; p, concave plug); (j) brood cells (from i) in plan view (cemented earth heavily stippled); (k-m) turrets from three nests showing variation in form. Scale lines: a and i, 2 cm; others, 1 cm.

Once the turret has been completed, the female casts further excavated soil over its rim with vigorous kicking movements of the hind legs so that a circular tumulus develops (Figure 3a). The downdraft of the female's wings as she enters and leaves the nest entrance usually results in the tumulus becoming annular.

The shaft is extended more or less vertically and widens slightly below the entrance to a diameter of 15-16 mm. Its walls are fairly smooth and unlined. However, in one nest a 6 cm section of shaft wall had been built in on one side where the substrate consisted of friable soil.

Cells were located at depths of 15-35 cm. They were urn-shaped and vertically orientated with their caps uppermost (Figure 4a). Most occurred singly but occasionally cell pairs were encountered where one cell rested upon the cap of the other (Figure 4h).

A newly constructed cell before provisioning consists of an ovoidal chamber at the lower end of the open shaft (Figure 4a). It has cemented earthen walls, trowelled smooth internally and coated with a clear, waxy, waterproof, lining. This smoothing and waxing continue a short distance into the shaft above the cell mouth. The wax lining is thickest (up to 0.13 mm) in the middle and lower parts of the cell and turns white and opaque with age.

Following provisioning and oviposition (see below), the cell is sealed with a complex earthen closure (Figure 4c). The first component, the cell cap, is a rather flat disc constructed in the narrowest part of the cell mouth. It is only slightly concave on the inner side, shows variable evidence of its spiral construction and regularly has a distinct 'micropyle' (often plugged with loose soil) located more or less centrally (Figure 4d). The cap is thinly lined on its lower (inner) surface with clear wax like the rest of the cell but the plug of soil in the micropyle is not waxed. Above the cap and separated from it by unconsolidated earth is a cemented concave plug (for which I coin the term 'supracap'), very smooth but not waxed on the concave upper surface. Unconsolidated soil is piled on this plug and a cemented wall seals the cell antechamber off from the shaft. The shaft is usually then extended laterally and downwards to form the next cell chamber. Consequently, as nests advance, the shaft descends in a series of steps and cells are built progressively deeper (Figure 4a).

The hard cemented walls and caps of cells permitted cells to be detected and removed intact from the soil when care was taken. However, as no discrete outer surface of a cell wall could be detected, I believe the female bees must simply impregnate the walls of the cell chamber with some cementing secretion prior to waxing them. Certainly, though, some sections of cell walls were built in, closing off old shafts and cell chambers.

Cells varied markedly in size, internal lengths ranging from 17-28 mm and diameters from 13.0-15.5 mm.

Having completed her cells, a female fills the shaft with loose soil then, three or four centimetres below the entrance, constructs a concave cemented earthen plug, smoothed but not waxed on the upper surface (Figure 4b). She then demolishes the entrance turret by wetting it with liquid from the mouth and biting away particles which she pushes down the shaft (Figure 5b). The nest is then abandoned. As nesting advances, nesting

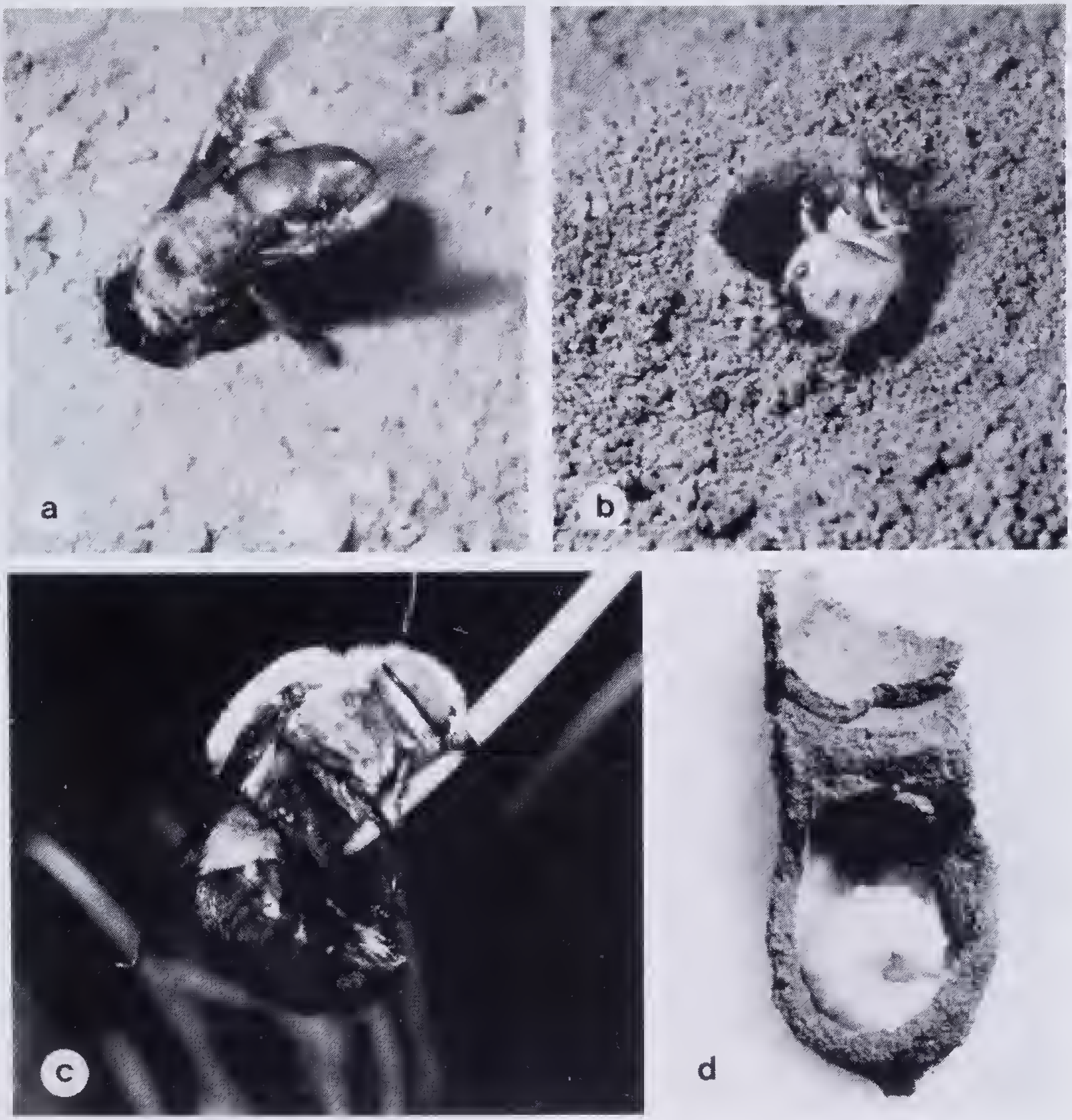

Figure 5 *Amegilla (Asaropoda) dawsoni:* (a) large male at an emergence shaft (a newly emerged virgin female was approaching the surface from within); (b) female demolishing her entrance turret following completion of the nest; (c) male in roosting posture grasping tip of terete leaf with mandibles alone; (d) brood cell opened to show dormant mature larva (note compound cell closure).

sites become littered with the bodies of dead females and I saw no evidence that females complete more than one nest in their lifetime.

Completed plugged nests with only 2 or 3 cells were excavated and no more than 5 fresh cells were associated with a single burrow.

Provisioning

The provision is chiefly liquid and occupies about 2/3 the depth of the cell (Figure 4c). The liquid fraction is clear and watery, apparently consisting of unthickened nectar, and rapidly soaks into the surrounding soil when a cell is cracked. Pollen occurs as a whitish sediment in the lower half of the provision and occasionally as wisps suspended in the upper fraction or floating as dry particles on the surface.

As one open freshly waxed cell was found with a substantial amount of dry pollen in its base, it appears that females accumulate several loads of dry pollen prior to commencing nectar deposition.

A thick ring of wax occurred at the meniscus of the provision in freshly closed cells (Figure 4c). Evidently, when a female coats the inside of the cell cap with wax she applies it in a liquid form so copiously that some of it flows down the cell walls and contacts the provision.

Immature stages

The slightly bowed egg, measuring *ca.* 4.5 mm long, rests in the surface of the provision on its ends, making no contact in the middle (Figure 4c).

The first instar larva also floats and feeds on the surface of the provision. Later, when most of the liquid fraction of the provision has been consumed and the larva has grown considerably, it lies on its side on the semi-solid pollen in the base of the cell. When all of the provision has been consumed, the near mature larva begins eating the wax lining of the cell walls. This activity was observed directly on opened cells in the laboratory. Additionally, it was noted that cells containing mature defaecating or post-defaecating larvae had no wax ring nor any wax lining and their walls readily absorbed drops of water placed on them.

Larval faecal material is deposited over the cell walls, usually thinly and more or less uniformly but occasionally as vertical streaks or discrete faeces. The cell cap and the upper fifth of the cell walls remain free of faecal material. In old cells, the pastel green faecal layer is usually lightly mouldy and may be peeled away.

No cocoon is spun and the mature defaecated larva curls into a C-shape, orientated vertically with its anterior end uppermost and becomes dormant (Figure 5d). How long larvae normally remain dormant was not determined but at least in some instances exceeds 12 months. During excavation of an active nesting area at Meedo Station in August 1980 I encountered numerous old cells containing mature larvae (but no pupae) amongst the freshly completed ones. Further excavation at the same site the following May produced 50 dormant mature larvae (but no other life stages). The larvae were returned to the laboratory in Perth where they were kept in their cells or in glass vials. Four pupated by June. The remainder failed to develop despite various attempts to break diapause by wetting their cells, refrigerating them for a month, or both. Although some died, turning dark brown and shrivelling, 25 survived for 8 years, becoming gradually more flaccid, and a few (in very flaccid condition) for 10 years.

Pupae were found in cells at Carnarvon in May and pharate adults in the first week of June, 1983, by Athol Douglas (personal communication) who also noted that most cells he examined at that time contained dormant larvae.

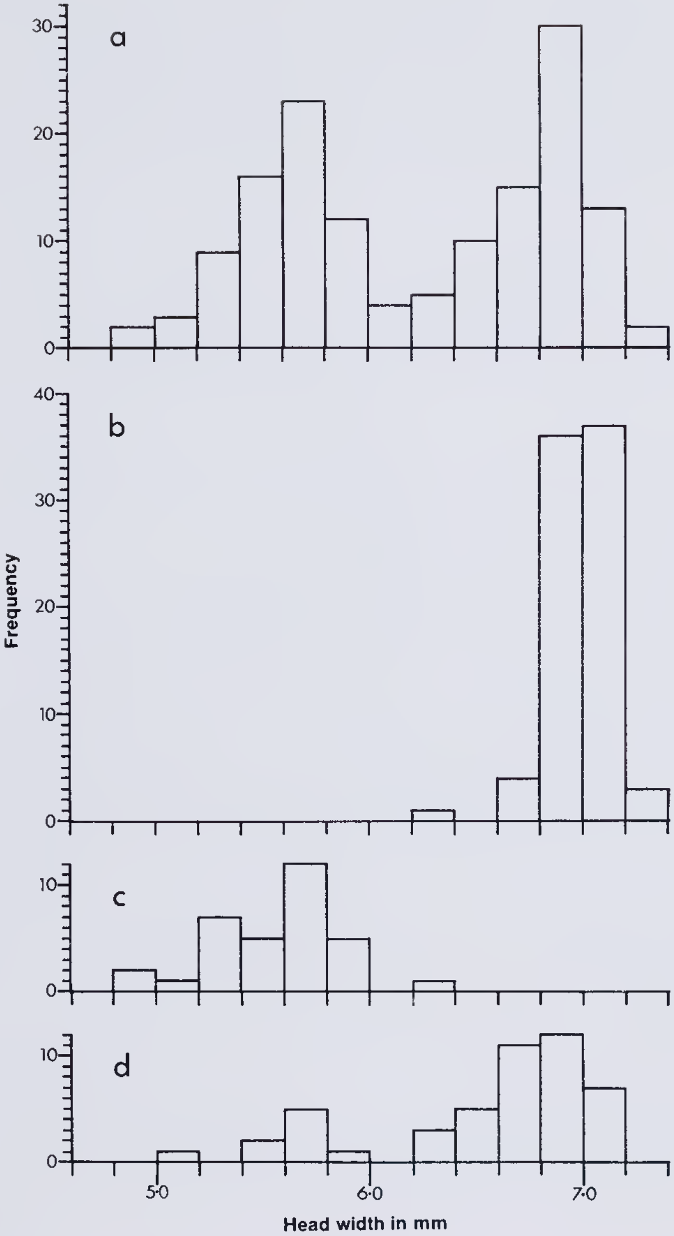

Figure 6 Size/frequency distributions of adults of *Amegilla (Asaropoda) dawsoni* based on head widths: (a) males and (b) females in pinned collection of the W.A. Museum; (c, d) males collected randomly at Meeberrie Station on 27 August 1988 while (c) patrolling flowers of *Eremophila fraseri* and (d) patrolling a nesting area.

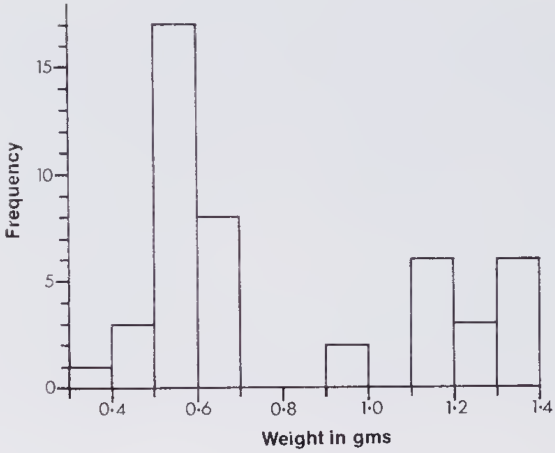

Figure 7 Weight/frequency distribution of 46 diapausing larvae of *Amegilla (Asaropoda) dawsoni* taken from brood cells at Meedo Station in May 1981.

Adult behaviour

Females

Nesting females roosted in the lower ends of their burrows overnight, the burrows remaining unplugged.

Flight activity commenced just prior to sunrise and continued throughout the day, beginning to trail off at sunset and ceasing within about 30 min. of it. Weather conditions do not seem to exert as much influence on flight activity as in most other bees for traffic at nesting areas was observed to commence in the early morning in temperatures as low as 7°C and in drizzling rain following overnight downpours that partly submerged some of the nesting aggregation.

Females departed swiftly from burrows without circling or after making only one circuit. On returning to the nesting area females often flew in a slow meandering flight, sometimes touching down hesitantly on one or more turrets before locating and plunging into their own.

Females approaching the nest entrance from within the burrow usually responded to the presence of an observer by emitting a shrill chirp (produced by vibration of the flight muscles and wings) and ducked back down the shaft, sometimes repeating this manoeuvre several times before emerging and flying off.

An observer arriving at an active nesting site is soon surrounded from head to feet by many loudly buzzing bees of both sexes. However, they simply mill about and do not attack and, providing the observer remains still, eventually lose interest and return to their usual activities. On one occasion, a corvid (crow or raven) was observed to glide down over a large nesting aggregation and immediately was pursued out of the area by a large swarm of bees.

At most active nesting aggregations there was at least one female flying from burrow to burrow as if lost. These females, which carried no pollen, frequently entered open turreted burrows and spent several minutes within before emerging and flying to another nearby burrow. Occasionally, they encountered nest occupants and struggles accompanied by loud buzzing ensued. Such encounters ended with one female (apparently the intruder) being evicted. Perhaps these wanderers are young females in search of abandoned or otherwise unoccupied burrows to usurp for their own use. If usurpers extend the work of foundresses, this could explain the exceptionally tall turrets occasionally observed in nesting aggregations.

Males

Many males were observed to spend the night roosting on foliage, usually that of shrubs with stiff, terete leaves. Each male grasps the tip of a leaf with its mandibles alone, the legs being folded beneath the body, and faces the leaf base (Figure 5c). Males were observed roosting solitarily or congregated on one shrub (each attached to a separate leaf). In fine sunny conditions males left their roosts about 1.5-2.0 hrs after sunrise. Other males appeared to overnight in burrows.

Males were observed to frequent both nesting areas and the forage plants. At nesting areas, they flew slowly over the ground (within 15 cm of the surface) following meandering paths and paid particular attention to holes without turrets (i.e. likely emergence holes) which they frequently inspected and sometimes entered briefly. They paid no attention to turreted burrows or females entering or leaving them.

Occasionally several males were observed to converge about a hole and, on such occasions, much chasing and jostling occurred with the largest male usually being successful in commandeering the entrance. The dominant male either hovered over the entrance or stood facing it with its antennae directed down the shaft (Figure 5a) and would enter the burrow periodically for a few seconds before backing out again. Evidently such behaviour was elicited by the approach of a virgin female towards the entrance from within. On two occasions females were observed to emerge from such burrows and were pounced on by the waiting males forming a buzzing ball which tumbled about on the ground. Within a few seconds, one male (the largest) succeeded in coupling with the female and the other males gradually dispersed. The female, mounted by the successful male, ran over the ground for some metres until the pair were hidden beneath some small plants and there coupling lasted for about two minutes. Mating was accompanied by convulsive twitches at the rate of about one every two seconds. Twitches appeared to be produced by sudden flexions of the male's hind legs which wrapped around the abdomen of the female and were accompanied by downward thrusts of his antennae.

At Meeberrie Station where males were marked for individual recognition, some very large males were found to remain at individual emergence holes over periods of hours. This close attention to emergence holes continued beyond sunset with increasingly longer stays down the shafts and I suspect (but did not confirm) that the males remained in the shafts overnight.

Cursory observations suggesting that males patrolling forage plants were generally of a smaller size class than those patrolling nesting areas were confirmed by random samples of males taken at Meeberrie Station on 27 August 1988 (Figure 6c, d). Perhaps small males, unable to compete successfully with large males for access to virgin females at the nest sites, adopt the alternative strategy of seeking mates at the forage plants. Large males probably visit flowers only to feed.

Associated organisms

Three old cells each contained a vacated silken cocoon consistent in form with those of Mutillidae. Each cocoon was of complex structure (Figure 4e): an inner, ovoid, multilayered cocoon 'proper' was suspended in a network of threads within a woven outer involucrum. The latter fitted flush against the side walls of the cell but formed a septum above the empty lower fourth of the cell. Two females of *Ephutomorpha* species were observed inspecting active burrows at one nesting site.

Many old cells excavated contained clusters of empty fly puparia. Several puparia were usually grouped together in each cell with their long axes vertical and occurred in the lower parts of closed cells or just above the constricted necks of open cells (Figure 4f, g). Two newly emerged adults of *Miltogramma rectangularis* Malloch (Diptera: Sarcophagidae) were found crawling across the ground at two sites where young bees were emerging but new nests were not yet being established and the flies were also commonly seen sitting on the ground or on turrets at active nesting sites. It is likely that the puparia observed were of this species. Within a few minutes of placing live flies into glass vials, I observed minute white maggots crawling vigorously over the vial walls. This indicates that the flies deposit early instar larvae rather than eggs into host cells.

Two maggots emerged from the neck of a dead but supple female bee collected from an active nesting site on Meedo Station on 30 August. One pupated after 12 days and, three weeks later, produced and adult fly identified as *Taylorimyia iota* (J. & T.) (Diptera: Sarcophagidae) (Ian Mackerras, pers. comm.). Numerous freshly dead female bees were collected and dissected subsequently at nesting sites but no further maggots or flies were encountered.

Amegilla (Asaropoda) species 2

Adults and nests of this species were observed at the Kennedy Range, 16 km WSW of Lyons River homestead, approximately 150 km inland from Carnarvon, W.A., on 30 August-1 September 1980.

The noisy patrolling activity of males betrayed the presence of six nest burrows in the level earthen floor of a shallow rock hollow at the base of a north-facing cliff. Each nest entrance was surmounted by a short turret. Some turrets were more or less vertical while the remainder exhibited varying degrees of curvature (Figure 4k-m). Females occasionally entered or left the burrows (one was captured as a WAM voucher specimen).

More burrows were located in a bare clay flat at the foot of the range pediment. Eight burrows were aggregated within about 1 m^2 while about as many again were found singly or in pairs further afield. A few nests were under construction and each had a curved entrance turret like those in the rock hollow. Most, however, had been closed and their turrets had been partially or wholly demolished.

One female returning to her nest became aware of a satellite fly following her and gave chase around and around several times before entering her nest. The fly (possibly a miltogrammine) was not captured.

One female was observed in the process of demolishing her turret. Periodically she brushed and wet it with her glossa, bit pieces off with her mandibles and thrust them behind her into the shaft entrance. This female was collected and her nest excavated. Her turret had curved 90^0, opening onto the ground surface (cf Figure 4k), and had an internal diameter of 10 mm as did the top of the shaft.

The vertical shaft was closed just below the ground surface by a cemented concave earthen plug below which, to a depth of 12 cm, it was loosely filled with soil. Beneath the loose fill was a 2 cm long barricade of cemented earth and a cluster of five sealed brood cells (Figure 4i, j). The cells were more or less vertical, side by side with their caps slightly overlapping.

The cell cluster was removed intact, except that two cells were accidentally cracked and their liquid provisions immediately soaked into the soil. The cells were opened and inspected in the laboratory on 10 September. The two damaged cells each contained an egg on the pollen residue from the provisions. One intact cell contained unused provision with a flaccid egg on its surface and two others contained larvae, one fully fed and the other about 3/4 grown and curled on the semisolid pollen provision in the base of its cell. Contaminants in two cells were the dismembered remains of several small black *Iridomyrmex* ants and moth wing scales contaminated another.

Brood cell architecture and provisions were virtually indistinguishable from those of *A. dawsoni.* Size alone could distinguish the cells of this species: internal length 14.5-15.0 mm, diameter 9.5-10.5 mm.

The two larvae found were observed biting at the wax lining of their cells and appeared to be ingesting it. The wax ring (which occurred at the level of the liquid provision surface in each freshly provisioned cell) had been virtually demolished in both cases.

The larvae were kept in their cells in capped vials at room temperature in Perth. On 22 September 1980, both were defaecating and smearing the faeces over their cell walls. This activity had ceased by 6 October. One pupated shortly before 12 October 1981 and gave rise to an adult female by 6 November. The other gave rise to an adult male on 5 September 1983, three years after nest construction.

Discussion

Only a very limited comparison may be made at this time between the biologies of the two *Asaropoda* species forming the subject of this paper and other members of the Anthophorini due to the paucity of information available. Discussion is made all the more difficult by the very unsatisfactory state of the alpha-level taxonomy of the Australian anthophorines.

Asaropoda species vary markedly in their phenology, doubtless as a consequence of the variety of climatic regimes in which they occur and the different flowering phenologies of their preferred food plants. *A. dawsoni*, a univoltine species with a winter/early spring flight season, contrasts with *A. ?bombiformis* which is bivoltine and has an early summer — late autumn flight season (Cardale 1968b).

Pronounced differences in preferred nesting sites are evident amongst *Amegilla* species. While *A. dawsoni* and Species 2 select flat, bare, clay soils as nesting sites, *A. ?bombiformis* and *A. pulchra* nests are recorded from sheltered, sloping or vertical soil beneath buildings (Michener 1960, Cardale 1968a, b) or in termite nests in tree hollows (author's unpublished observations). *A. pulchra* (or closely related species) also utilizes adobe walls, soft mortar, vacated nests of mud-dauber wasps (Sphecinae, Eumeninae) and consolidated clay soils in the floors of caves (Rayment 1944 and author's unpublished observations).

Asaropoda females make much use of liquid during nest construction, applying it freely from the mouth. Brooks (1983) has recorded how females of *Anthophora bomboides* may make up to 80 trips a day to collect water. However, *Amegilla* females are not known to visit water (nor are any other solitary bees in Australia) and I suspect they use nectar to wet the soil.

Brooks (1983) described attempted nest usurpation behaviour in females of *Anthophora bomboides* and regarded it as a regular phenomenon which ensured that most abandoned incomplete nests were quickly reoccupied. As almost identical behaviour was observed in *Am. dawsoni*, it may be a trait of the Anthophorini.

Communal aggressive behaviour towards intruders (without stinging) at nesting aggregations and individual female aggression towards parasites as recorded for *Asaropoda* has also been recorded for *Anthophora edwardsii* by Thorp (1969).

Entrance turrets are evidently characteristic of some but not all species of *Asaropoda*. They were a constant feature of the nests of *A. dawsoni* and *A.* species 2 and Rayment (1951) recorded one at a nest of *A. rickae* (Rayment). However, no turrets were noted by Cardale (1968b) nor Rayment (1935, 1951) for *A. ?bombiformis* and *A. rufa* nests, respectively. Turrets are unknown for *Zonamegilla* but are constructed by some species of *Anthophora* (Brooks 1983; Thorp 1969).

On the flat, exposed areas where *A. dawsoni* habitually nest, the turrets would serve to prevent wind-blown debris and especially excavated soil from entering shafts and possibly contaminating the provisions of open cells.

Below ground, the nests of *A. dawsoni* and Species 2 are generally very similar and do not differ dramatically from nests of other Anthophorini. Perhaps the most distinctive feature of *Asaropoda* nests is the complexity of the cell closure. Each cell of *A. dawsoni* has three cemented closures (except when built in series): the cell cap, the supracap and a rough plug sealing the access burrow off from the shaft. The supracap (a cemented, concave, earthen plug, smoothed on its upper concave surface) and called the "false cap" by Cardale (1968b) is a constant feature of *Asaropoda* cells. I do not think the supracap can be equated to the "antecap" of *Anthophora* (Brooks 1983) which appears to be the homologue of the "barricade" of *Amegilla pulchra* (Cardale 1968a) and seals off the bottom of the shaft after the last cell has been closed. However, Thorp (1969) recorded that "secondary caps", resembling the bottoms of smooth but unlined cells, were present above cell caps in fewer than 10% of nests of *Anthophora edwardsii.*

The sub-surface shaft plugs of *A. dawsoni* and Species 2 appear to have no equivalent in *A. pulchra* nests but may be the homologue of the plugs constructed in the entrances of shafts by *Anthophora bomboides* Kirby (Brooks 1983).

The range of forage plants utilized by *A. dawsoni* is very restricted compared with the great range of plants utilized by *A. pulchra.* However, the four genera visited are not closely related. Sonication (buzzing) of poricidal anthers as observed for females of *A. dawsoni* is a common and well documented technique used by bees to obtain pollen (Buchmann 1983). Anderson and Symon (1988) recorded three *Amegilla* species (none in *Asaropoda*) sonicating flowers of various *Solanum species.*

Provisions of Anthophorini are generally described as a sour-smelling semiliquid paste or batter. In *Amegilla pulchra,* the pollen and honey are uniformly mixed and usually form a runny opaque cream or yellowish paste. Those of *A. ?bombiformis* were described as being "of thicker consistency and more pleasant odour" by Cardale (1968b). Rayment (1944) reported that females of the '*Anthophora zonata* group' (= *Amegilla (Zonamegilla)* and *A. (Notomegilla)* species) often sit in the sun to 'ripen' (i.e. thicken) the nectar and he described the regurgitation process. However, similar behaviour was not observed for *A. dawsoni* and Species 2 whose provisions are quite different in having a substantial clear watery fraction above a pollen sediment. Consequently, I suspect that they provision with unthickened nectar.

The ingestion of the wax lining of brood cells by larvae of *A. dawsoni* and Species 2 is of interest as similar behaviour was reported for the American species, *Anthophora abrupta* Say by Norden *et al* (1980). These authors suggested that wax-ingestion was a highly specialized behaviour that did not occur in some other species of *Anthophora.* Given also that it does not occur in *Amegilla (Zonamegilla) pulchra,* the behaviour has probably arisen independently in *Anthophora* and *Asaropoda* species.

Amongst the common enemies of Anthophorini are cuckoo bees of the tribe Melectini. Several species of *Thyreus* occur widely in Australia and *T. lugubris* (Smith) has been reared from a cell of *Amegilla ?bombiformis* Cardale (1968c). However, *A. dawsoni* appears to be free from *Thyreus* attack and there is no species of *Thyreus* approximating it in body size.

As Cardale (1968c) observed for *A. pulchra,* sarcophagid flies of the genus *Miltogramma* appear to be the prime enemy of *A. dawsoni.* Given the presence of clusters of puparia in the necks of some uncapped cells, the flies must breed on the hosts' provisions rather than on host immatures, a conclusion consistent with Cardale's observations and the prevailing picture of Miltogrammini as cleptoparasites (Spofford *et al* 1989). The fly reared from an adult female, *Taylorimyia iota,* is recorded as an internal parasite of Orthoptera (Key 1970).

An interesting question is how the delicate *Miltogramma* adults escape from the host's capped brood cells and penetrate the complex cemented cell closures. Cardale (1968c) observed perforations in the cell caps of *A. pulchra* from which flies had emerged but did not record how they were made.

Male dimorphism and associated behavioural differences as observed in *A. dawsoni* are not known amongst other Anthophorini. However, rather similar variation and behavioural differences are reported for some species of the American genus *Centris* (Anthophorinae: Centridini) by Alcock *et al* (1976, 1977) and Chemsak (1985). Males of *C. pallida* Fox vary markedly in size and the size/frequency distribution of males in a population is strongly skewed with small size classes predominating. Like *A. dawsoni*, the *Centris* species are large, robust, hairy bees and often nest in huge aggregations.

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A new species of *Rattus* from the mountains of West Flores, Indonesia

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Abstract

Rattus hainaldi sp. nov. is described from Gunung Ranakah near Ruteng, West Flores, from a single adult male collected from lower montane rainforest at *ca.* 1300 m altitude. A juvenile male from nearby Ranamese is tentatively referred to this species.

This is the first endemic rodent species in Nusa Tenggara placed unequivocally in *Rattus*.

Introduction

Musser (1981) notes that species of native *Rattus* seem to be present on all the archipelagos and the continent east of the Sunda Shelf, except for the Lesser Sunda Islands (Nusa Tenggara). He writes further (p. 168) that "whether this pattern is real or whether it simply reflects insufficient biological exploration on Nusa Tenggara is important to determine in order to reveal the source of native *Rattus* in the Moluccas, the New Guinea area, and the Australian region". He considers that the *Rattus* known from Nusa Tenggara (*R. exulans*, *R. argentiventer*, *R. norvegicus* and *R. rattus*) are introduced human commensals, but allows (p. 166) the possibility that one of the two former species may prove to be native. Recently, Kitchener *et al.* (1991) described a new species of rodent from south west Timor, Nusa Tenggara, which they tentatively placed in *Rattus*.

As part of a biological survey of Nusa Tenggara by the Western Australian Museum and the Museum Zoologicum Bogoriense, initiated in 1987 and still continuing, two expeditions have been made to Flores I. (October 1989 and May 1990). In the first of these expeditions, to Central and East Flores, a specimen of a long-nosed murid, *Paulamys* cf. *P. naso*, initially known only from Holocene and Pleistocene fossils (Musser 1981; Musser *et al.* 1986) was collected in mountainous country on Gunung Kelimutu (Kitchener *et al.* 1991). On the second expedition, to West Flores, a single specimen of a distinct small, long-tailed *Rattus* was collected near Desa Longko, Manggarai District (Figure 1). This specimen is herein described as a new species. A juvenile *Rattus* collected from nearby Ranamese is tentatively referred to this species.

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Figure 1: Location in Nusa Tenggara of type locality of *Rattus hainaldi* (arrowed).

Methodology

Measurements, in mm, and descriptions

External measurements were recorded from *R. hainaldi* holotype and WAM M33039 and *R. exulans* following their preservation in 70% ethanol, weight was taken in the field prior to fixation. Cranial and dental measurements were taken with dial calipers to the nearest tenth millimetre. Measurement points are mostly illustrated in Musser (1970) and described in Musser and Newcomb (1983). Measurements not in Musser (1970) are: nasal projection length, length between the distal tip of nasal and the anterior edge of premaxilla beneath nasal; condyle to dorsal incisor base, length from posterior edge of dentary condyle to anterior point of dentary between incisors on dorsal aspect; M_1 to dorsal incisor base, length from anterior face of M_1 to anterior point of dentary between incisors on dorsal aspect; dentary height at M_1, height of dentary at middle of M_1 anterior labial cusp perpendicular to dentary ventral edge. Description of occlusal structure of teeth follows Musser and Newcomb (1983). Terminology of cranial bones and foramina is from Musser (1981).

Colour

Pelage and skin colour where they follow Ridgway (1912) are capitalized.

Systematics

Rattus hainaldi sp. nov.

(Table 1, Figures 2-7)

Holotype

Western Australian Museum, WAM M32877*, adult male, weight 81 gm, body fixed in 10% formalin, preserved in 70% ethanol; skull and dentaries separate; collected in commercial 'break-back' trap on 8 May 1990 by Dr Chris Watts.

Type locality

On a steep slope of the active volcano Gunung Ranakah, at an altitude *ca.* 1300 m (Figure 2), above KampongRobo, Desa Longko, 8 km SSE Ruteng, W. Flores (8°35'S, 120°33'E). The vegetation at this site is, following the classification of Whitmore (1984), lowland montane forest and is described by Ron Johnstone (pers. comm.) as "tall to moderately tall (15-35 m) montane forest. Canopy and emergent trees (some with lichen 'beards') included the following genera: *Terminalia, Garuga, Ficus, Celtis, Melia* and *Albizia* (Figure 3). Lower strata consisted mostly of slender trees and shrubs and some vines. The ground had litter that was sparse on slopes but dense in gullies with occasional ferns and some moss. Forest edges and where trees had been felled were overgrown with a white flowering composite 2-3 m high".

Diagnosis

Rattus hainaldi is distinguished from all other South East Asian species of *Rattus* described in the literature by a combination of: small body; tail considerably longer than snout to vent length (161 v. 133), bicoloured with whitish undersurface; dorsal pelage orange brown flecked with dark brown; ventral pelage creamy white but on chest and

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*Final disposition will be the collections of the Museum Zoologicum Bogoriense, Bogor.

Figure 2: Gunung Ranaka, near Ruteng, Flores I., the type locality of *Rattus hainaldi* is on slopes in foreground. Photo: R.A. How.

particularly more posteriorly flecked with pale grey; pelage soft, with long guard hairs on dorsum and flanks; skull small, greatest skull length 35.1, and generally slight; postorbital and temporal ridges low; incisive foramen moderately short (2.4) and broad; bulla moderate, averaging 18 percent of greatest skull length, and rostrum short and moderately broad.

Of the recorded *Rattus* species of Flores (*R. exulans, R. argentiventer, R. rattus* and *R. norvegicus*) it could only be confused with *R. exulans*. It differs from Floresian *Rattus exulans* in being generally larger (see Table 1, and Figures 5, 6) and more robust; the anterodorsal edge of zygomatic plate projects less anteriorly; nasals blunt rather than angular, terminating closer to anterior edge of premaxilla; rostrum less curved anteriorly in lateral profile; interparietal wider and narrower; incisive foramen shorter relative to palatal length 0.32 *v.* 0.37 (0.35-0.39); postorbital and temporal ridges less pronounced, terminate before sharp ventral inflection of parietal/squamosal suture rather than reaching to that inflection and occasionally posterior to it; ventral masseteric ridge stronger and more sharply curved dorsally; dentary deeper, ratio of dentary height below M_1 to dentary length 0.29 *v.* 0.25 (0.23-0.27); pelage softer with numerous long guard

Figure 3: Vegetation at trap site of type locality of *Rattus hainaldi*. Photo R.E. Johnstone.

hairs, particularly on back and flanks that are absent in *R.* exulans; feet darker coloured dorsally.

Description

Skull and dentary (Table 1, Figure 4)

Skull small with moderate length rostrum, palatal length 51% of greatest skull length; zygomatic breadth moderately wide (18); nasal short, terminate posterior to orbit, internal anterior edge, slightly inflated anteriorly, distal tip only very slightly rounded; rostrum short and moderately broad; slight dorsal ridges outline interorbital region, originate *ca.* 1 mm posterior to frontal — nasal suture and posteriorly traverse dorsal margin of postorbital and temporal regions, highest in postorbital region and decrease in size immediately posterior to frontal — parietal suture, very slight posterior to point of downward inflection of parietal-squamosal suture; interparietal large; between slight temporal ridge and zygomatic root braincase slopes slightly and gently outwards; postglenoid vacuity moderately spacious; zygomatic plate anterior edge slightly curved forward, its anterodorsal inflection well posterior to its most anteroventral point; incisive

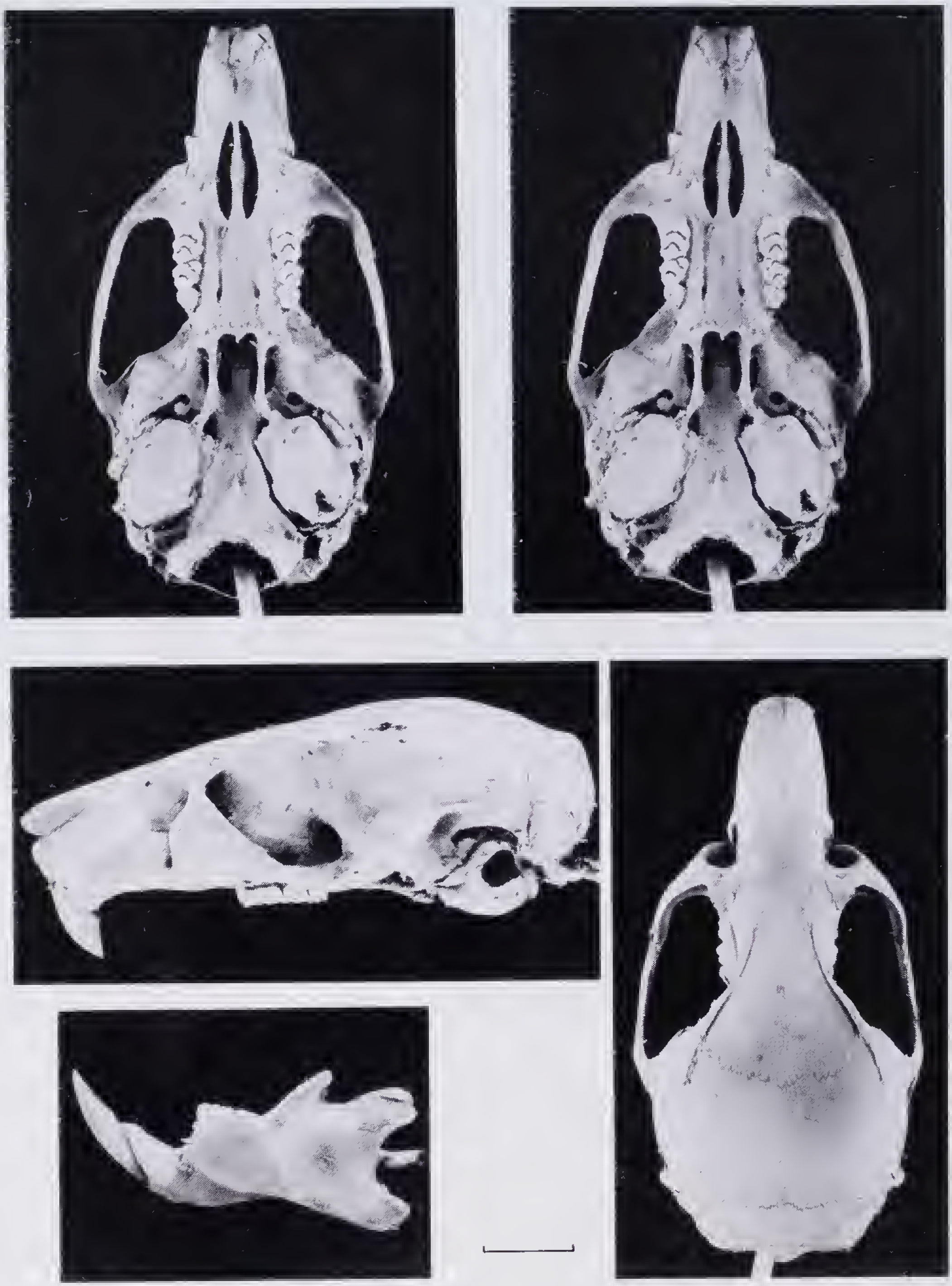

Figure 4: Skull and mandible of *Rattus hainaldi*; ventral view as stereopairs. Scale line, 5 mm.

Figure 5: Dorsal (A, B) and ventral (A^1, B^1) views of A,A^1 — *Rattus hainaldi* holotype; B,B^1 — *R. exulans,* WAM M32609 (Flores). Scale line, 5 mm.

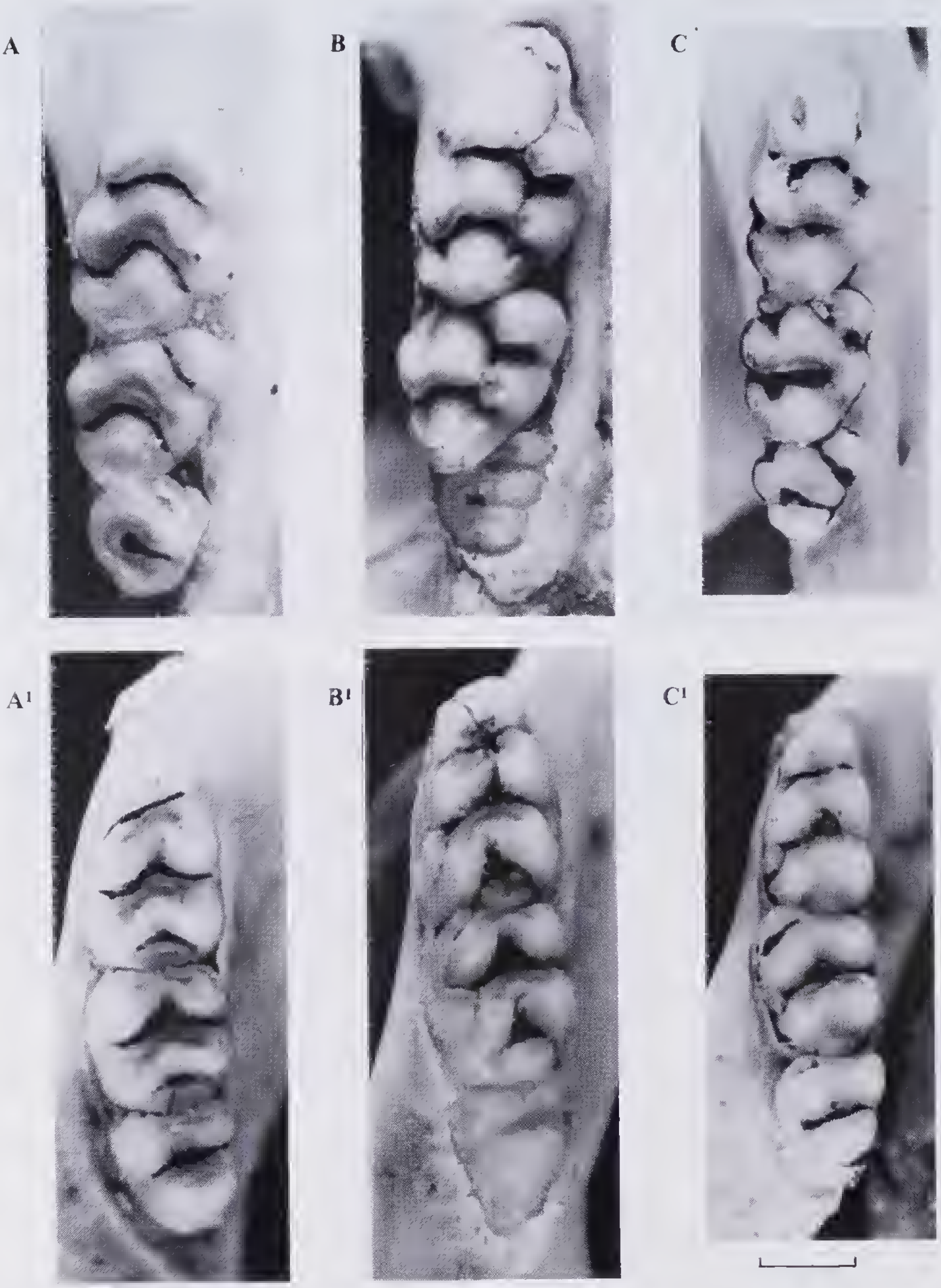

Figure 6: Left hand side upper (A-C) and lower (A^1-C^1) molar rows of: A,A^1 — *Rattus hainaldi* holotype, B,B^1 — *R.* sp. cf. *R. hainaldi* WAM M33039 and C,C^1 *R. exulans ephippium*, WAM M32609 (Flores I.). Scale line, 1 mm.

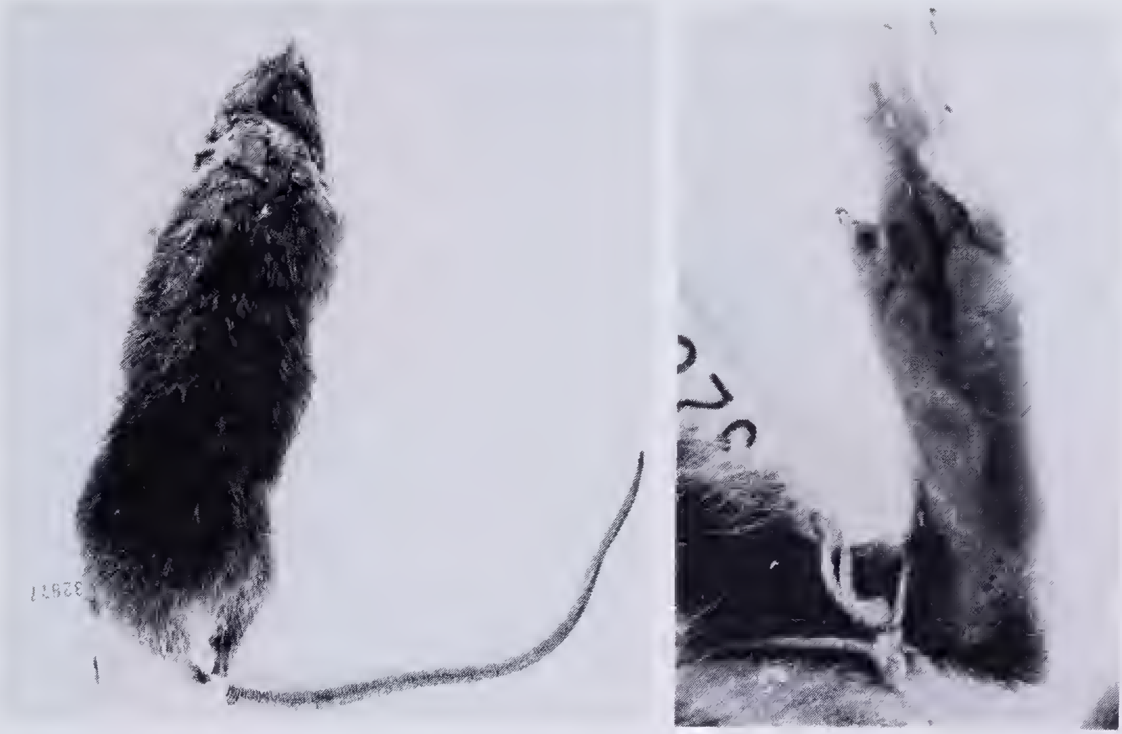

Figure 7: Alcohol preserved specimen of carcase and pes of *Rattus hainaldi* holotype.

foramen short, moderately broad, terminate posteriorly in line level with M^1 anterior face; maxilla — premaxilla suture located anterior of mid point of incisive foramen lateral edge; mesopterygoid fossa and palatal bridge moderately wide; palatal bridge extends *ca.* 1.2 posterior to M^3 posterior edge with short median spine; ventral surface of palatal bridge mostly smooth with two lateral and shallow palatal grooves; posterior palatine foramen small, oval, in line with M^2 posterior edge, palate pitted with *ca.* 32 tiny vascular foramina which are concentrated in rugose area at posterior edge; pterygoid fossa moderately wide and deep; foramen ovale small, oval, and slightly excavated; sphenopalatine vacuity long, extends to pterygoid process mid length; sphenopterygoid vacuity large; sphenopalatine foramen located dorsal to M^2, well anterior to small suboval dorsal palatine foramen

Dentary robust, below M_1 deep, anterior to M_1 short, robust and moderately curved; masseteric ridge strong and sharply curved dorsally.

Dentition (Table 1, Figure 6)

Upper incisors opisthodont, anterior surface with brown-orange enamel; lower incisors with only a trace of pale orange enamel on anterior face. Occlusal pattern of upper and lower incisors in *R. hainaldi* holotype and WAM M33039 are shown in Figure 6; toothrows of moderate length in relation to palatal bridge. General morphology of molars and their root pattern similar to those in many species of *Rattus*

Table 1: Skull, dentary and teeth measurements (in mm) for *Rattus hainaldi* holotype, *R.* sp. cf. *R. hainaldi* WAM M33039 and *R. exulans* from Flores I. The latter two species as mean ± standard deviation (range), and weight (gm).

	R. hainaldi		*R. exulans* (Flores)	
	Holotype	Referred juvenile	N = 10♂♂	
Measurement/weight				
Weight (gm)	81	22.6	49.2 ± 11.2	(31 — 72)
Snout to vent length	133.4	81.2	109.5 ± 10.4	(93.8 — 123.5)
Tail length	161.1	129.2	130.2 ± 13.9	(101.9 — 146.4)
Hind foot length	29.5	26.6	25.0 ± 1.0	(23.7 — 26.6)
Ear length	21.1	16.9	16.5 ± 15.6	(15.9 — 18.4)
Greatest skull length	35.1	29.1	31.6 ± 1.5	(30.2 — 33.8)
Condylobasal length	32.4	25.8	29.1 ± 1.1	(27.7 — 31.1)
Zygomatic breadth	18.0	13.9	14.8 ± 0.2	(14.2 — 16.0)
Interorbital breadth	5.3	4.6	4.7 ± 0.1	(4.6 — 4.9)
Nasal length	13.2	9.6	11.6 ± 0.8	(10.9 — 12.8)
Nasal breadth	4.3	3.7	3.2 ± 0.2	(3.0 — 3.5)
Nasal projection length	0.1	—	0.8 ± 0.2	(0.6 — 1.0)
Rostrum length	10.7	8.8	9.9 ± 0.5	(9.3 — 10.3)
Rostrum breadth	6.5	4.9	5.4 ± 0.3	(4.9 — 5.9)
Braincase breadth	15.3	13.9	13.3 ± 0.3	(12.6 — 13.7)
Braincase height	10.5	9.9	9.0 ± 0.3	(8.6 — 9.6)
Zygomatic plate breadth	3.5	2.1	3.1 ± 0.2	(2.8 — 3.4)
Interparietal breadth	10.7	10.3	9.5 ± 0.3	(9.1 — 9.9)
Interparietal length	4.0	4.7	4.9 ± 0.3	(4.4 — 5.3)
Breadth across incisor tips	1.9	1.5	1.5 ± 0.1	(1.4 — 1.7)
Diastema length	8.7	6.6	8.3 ± 0.5	(7.6 — 9.1)
Palatal length	18.0	14.6	16.2 ± 0.8	(15.3 — 17.8)
Post palatal length	12.1	9.3	10.6 ± 0.5	(9.9 — 11.3)
Palatal bridge length	6.8	5.8	6.0 ± 0.5	(5.4 — 7.0)
Palatal bridge breadth at M^1	4.0	2.8	3.2 ± 0.3	(2.7 — 3.5)
Palatal bridge breadth at M^3	4.7	—	3.7 ± 0.4	(3.1 — 4.3)
Mesopterygoid fossa breadth	2.4	2.0	2.0 ± 0.1	(1.8 — 2.2)
Incisive foramina length	5.8	4.4	5.9 ± 0.2	(5.7 — 6.2)
Incisive foramina breadth	2.4	1.8	2.2 ± 0.2	(1.9 — 2.5)
Bulla length	6.4	5.6	5.8 ± 0.2	(5.6 — 6.1)
Bulla height	5.7	5.2	5.2 ± 0.2	(4.9 — 5.5)
M$^{1-3}$ length (crown)	5.4	—	5.2 ± 0.2	(5.0 — 5.4)
M$^{1-3}$ length (alveolar)	5.7	—	5.4 ± 0.2	(5.1 — 5.7)
M^1 breadth (crown)	1.7	1.9	1.6 ± 0.1	(1.5 — 1.7)
M^1 breadth (alveolar)	1.5	1.8	1.4 ± 0.1	(1.3 — 1.6)
M^2 breadth (crown)	1.6	1.8	1.5 ± 0.1	(1.4 — 1.7)
M^2 breadth (alveolar)	1.5	1.8	1.3 ± 0.1	(1.2 — 1.6)
M^3 breadth (crown)	1.2	—	1.2 ± 0.1	(1.1 — 1.2)
M^3 breadth (alveolar)	1.2	—	1.0 ± 0.1	(0.9 — 1.1)
M$_{1-3}$ length (crown)	5.5	—	4.9 ± 0.2	(4.6 — 5.2)
Condyle to dorsal incisor base	18.9	15.7	17.2 ± 0.9	(16.3 — 18.8)
M^1 to dorsal incisor base	5.2	4.8	4.9 ± 0.3	(4.3 — 5.4)
Dentary height at M$_1$	5.4	4.1	4.3 ± 0.2	(4.0 — 4.5)

(Musser and Newcomb 1983), particularly to *R. exulans ephippium* (Figure 6). Upper molar labial cusps more developed than their lingual cusps; M^2 with t3 barely perceptible; M^{1-2} with posterior cingulum vestigial; M_1 anterior lingual and labial cusps subequal.

Pelage and skin (Figure 7)

Fur soft and moderately long, on dorsum hairs 10-11 long; on flanks *ca.* 13 long and on ventral surfaces *ca.* 8 long; scattered throughout dorsum are numerous guard hairs which range in length from 13 behind shoulders to up to 35 on lower back and flanks. These guard hairs creamy white at base and tipped with Drab. On lower back and flanks these hairs tipped with creamy white. Predominant colour of dorsal surface Clay Color (orange brown) flecked with Hair Brown (dark brown); on flanks this merges gradually into Cream Buff and to Pale Smoke Gray (pale grey) on inside of arms and legs and to creamy white on throat, chest and abdomen; chest and abdomen strongly flecked with a light grey. Scrotum creamy white; over much of body basal hair colour Neutral Gray (blue grey) but on dorsum a darker Deep Gray.

Hair on fingers white, reaches tip of claws, dorsal and palmar surface of manus Pale Olive Buff to White, flecked at base with Drab. Undersurface of manus Cream Buff. Hairs on distal phalanx of toes white, reach to just in front of claw; plantar surface of pes Lilac Gray with pads Cream Buff, dorsal surface creamy white internally but mostly Light Drab.

Ears moderately long (21.5), smoothly rounded and thinly covered with short Drab hairs.

Tail long (161.1), 121% of snout to vent length; basal one-third with 10 scales/cm, middle one-third 12 scales/cm and distal one-third 16 scales/cm; dorsal skin colour Drab, ventrally Pale Smoke Gray to almost White at base; dorsal hairs Drab; ventral hairs: at basal 2/5 white and 2 long, middle 2/5 Pale Smoke Gray and *ca.* 3 long, distal 1/5 increasingly Drab, *ca.* 4.5 long, distal hairs Drab, 6 long.

Vibrissae

Forearm with: 6 white ulnar carpals *ca.* 11 long; 3 white medial antebrachials *ca.* 9 long; and 2 white anconeals *ca.* 10 long. Each side of face with: numerous long (up to 60) mysticials, these blackish dorsally and much shorter *(ca.* 20) and white ventrally; a single black genal vibrissae, *ca.* 30 long; 6 submentals, *ca.* 6 long; and 6 white interramals, *ca.* 10 long.

Pes and manus (Figure 7)

Moderately long: pes 29.5, manus 14.8; thumb very short (*ca.* 2) with flat nail. Pes with 6 moderately large pads, smooth with subsurface striae; interdigital pads large, separate, hypothenar pad one-third size and 0.4 posterior to interdigital pad at base of digit V (which has a small oblong, posterolateral accessory pad; thenar pad elongate, 4.7 long).

Figure 8: Vegetation at Ranamese, Flores, site of capture of *Rattus* sp. cf. *R. hainaldi* WAM M33039. Photo D. King.

Remarks

The phylogenetic affinities of *Rattus hainaldi* will have to be determined by comparing its features, both morphological and biochemical, with native *Rattus* like species in the Indo-Australian region.

Etymology

This species is named in memory of the late Mr Hainald, Head, IPTEK, Lembaga Ilmu Pengetahuan Indonesia (LIPI), Jakarta Selatan, for his untiring and gracious efforts to facilitate the bureaucratic aspects of this series of expeditions to Nusa Tenggara.

Tentatively referred specimen

Collection

WAM M33039, juvenile male, weight 22.6 gm, body fixed in 10% formalin, preserved in 70% ethanol; skull and dentaries separate; liver and blood separate, preserved in liquid nitrogen in the field and in an ultra freeze refrigerator at the Western Australian Museum; collected in commercial 'break-back' trap on 27 May 1991 by the authors above Lake Ranamese, at an altitude of 1250 m (8°36′S, 120°34′E), *ca.* 20 km E

Figure 9: *Rattus* sp. cf. *R. hainaldi* WAM M33039 photographed shortly after its capture.
Photo R.E. Johnstone.

Kampong Robo. Vegetation at this site is a low montane forest (Figure 8) with many floristic elements in common with the type locality, but with a considerably denser (up to 15 cm) layer of leaf litter, denser moss and lichen, and a much more abundant fern layer.

Description

This specimen is a juvenile, M^3 not yet erupted above gum line. Its measurements are in Table 1. The shape of its skull, dentary and teeth are shown in Figure 10 and its photo in life in Figure 9. It shares many features with the holotype of *R. hainaldi* but differs as follows: interparietal relatively longer than it is broad 0.46 *v.* 0.37; M^1 with small anterior lingual accessory cusp which is absent in *R. hainaldi*; M_{1-2} posterior cingulum appear slightly more oval even allowing for their reduced wear; M_1 anterior lingual cusp appears relatively larger than its associated labial cusp; M_{1-2} anterior lamella appears to be at a sharper angle to the posterior lamella; M_{1-2} posterior labial cusplets appear much larger. These differences may all be a function of age and wear, but without specimens of intermediate age to examine, we cannot be certain they are conspecific. Certainly the relatively large size of interparietal may be unimportant. The measurement of a large

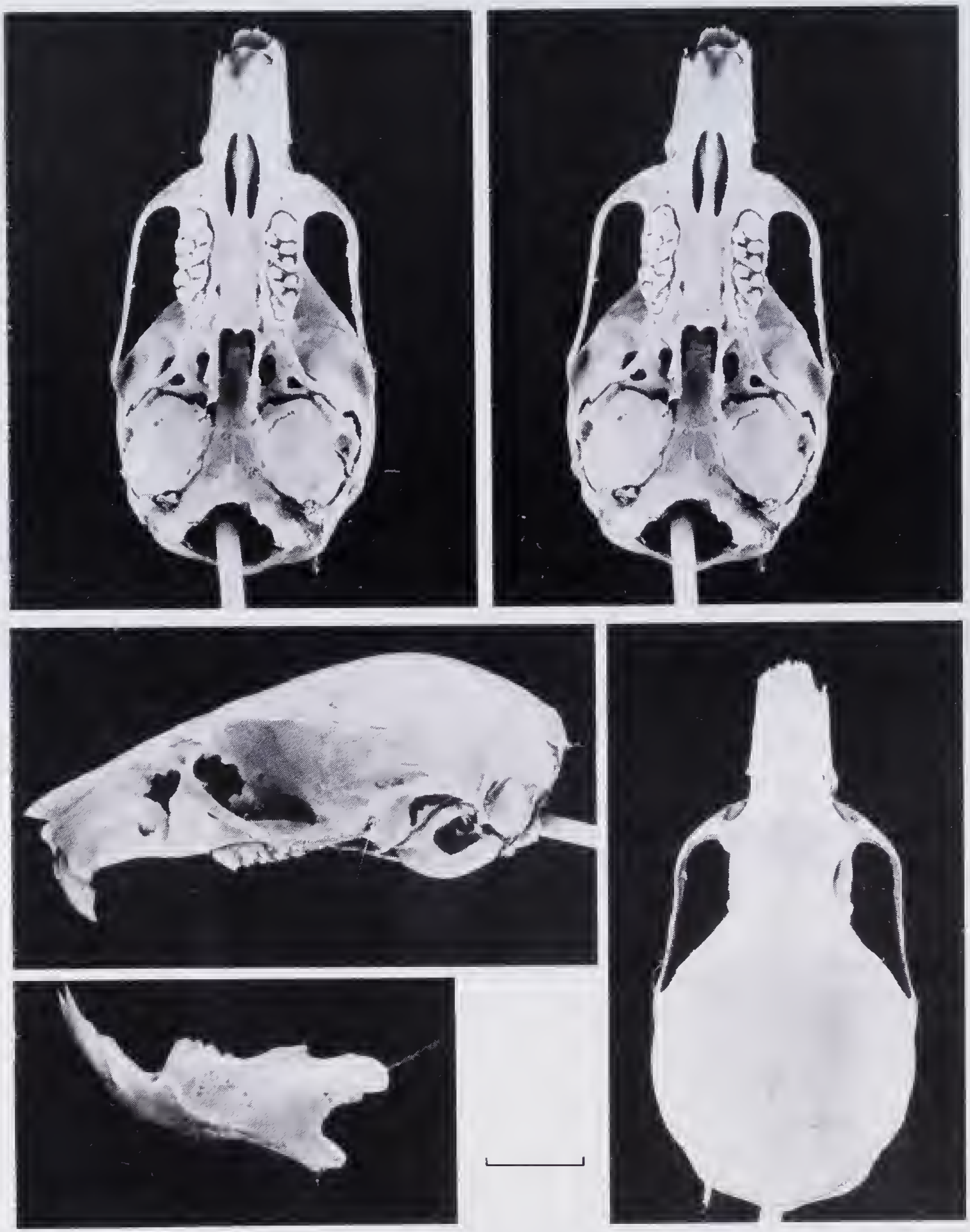

Figure 10: Skull and mandible of *Rattus* sp. cf. *R. hainaldi* WAM M33039; ventral view as steropairs. Scale line, 5 mm.

number of specimens of *R. exulans* in Nusa Tenggara revealed no correlation between age (judged by greatest skull length and molar tooth eruption and wear) and relative size of the interparietal. Frequently, juveniles had considerably larger interparietals than adults.

Colour of pelage of WAM M33039 darker than holotype with Dark Neutral Grey of underfur showing through all over body — this tipped with Chamois (orange drab) on flanks and shoulder and creamy white on abdomen, chest, feet and hands. Tail coloured as for *R. hainaldi* except that ventral surface of tail not as markedly pale. The development of long guard hairs are obvious on back and flanks.

Allozyme elctrophoresis, involving some 35 loci, has been carried out on this referred specimen with reference to *Rattus exulans*, *R. rattus*, *R. argentiventer* (from Flores) and *R. tiomanicus* (from Java). These data, which will be published separately, indicate that this referred specimen is quite distinct genetically from these other species (Dr L. Schmitt, pers. comm.).

Acknowledgement

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Ken Aplin, Western Australian Museum, and Guy Musser, American Museum of Natural History, kindly read and constructively commented on the manuscript. Norah Cooper, Western Australian Museum, prepared all the photographs.

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Anne Nevin, Western Australian Museum, typed the manuscript.

Other specimens measured

Rattus exulans ephippium (all adult males, Flores I.)

Desa Woloara: WAM (M32012, M32013, M32043, M32044, M32046, M32047, M32071, M32081); Desa Daraloeng: WAM M32609; Desa Longko: WAM 32808.

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A provisional review of the genus *Stenogobius* with descriptions of a new subgenus and thirteen new species. (Pisces: Teleostei: Gobiidae).

Ronald E. Watson*

Abstract

The gobiid genus *Stenogobius* Bleeker of the tropical Indo-Pacific is reviewed. The genus includes two subgenera, of which one is described as new, and 23 species, 13 are described as new. The subgenus *Stenogobius* Bleeker is of the Indian Ocean region and extreme western Pacific consisting of eight species included in two species groups; *Insularigobius*, subgen. nov. is known only from islands and consists of 15 species within two species groups. The subgenus *Stenogobius* is represented by *S. gymnopomus* (Bleeker), *S. kenyae* Smith and *S. macropterus* (Duncker) of Indian Ocean drainages and *S. ingeri*, sp. nov. and *S. mekongensis*, sp. nov. of South China Sea drainages all of which form one species group; *S. laterisquamatus* (Weber), *S. ophthalmoporus* (Bleeker) and *S. psilosinionus*, sp. nov. from the extreme western Pacific form the second species group. The subgenus *Insularigobius* is represented by *Stenogobius caudimaculosus*, sp. nov., *S. genivittatus* (Valenciennes), *S. hawaiiensis*, sp. nov., *S. marqueti*, sp. nov., *S. randalli*, sp. nov. and *S. squamosus*, sp. nov. from the central Pacific and *S. alleni*, sp. nov., *S. blokzeyli* (Bleeker), *S. fehlmanni*, sp. nov., *S. hoesei*, sp. nov., *S. kyphosus*, sp. nov., *S. marinus*, sp. nov. and *S. zurstrasseni* (Popta) of the western Pacific form one species group; *S. polyzona* (Bleeker) from the western Indian Ocean and *S. beauforti* (Weber) from northern coastal streams of New Guinea form another distinctive group. The subgenus *Stenogobius* differs from *Insularigobius* by a combination of features which include coloration, counts of fin rays, rows of teeth, scales, color pattern on juveniles, sexual dimorphic and sexual dichromatic differences. Endemism is frequent in *Stenogobius* with species occuring within particular island groups, on particular islands or within discrete geographical regions.

Introduction

The genus *Stenogobius* was first established by Bleeker (1874: 317) and included three subgenera; *Stenogobius*, *Oligolepis*, and *Gnatholepis*. Jordan & Seale (1905: 796) elevated *Gnatholepis* to generic level with their account of *G. deltoides*. *Oligolepis* was elevated to generic level by Koumans (1935: 141) with his account of *O. acutipennis*. Since the time of their original descriptions and subsequent elevation to generic level no questions have been raised over the validity of *Oligolepis* and *Gnatholepis*, but *Stenogobius* has been questioned time and time again. Due to the controversy over the validity of *Stenogobius* it has usually been placed in the genus *Awaous* Valenciennes (1837: 96) or its junior synonym *Chonophorus* Poey (1860: 274).

Stenogobius can be separated from *Awaous* most notably by the following characteristics: Gill rakers detached, rudimentary and not enclosed by elongate papillae; lack of papillae on gill structure, interior of gill cover and on pallate; by having glossohyal bone truncate (somewhat bilobate on *Awaous*); lower jaw terminal (inferior on *Awaous*); pelvic disk not being adherent to body, frenum between pelvic spines without a small fold and pocket near base; caudal fin oblong and somewhat pointed on

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male (always rounded on *Awaous*); sexual dimorphism and dichromatism generally well developed. *Stenogobius* is limited to coastal plains in fresh water to near marine conditions. *Awaous* is occasionally reported from brackish water, but is most often found in fresh water where it is known to ascend streams to relatively high elevations (1000 meters).

In the past, much difficulty has existed over the identification of the species and the numbers that exist. Consequently most forms have been identified either as *Stenogobius genivittatus* (Valenciennes, 1837: 64) or *S. gymnopomus* (Bleeker, 1853a: 270). In Koumans (1953: 35) six species were placed in synonymy with *Stenogobius genivittatus*, of these five are considered valid, four are placed within the subgenus *Insularigobius* and one in the subgenus *Stenogobius*.

During the course of this study it was found that species are differentiated by various proportional measurements and/or by certain zones of squamation. In order to identify these differences it is best to have large samples from specific localities. Two distinctive groups were discovered and *Stenogobius* is herein divided into two subgenera. One of these subgenera has obvious external differences in color or squamation, while the other has very strong sexual dimorphic and dichromatic differences. The genus appears to be represented by 30 species. This study details 23 species of which 13 are described as new. There is considerable difference in the length of species, *Stenogobius alleni*, sp. nov., has so far been recorded with a maximum size of 39.1mm SL; on the other hand the largest, *S. laterisquamatus* (Weber, 1908: 261) was recorded at 197.1mm SL.

The two subgenera of *Stenogobius* are divided into two species groups that are strongly correlated to major geographic regions of the Indian and Pacific Oceans. This observation agrees with the biogeographical interpretation of the Pacific Plate presented by Springer (1982).

Stenogobius shows a high degree of endemism with the island of New Guinea being represented by the largest number of species followed by the Marquesas Islands. On the accounts of new species it could be argued that these may simply represent populations or varieties, especially in *Insularigobius*. This factor was taken into consideration and no clear intergradation could be substantiated. Distinct differences of related forms in close proximity could be found in the Papua New Guinea region and the Marquesas Islands.

Many of the collections from RMNH have proven to be problematic with some lots having more specimens present than just the type material. Through reading original literature attempts have been made to identify probable types. This situation exists with many of the Bleeker types.

Methods

Methods follow those utilized by Watson & Lachner (1985). All lengths of specimens are expressed in standard length (SL) to the nearest tenth of a millimeter (mm). Jaw length was measured from anterior tip of upper jaw to posterior edge of maxilla. Formula for rows of teeth is referred to as follows; two to four rows of teeth present anteriorly and two laterally the formula reads 2-4+2, the first half of the formula always refers to the anterior rows of the teeth and the second portion to the lateral rows. Scales in a horizontal series from upper pectoral base and along the middle of the body laterally to the central hypural base; transverse scale series, count starting at spine of second dorsal fin counting back and down to anal fin. Body depth is measured from anterior base of second dorsal fin to belly, this measurement taken only from males as females vary considerably from gravid to nongravid state.

Abbreviations

Abbreviations used to designate institutions and collections cited follow Leviton et al (1985), except collections formerly of the Laboratory of Ichthyology, the Crown Prince's Palace (LICPP) which are here regarded as the Laboratory of Ichthyology, Akasaka Imperial Palace (LIAIP) following Akihito & Sakamoto (1989).

Abbreviations for cephalic sensory system follow Lachner & McKinney (1974): ANA, anterior nasal; NA, nasal; AITO, anterior interorbital; PITO, posterior interorbital; AOT, anterior otic; POT, posterior otic; IT, intertemporal; AT, anterior temporal; PT, posterior temporal; POP1,2,3, preopercular.

Abbreviations utilized to represent certain physical characteristics and measurements: A, anal fin; C, caudal fin; D, dorsal fin; LS, scales in horizontal series; P, pectoral fin; PD, predorsal midline scale count; TRB, transverse scale series.

Information and collection data pertaining species from KFRS follow Kailola (1975).

Accounts of species are arranged alphabetically after the nominal for each species group or complex. Species are arranged alphabetically by subgenus in tabular data.

Systematics

Genus *Stenogobius* Bleeker 1874: 317

Type species

Gobius gymnopomus Bleeker 1853a: 270 (type locality: Priaman, Sumatra) by original designation.

A small to relatively large sized (approximately 40 to 200mm SL), tropical Indo-Pacific goby usually inhabiting freshwater streams and rivers, occasionally marine environments; body elongate, subcylindrical and slightly compressed; head subcylindrical and slightly compressed; length of snout and width of interorbital space varies considerably with size and age of specimen; mouth terminal, lower jaw not protruding and slightly oblique, upper jaw protractile; opercle and preopercle without spines and edges smooth; six spines in first dorsal fin, first dorsal fin may or may not be free from second dorsal fin, often first dorsal fin on males not free while free on females, or free on young males and not on older males; pectoral fin rounded with upper rays free, not feathery in appearance, rays numbering 14-17; pelvic fin always I,5, fifth rays of each fin joined together its entire length to form a cup-like disk not adherent to body, pointed posteriorly on males and rounded on females; origin of second dorsal fin slightly anterior to anus; caudal fin oblong, rounded on females and juveniles, pointed on males, almost always with 13 branched rays; fleshy papillae on shoulder girdle numbering from zero to five; all cutaneous sensory papillae oriented transversely in each row as defined in Hoese

(1983); pterygiophores 3(12210), as defined by Lachner & McKinney (1974: 875); vertebrate (including urostyle) 10+16=26; branchiostelgal rays five; gillrakers either absent or present as few detached rudiments; scales on body laterally ctenoid with single row of ctenii extending from behind pectoral base on adults and from posterior portion of nape above opercle on young specimens extending posteriorly on caudal fin base; scales on pectoral base, belly, breast, opercle and cheek cycloid; predorsal midline scales always cycloid when present, midline variable ranging from naked to fully scaled (Figures 1a, 1b & 1c); small cycloid scales may be present at bases of second dorsal and anal fins; teeth conical and recurved forming irregular rows, outer row most pronounced, adult males often with canine-like teeth, upper jaw teeth 1-6+0-3, lower jaw teeth 2-7+1-3, number of teeth sexually dimorphic with males possessing more and larger teeth than females, teeth absent from vomer and palatine; teeth on pharyngeals conical, not recurved: tongue slightly truncate to emarginate; gill opening restricted, isthmus broad extending ventrally to pectoral base; anterior nares in short tube, posterior nares without tube; cephalic sensory pore system ANA, NA, AITO, AOT, IT, AT, PT and POP1,2,3 (always paired), and PITO (singular), (Figure 2); dark mark on upper pectoral base, blackish in preservation, black with bluish tinge in life; sexual dimorphism usually developed; sexual papilla of males (Figure 3a) wedge shaped, on females (Figure 3b) the sexual papilla bulbous; sexual dichromatism may or may not be well developed; gut contents mainly with large amounts of fine sand particles, detritus, algae and tiny aquatic organisms; members of genus are substrate divers which seek shelter in the substrate when threatened or as evening falls.

Reproduction has been observed in *Stenogobius (Insularigobius) hawaiiensis*, sp. nov.; courtship involved males with fins extended, mouth open and gill covers extended outwards, dominate male drove away all other prospective males; females appear disinterested in this activity; the breeding site of the one observation was a length of electrical conduit about 300mm in length and approximately 50mm in diameter; the submissive female entered the selected site followed by the male; eggs were deposited on the roof of the conduit approximately 100mm from the entrance and cared for by the male, female was driven away after egg laying activity was completed; number of eggs could not be determined; length of incubation could not be determined as site was disrupted by flooding the following day.

Key to subgenera of *Stenogobius*

1a. Blackish bar under eye vertical and somewhat V-shaped extending from below eye to corner of jaw; dorsal and anal fins almost always with 10 rays; pectoral fin rays almost always 16, one species 15; jaw lengths not sexually dimorphic, usually less than 10% of SL; first dorsal fin higher than second with spines generally filamentous on both sexes, spines usually do not flex sharply posteriorly when fin is erect; body coloration not usually sexually dichromatic; juveniles with little or no markings over body, suborbital bar tiny . . . *Stenogobius* Bleeker 1874.

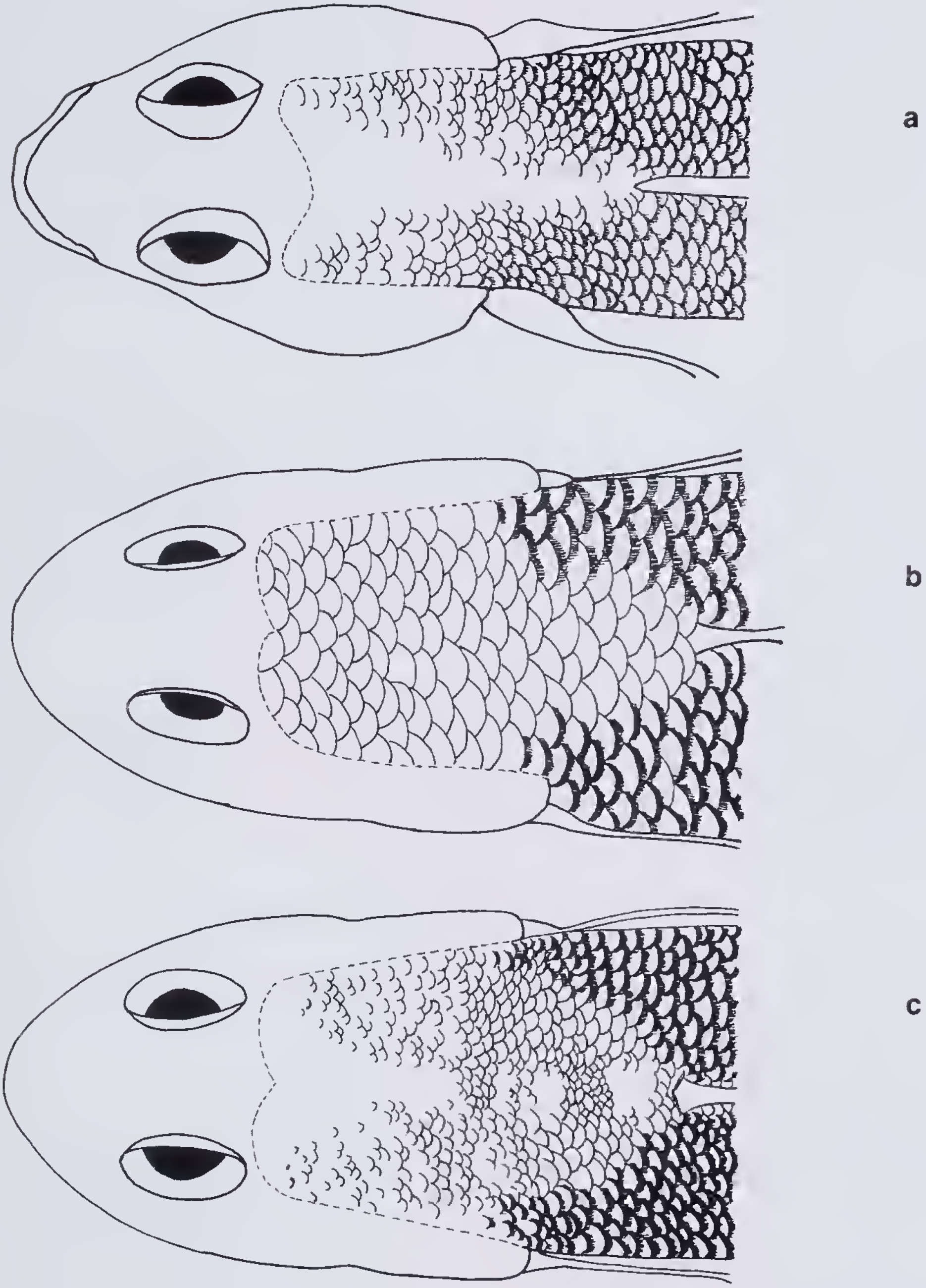

Figure 1 **a:** Predorsal midline naked anterior to first dorsal fin; **b:** Predorsal midline completely scaled with large scales; **c:** Predorsal midline appearing patchy.

1b. Blackish bar under eye oblique and normally broad extending from below eye to lower edge of preopercle; dorsal and anal fins almost always with 11 rays; pectoral fin rays almost always 15; jaw length usually sexually dimorphic with males having lengths usually greater than 10% of SL and females usually less than 10% of SL; spines of first dorsal fin generally flex posteriorly when erect becoming parallel with body axis, first dorsal fin usually same height as second dorsal fin, spines generally not filamentous on males of most species, never filamentous on females; species sexually dichromatic; juveniles with spotting and bars over body, suborbital bar distinct . . . *Insularigobius*, subgen. nov.

Subgenus *Stenogobius* Bleeker

(Tables 1-4)

Diagnosis

Dorsal fin almost always VI-I,10; anal fin almost always I,10; pectoral fin rays 14-17, usually 16, one species 15; first dorsal fin normally higher than second dorsal fin with spines long and filamentous; jaw lengths not strongly sexually dimorphic and normally less than 10% of SL; body and fin markings somewhat distinctive; sensory papillae on lower preopercle in one or two rows (Figure 4a & 4b), either pattern may be present on individuals of the same species; sexual dichromatism not always apparent; blackish markings on upper pectoral base divided with one spot visible on upper pectoral base and another under gill cover.

Juveniles generally lack pigmentation, except for a narrow V-shaped bar below eye and banding on first dorsal fin. Some species may have close affinities with continental land masses. The *Stenogobius gymnopomus* species group occurs in the Indian Ocean and the South China Sea; *S. ophthalmoporus* species group occurs in the eastern Indo-Australian Archipelago which is included in the western Pacific.

Key to species of the subgenus *Stenogobius*

1a. Pectoral rays 15 to 17, usually 16 ....2.
1b. Pectoral rays 14 to 15, usually 15; Sri Lanka .....*S. macropterus* (Duncker 1912).

2a. Predorsal midline always fully scaled ....3.
2b. Predorsal midline usually naked ....5.

3a. Scales in horizontal series 47 to 53 ....4.
3b. Scales in horizontal series 52 to 61; northern New Guinea
.... *S. laterisquamatus* (Weber 1908).

4a. Predorsal scales 10 to 15; east Africa .... *S. kenyae* Smith 1959.
4b. Predorsal scales 16 to 22; Vietnam to Japan, southward to
Sulawesi and Ambon, Indonesia.............. *S. ophthalmoporus* (Bleeker 1853).

5a. Cheek always naked ....6.
5b. Cheek always scaled; southern New Guinea ....*S. psilosinionus*, sp. nov.

6a. First dorsal fin with two black bands on basal half of fin .... 7.

6b. First dorsal fin with black crescentic shaped marking at base and a black band medially; Jawa and Sumatera, Indonesia and Andaman Islands .... *S. gymnopomus* (Bleeker 1853).

7a. Predorsal midline never entirely naked, usually with naked patches, three to 20 small scales present; posterior nostril on a line below lower edge of pupil; body depth 19 to 22% of SL in males; Mekong River Delta, Vietnam .... *S. mekongensis*, sp. nov.

7b. Predorsal midline naked or with up to four scales anterior to first dorsal fin; posterior nostril on a line with center pupil; body depth 16 to 20% of SL in males; Sabah, Malaysia .... *S. ingeri*, sp. nov.

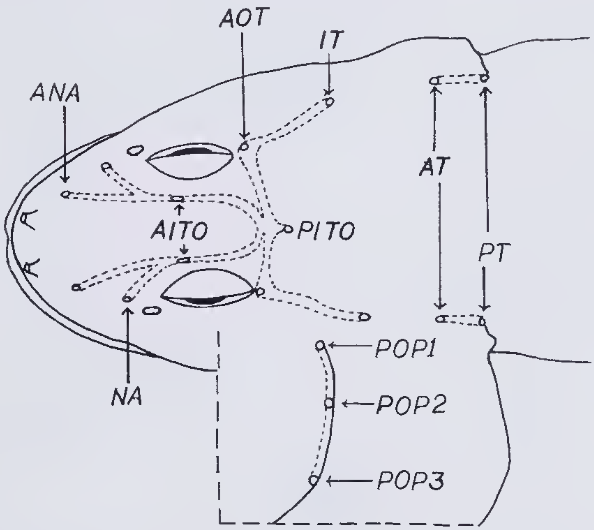

Figure 2 Cephalic sensory pore system.

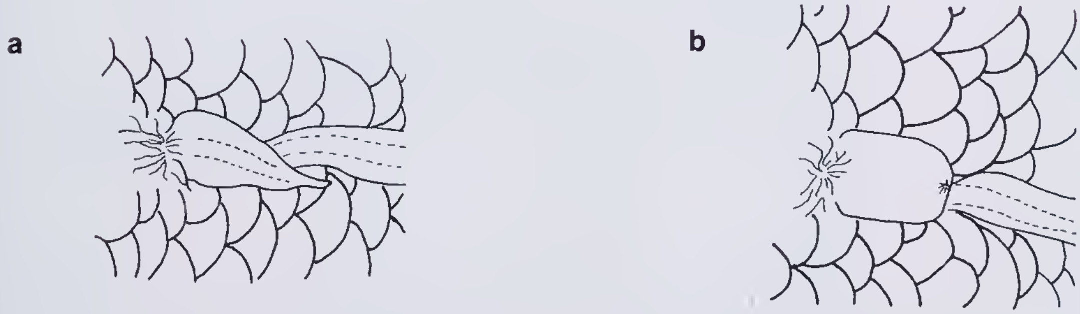

Figure 3 **a:** Sexual papilla of male; **b:** Sexual papilla of female.

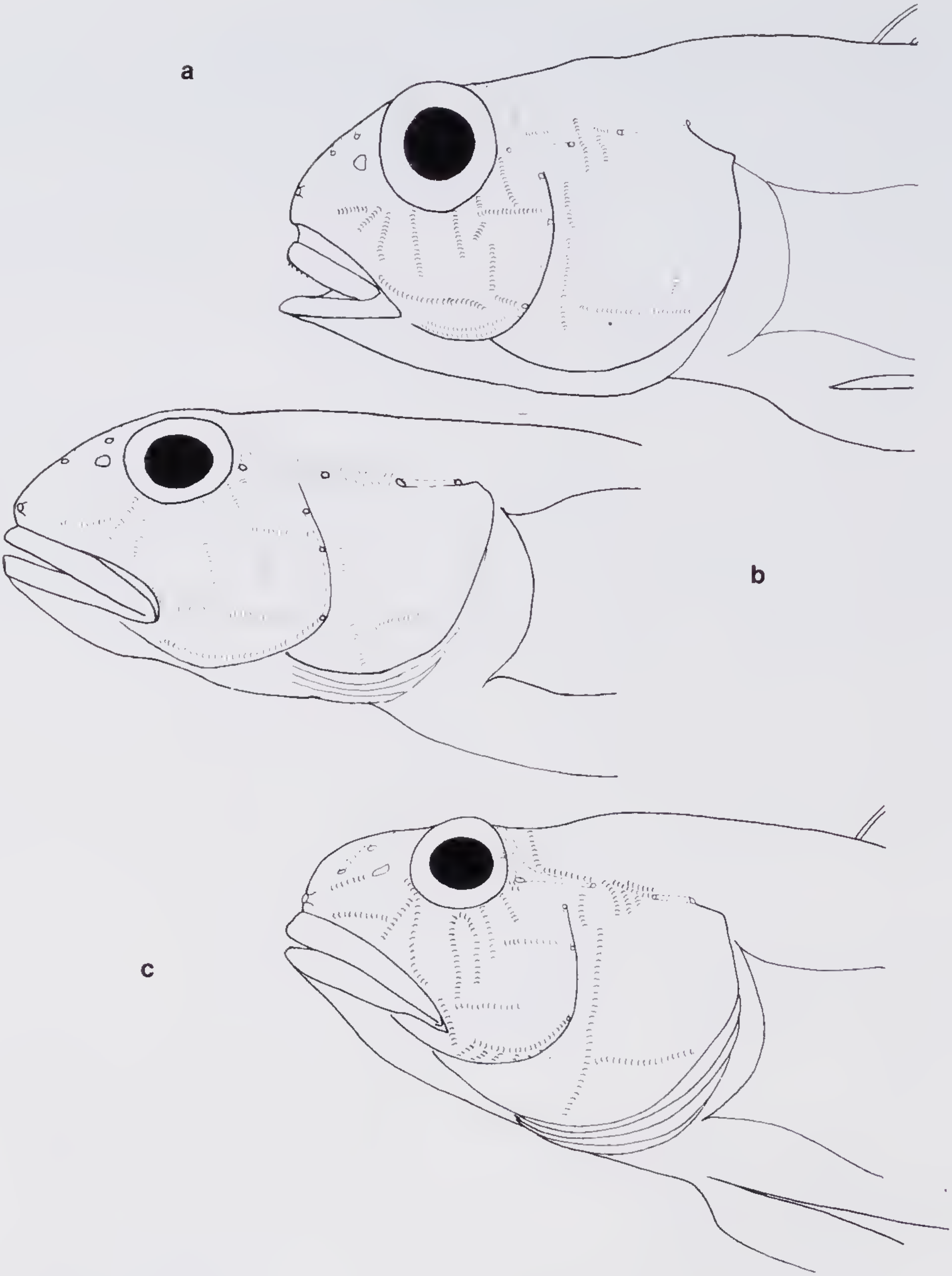

Figure 4 Cutaneous sensory papillae found on some individuals of the subgenus *Stenogobius;* **b:** Cutaneous sensory papillae found on some individuals of the subgenus *Stenogobius* and the *S. polyzona* species group; **c:** Cutaneous sensory papillae found on members of the *Stenogobius genivittatus* species group.

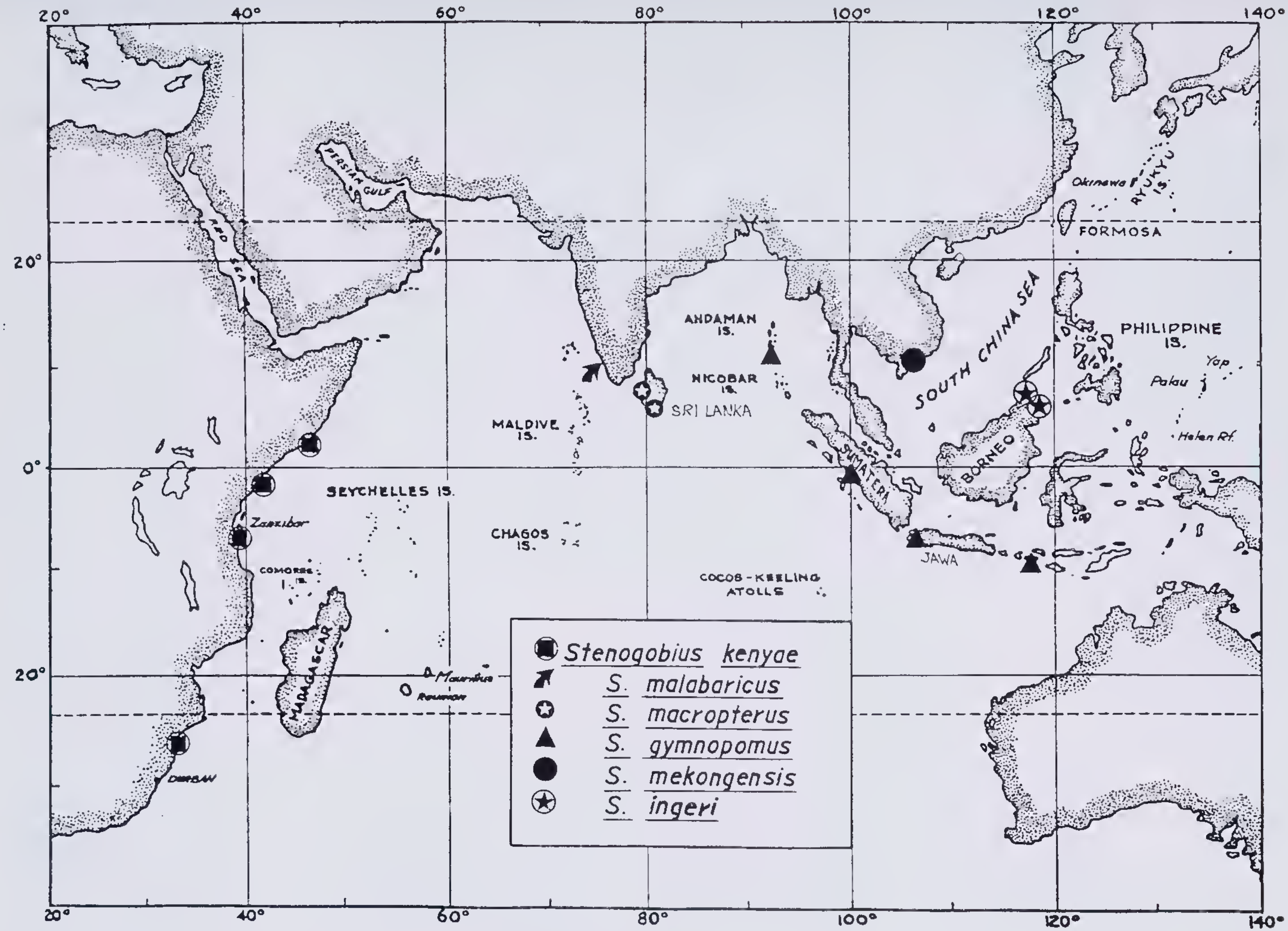

Figure 5 Distributional map of *Stenogobius gymnopomus* species group.

Table 1 Morphometrics in species of the subgenus *Stenogobius* in percent of the standard length.

Species	Jaw length in males				
	6	7	8	9	10
S. gymnopomus			3	5	1
S. ingeri				12	3
S. kenyae				2	3
S. laterisquamatus			2	2	2
S. macropterus				2	1
S. mekongensis			1	—	3
S. ophthalmoporus		1	3	7	3
S. psilosinionus		1	4	4	4

	Jaw length in females				
	6	7	8	9	10
S. gymnopomus			4	2	1
S. ingeri	1	—	8	1	
S. kenyae				5	
S. laterisquamatus			4	2	
S. macropterus				1	
S. mekongensis			2	1	
S. ophthalmoporus			4	4	
S. psilosinionus		3	10	5	1

	Caudal peduncle depth					
	8	9	10	11	12	13
S. gymnopomus				8	9	
S. ingeri	1	1	11	11	1	
S. kenyae	1	—	—	5	4	
S. laterisquamatus		3	6	3	2	
S. macropterus				2	1	1
S. mekongensis				4	3	
S. ophthalmoporus			3	8	8	3
S. psilosinionus			1	13	16	2

	Caudal peduncle length							
	14	15	16	17	18	19	20	21
S. gymnopomus	2	—	6	5	2	2		
S. ingeri	1	5	6	11	1			
S. kenyae			1	5	3	1		
S. laterisquamatus			1	1	6	4	1	1
S. macropterus	1	—	1	2				
S. mekongensis				5	2			
S. ophthalmoporus		2	6	8	6	1		
S. psilosinionus		1	3	16	9	3		

Table 1 (continued)

	Body depth at second dorsal fin origin in males								
	16	17	18	19	20	21	22	23	24
S. gymnopomus					2	3	2		
S. ingeri	1	3	4	2	1				
S. kenyae				3	—	1			
S. laterisquamatus				2	1	1			
S. macropterus						2	1		
S. mekongensis				1	—	1	1		
S. ophthalmoporus				2	5	3	3	—	1
S. psilosinionus		1	1	1	3	4	1	1	

	Head length						
	22	23	24	25	26	27	28
S. gymnopomus	1	5	4	5	2		
S. ingeri	1	—	9	14	1	—	2
S. kenyae		2	3	1	1	3	
S. laterisquamatus	2	3	5	2	1		
S. macropterus			1	2	1		
S. mekongensis		2	3	1	1		
S. ophthalmoporus	1	9	4	5	1	—	1
S. psilosinionus			7	12	10	1	2

	Preanal length									
	50	51	52	53	54	55	56	57	58	59
S. gymnopomus				2	3	2	7	3		
S. ingeri				3	4	7	6	3	1	1
S. kenyae			1	3	1	3	2	1	—	1
S. laterisquamatus	1	—	2	2	1	1	2	4		
S. macropterus					1	2	1			
S. mekongensis				1	2	1	2	1		
S. ophthalmoporus		1	—	4	6	4	3	4		
S. psilosinionus				2	4	6	7	5	2	2

Stenogobius (Stenogobius) gymnopomus **species group.**

(Figures 5, 6a, 6b, 6c, 6d, 6e & 6f)

This species group is from the Indian Ocean with one species showing strong affinities to continental masses. The group is identifiable in having cheek naked; opercle almost always naked; predorsal midline usually naked or with naked patches, one species fully scaled; pectoral base naked or with scales primarily on central region of base, these may extend downward to lower base; usually three crescentic bars between second dorsal and anal fins.

Sexual dimorphic characteristics developed; male genital papilla somewhat conical and slightly depressed appearing wedge-shaped, about three times the length of the length, length varies with size and age of specimen; on females genital papilla cylindrical with a rounded tip, about two times the length of base, appearing bulbous; all unpaired fins and filamentous spines of first dorsal fin longer on males than females.

This group is currently represented by five species of which two are described as new.

Stenogobius (Stenogobius) gymnopomus (Bleeker 1853)

(Figure 7)

Gobius gymnopomus Bleeker, 1853a: 270 (type locality: Priaman, Sumatra)

Gobius richardsonii Bleeker, 1853b: 508 (type locality: Padang, Sumatra)

Gobius gymnopomus. — Bleeker, 1859: 116

Gobius richardsonii.— Bleeker, 1859: 118

Gobius gymnopomus. — Gunther, 1861: 65

Stenogobius gymnopomus.— Bleeker, 1874: 317

Stenogobius gymnopomus. — Koumans, 1953: 34

Material examined

Twenty specimens from Indonesia and the Andaman Islands totalling nine males, seven females, four juveniles; size range 32.9 to 75.3, largest male 74.0, largest female 75.3, smallest gravid female 64.7.

Probable holotype

RMNH 4552, male (62.8), Priaman, Sumatra, Dutch East Indies, 1850, I. Pfieffer.

Additional material

IRSNB 19.853, 11(32.9-65.0), five males, two females, four juveniles, river at village of Nayapuram (Knappuram), South Andaman, Andaman Islands, 14 December 1974, J.-P. Gosse; MZB 4406, female (63.1), Ciawi, Sumur, Pandegland, Jawa Barat, Indonesia, 22 January 1982, Voetikno; MZB 4415, female (64.7), Selatan di Desa Cisiih, S. Cisiih, Sumur, Pandeglang, Jawa Barat, Indonesia, 23 January 1982, D. Wowor & D.I. Hartot; RMNH 4552, 5(67.5-75.3), three males, two females from same container as probable holotype, probably includes holotype for *Gobius richardsonii,* whose type locality is Padang, Sumatra in freshwater; SMF 6582, female (67.5), Brang-Nee River, Sumbawa, Dutch East Indies, January 1910, J. Elbert.

Diagnosis

Cheek naked; opercle naked; central pectoral base sometimes scaled; breast and belly anteriorly naked; predorsal region naked or with few scales anterior to first dorsal fin; first dorsal fin with blackish mark on posterior half of fin near base, marking darkest posterior to fifth spine appearing slightly crescentic; pectoral fin rays 16.

Relationship

This species appears very close to *Stenogobius macropterus*, but differs by dorsal fin marking and having 16 pectoral fin rays.

Description

D VI-I,9 to VI-I,10, almost always VI-I,10; A I,10; P 15 to 17, usually 16. LS 49 to 53, usually 50 to 52; TRB 11 to 13, usually 11 to 12; PD either naked or with scales near anterior base of first dorsal fin; cheek naked; opercle naked; pectoral base, usually

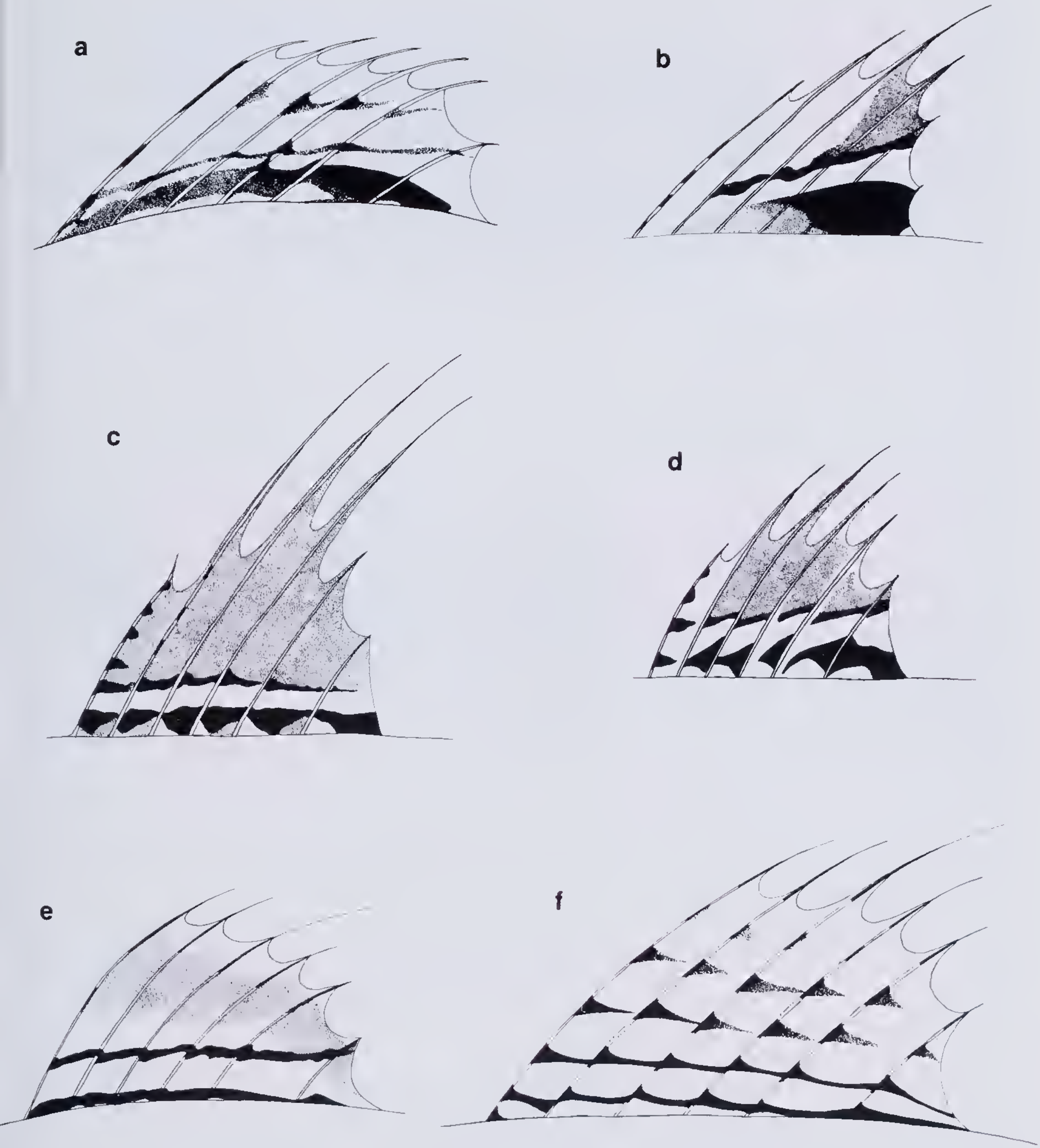

Figure 6 **a:** First dorsal fin of *Stenogobius gymnopomus;* **b:** First dorsal fin of *Stenogobius macropterus;* **c:** First dorsal fin of male of *Stenogobius kenyae;* **d:** First dorsal fin of female of *Stenogobius kenyae;* **e:** First dorsal fin of *Stenogobius ingeri;* **f:** First dorsal fin of *Stenogobius mekongensis.*

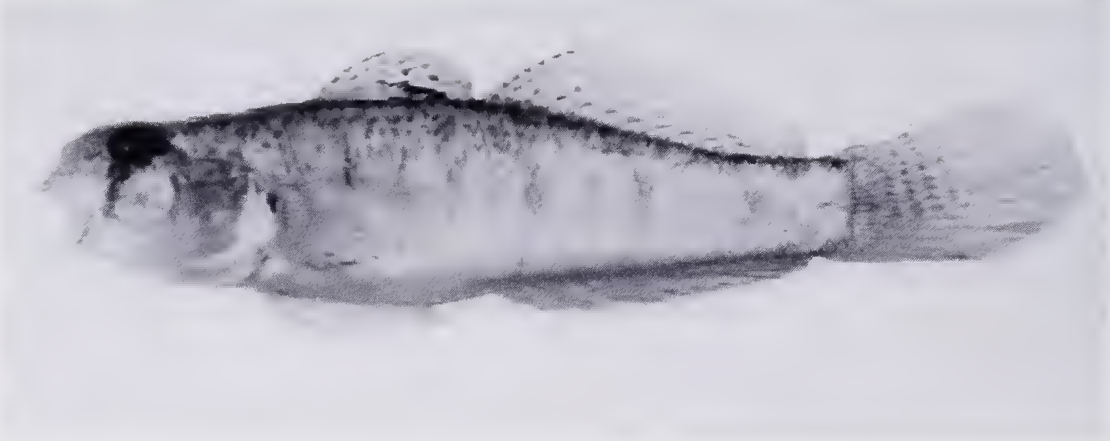

Figure 7 *Stenogobius gymnopomus* (Bleeker), MZB 4415, female (67.7), Jawa Barat, Indonesia.

naked; anterior region of belly naked; breast naked. Jaw extending under anterior edge of eye. Upper jaw teeth, males 3+2; females 1-3+1. Lower jaw teeth, males 3-4+2, females 1-3+1-2.

Color in preservation: Background straw-yellow; snout slightly dusky with some blackish spotting; short black diagonal bar in front of eye; upper jaw dusky anteriorly; lower jaw with small dusky spot at anterior tip; some dusky spotting on cheek and upper opercle; nape with much black speckling, continuing posteriorly, but becoming less distinct; three faint brownish or blackish bars between second dorsal and anal fins, two brownish or blackish bars below the first dorsal fin; very faint dusky patch between each crescentic bar along midline; body ventrally without noticeable markings. First dorsal fin with black band along lower base, very faint anteriorly, posterior to fifth spine band intensifies then descends, disappearing between sixth spine and posterior base of fin, this band appearing crescentic, medially faint black band extending length of fin, both bands separated by translucent band, remainder of fin slightly dusky; spine on second dorsal fin with six black marks, remainder of fin with six even rows of black spots appearing on membrane between rays and spine; caudal fin with eight vertical bars formed by blackish pigmentation on membrane between rays and upper two-thirds of fin, most pronounced on upper anterior portion of fin, rest of fin slightly dusky; anal fin slightly dusky with dusky margin; pelvic disk without pigmentation on females, dusky between rays on males; pectoral fin without pigmentation.

Color in life: Life colors after Bleeker's original account based on the holotype. Upper body color green and yellow below; back sprinkled with dark spots; below dorsal fin three curved and angular dark streaks, angled convexly posteriorly; transverse dark band below eye; snout with irregular dark bands; spinous dorsal fin with violet base, middle streaked lengthwise in yellow, upper reddish-violet with yellow marks, dark rays violet-green with yellow marks, double margin of yellow and reddish-violet; pectoral fin yellow with black spot on upper base; pelvic disk violet; anal fin reddish-violet with

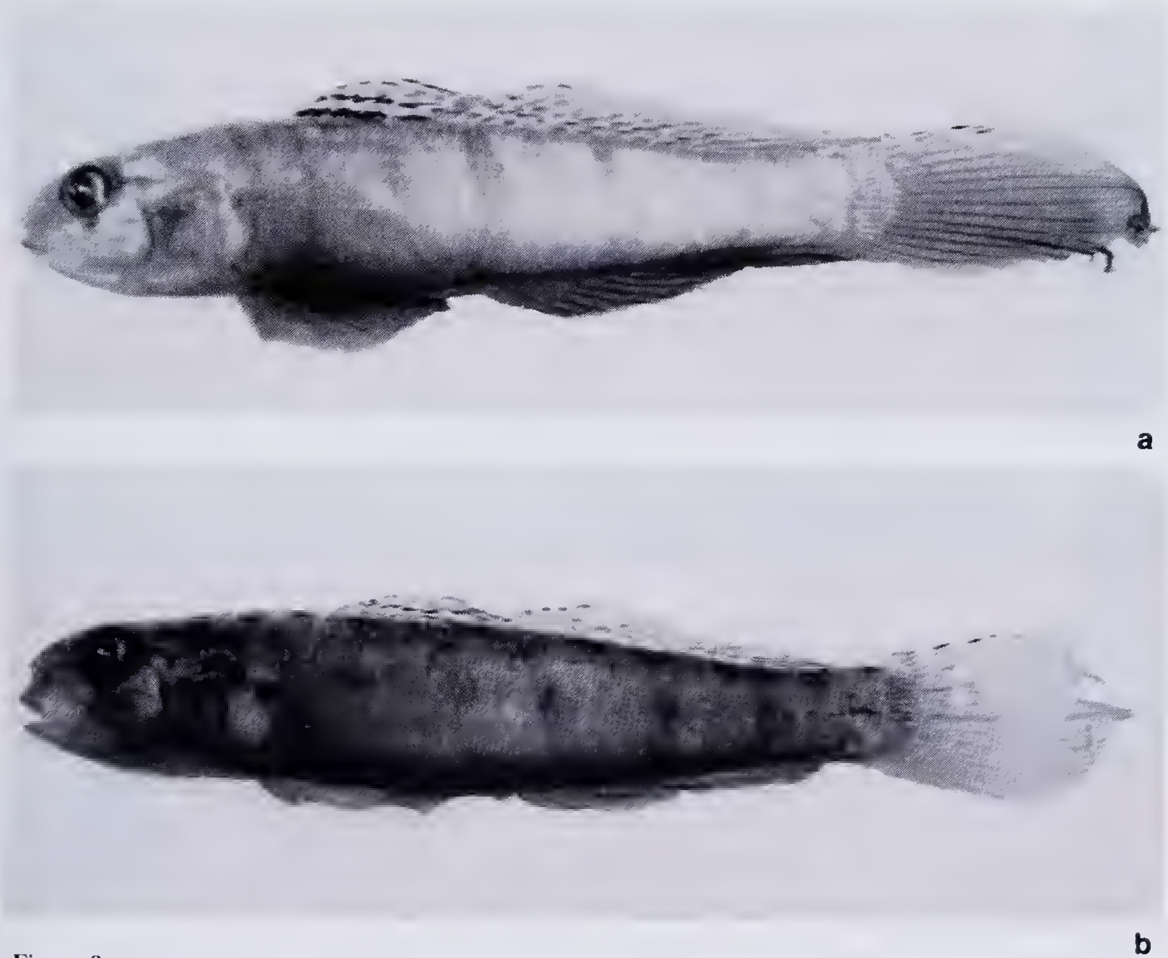

Figure 8 **a:** *Stenogobius ingeri*, sp. nov., FMNH 68462, HOLOTYPE, male (68.7), Sabah, Malaysia; **b:** *Stenogobius ingeri*, sp. nov., NSMT P.41080, PARATYPE, female (51.4), Sabah, Malaysia.

double margin of violet and orange; caudal fin with violet and greenish marks above double margin of yellow and reddish-violet.

Bleeker does not equate dark to a specific color.

Remarks

Distribution: Known from the Indian Ocean slopes of Sumatera, Jawa and Sumbawa in western Indonesia and the Andaman Islands.

Ecology

Reported from rivers and estuaries near mouths of rivers in both marine and fresh water conditions.

Stenogobius (Stenogobius) ingeri, sp. nov.
(Figures 8a & 8b)

Stenogobius (Stenogobius) ingeri, sp. nov. (type locality: Sungei Marikut, Kalabakan, Tawau District, Sabah, Malaysia)

Stenogobius gymnopomus. — Inger & Chin, 1962: 179

Material examined

Thirty three specimens from Sabah, Malaysia, totalling 16 males, 14 females, three juveniles; size range 26.0 to 68.7, largest male 68.7, largest female 62.9, smallest gravid female 41.1.

Holotype

FMNH 68462, male (68.7), Sungei Marikut, Kalabakan, Tawau District, Sabah, Malaysia, 16 June 1956, R.F. Inger.

Paratypes

AMS I.25616-001, two males (41.7-53.9), same collection data as holotype; FMNH 68458, male (60.8), Kinabatangan District, Sabah, Malaysia, 21 June 1956, R.F. Inger & P.K. Chin; FMNH 68461, two females (42.2-62.0), Sungei Maga, Kalabakan, Tawau District, Sabah, Malaysia, 11 June 1956, R.F. Inger; FMNH 96569, 12(26.0-63.0), six males, six females, same collection data as holotype; LIAIP 1956008, 2(26.0-42.0), one female, one juvenile, Kinabatangan District, Sabah, Malaysia, 6 June 1956, R.F. Inger; MZB 5650, two males (36.6-40.1), same collection data as holotype; NSMT P.41079, male (35.8), same collection data as holotype; NSMT P.41080, female (51.4), same collection data as holotype; SMF 20497, two males (35.6-49.0), same collection data as holotype; USNM 278369, 2(41.1-64.4), one male, one female, same collection data as holotype.

Diagnosis

Cheek naked; opercle naked; central pectoral base usually naked; belly anteriorly naked; breast naked; predorsal midline naked or with few scales anterior to first dorsal fin; body depth of males 16 to 20% of SL, usually 17 to 19%; first dorsal fin with two parallel black bands extending basally and medially entire length of fin.

Relationship

This species appears most closely related to *Stenogobius mekongensis* and more distantly to *S. kenyae*. It differs from *Stenogobius kenyae* by having predorsal region mostly naked, if scales are present these are always tiny; it differs from *S. mekongensis* by being more slender, and with fewer scales on predorsal midline and opercle naked.

Description

D VI-I,10 to VI-I,11, usually VI-I,10; A I,10; P 15 to 17, usually 16. LS 49 to 54, usually 50 to 53; TRB 11 to 13, usually 11 to 12; PD usually naked; cheek naked; opercle naked; pectoral base usually naked; belly anteriorly naked; breast naked. Jaw reaching under anterior edge of eye. Upper jaw teeth, males 2-3+1-2; females 1-2+1. Lower jaw teeth, males 3-4+2; females 2-3+1-2.

Color in preservation: Background slightly brownish; three well developed, broad crescentic blackish bars between second dorsal and anal fins, two or three faint blackish bars below first dorsal fin; dusky spot at hypural base; body ventrally without notable markings. Snout slightly dusky, may have some weak spotting; upper jaw slightly dusky, lower jaw with small dusky spot on anterior tip; cheek without spotting; upper opercle

Table 2a Fin length in males of species belonging to the subgenus *Stenogobius*, expressed to the nearest whole percent of the standard length.

	Second dorsal fin length																							
	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61
S. gymnopomus		1	—	1	1	2	—	1	2	—	—	—	1											
S. ingeri				1	—	2	1	2	1	2	1	1	—	—	1	2	—	—	—	1				
S. kenyae											1	—	1	1	1									
S. laterisquamatus									1	1	—	1	—	1	1	1								
S. macropterus										1	—	—	—	—	—	—	2							
S. mekongensis					1	—	1	—	—	—	—	1	—	—	1									
S. ophthalmoporus	1	—	—	—	2	—	—	—	—	1	—	—	1	—	1	3	1	2	1					
S. psilosinionus	1	—	—	—	—	—	2	—	—	—	1	1	1	1	—	—	2	2	—	—	1	—	—	1

	Anal fin length																	
	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55
S. gymnopomus		1	1	1	2	1	2	—	—	—	1							
S. ingeri			2	1	—	2	1	2	1	2	1	1	1	—	—	—	—	1
S. kenyae										1	1	1	1					
S. laterisquamatus								2	1	—	—	1	—	1	1			
S. macropterus								1	—	—	—	—	1	1				
S. mekongensis					1	—	—	—	2	—	1							
S. ophthalmoporus	1	—	1	—	1	—	1	—	—	1	1	—	2	2	1	2	1	
S. psilosinonus		1	1	—	2	—	—	1	2	—	—	2	—	2	—	1	—	1

	Caudal fin length																							
	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
S. gymnopomus	1	—	1	2	—	—	—	1	—	—	—	—	—	—	—	1								
S. ingeri					1	—	2	2	—	—	2	—	2	—	1	—	2	—	1	1	—	—	1	
S. kenyae													1	—	1	1	1							
S. laterisquamatus															1	1	—	—	—	1				1
S. macropterus												1	—	—	—	—	1	—	—	—	—	—	—	1
S. mekongensis					1	—	—	—	—	—	—	—	—	—	1	—	1							
S. ophthalmoporus															1	—	1	—	2	2	—	1	1	1
S. psilosinionus										1	—	2	1	—	1	1	2	—	1	—	1	—	2	

Table 2b Fin lengths in females of species belonging to the subgenus *Stenogobius*, expressed to the nearest whole percent of the standard length.

	Second dorsal fin length										
	35	36	37	38	39	40	41	42	43	44	45
S. gymnopomus						2	1	2	—	1	
S. ingeri	1	1	2	3	2	—	1				
S. kenyae					2	—	2	1			
S. laterisquamatus		1	1	—	1	1	2				
S. macropterus										1	
S. mekongensis								2	1		
S. ophthalmoporus					1	2	1	1	1	—	1
S. psilosinionus	1	1	2	—	2	3	3	4	2	1	

	Anal fin length											
	33	34	35	36	37	38	39	40	41	42	43	44
S. gymnopomus								2	3	1	—	1
S. ingeri	1	—	—	3	3	2	1					
S. kenyae					1	1	2	1				
S. laterisquamatus			1	2	—	2	—	1				
S. macropterus											1	
S. mekongensis									2	1		
S. ophthalmoporus						2	3	1	—	—	—	1
S. psilosinionus			1	4	3	2	8	1				

	Caudal fin length												
	24	25	26	27	28	29	30	31	32	33	34	35	36
S. gymnopomus				1	—	3	—	1					
S. ingeri			2	1	—	3	2						
S. kenyae						1	1	—	2				
S. laterisquamatus				1	2	1	—	1	1				
S. macropterus												1	
S. mekongensis					1	1	—	—	—	—	1		
S. ophthalmoporus				1	—	2	1	—	—	—	—	—	1
S. psilosinionus			2	—	1	1	2	3	4	5			

may have two or three blackish bands; nape with four blackish bands that may appear as divided symmetrical spots on large specimens, similar banding along dorsum to caudal peduncle, not distinctive posteriorly. First dorsal fin with black band along entire base, medially another black band extending length of fin, these are separated by a translucent band, distally fin is dusky, tips of the first four spines black; spine on second dorsal fin with black marks anteriorly, three to four rows formed by dusky spots on membrane between rays extending length of fin; caudal fin light above with some dusky markings on upper anterior half of fin, darkest along margin, lower half of fin dusky; anal fin and pelvic disk dusky on males, pelvic disk translucent on females, anal fin also translucent, but with dusky margin.

Remarks

Distribution: Known only from the Malaysian province of Sabah on northeastern Borneo.

Ecology: Specimens examined were collected from streams and rivers in fresh water near the coast.

Etymology: This species is named for Robert F. Inger who collected all known specimens.

Stenogobius (Stenogobius) kenyae Smith 1959

(Figure 9)

Stenogobius kenyae Smith, 1959: 190 (type locality: Sabaki River, Kenya)

Stenogobius gymnopomus. — Smith, 1959: 190 (Somalia)

Material examined

Ten specimens from the eastern coastal region of Africa, totalling five males, five females; size range 26.8 to 83.6, largest male 83.6, largest female 64.1, smallest gravid female 58.6.

Paratypes

RUSI 878, 3(58.6-83.6), one male, two females, Sabaki River, Kenya.

Additional material

CAS-SU 31507, male (60.4), Msimbazi Creek, Dar-Es-Salaam, Tanzania, 26 April 1934, A.W.C.T. Herre; NMC 81-193, two females (38.9-44.7), Rufiji River at Utete, east end of town adjacent to Lake Chemchem, Tanzania, 30 July 1979, A.J. Hopson *et al;* NMC 81-194, male (51.0), Rufiji River mouth shore at Ndundu ferry landing, Tanzania, 31 July 1979, A.J. Hopson et al; RUSI 5456, male (26.8), Sodwana Bay, Kwazulu, South Africa, 25 November 1975; ZMH 19307, 2(41.2-58.5), one male, one female, Giuba River, Giumbo, Somalia, 14 December 1926, D. Vinciguerra.

Diagnosis

Cheek naked; opercle usually naked, may have few large scales; pectoral base naked; belly usually naked, may have few thin scales; breast usually naked, may have one to five scales; predorsal region fully scaled with large scales numbering 10 to 15; first dorsal fin with two parallel black bands on basal half of fin.

Relationship

This species appears most closely related to *Stenogobius ingeri* and *S. mekongensis;* it can be distinguished from these forms by the presence of large scales on the predorsal midline.

Description

D VI-I,10 to VI-I,11, usually VI-I,10; A I,10 to I,11, usually I,10; P 15 to 16. LS 47 to 53; TRB 11 to 12, usually 12; PD 10 to 15; cheek naked; opercle usually naked; pectoral base naked; belly anteriorly naked or with few thin scales; breast naked or with few embedded scales. Jaw reaching under anterior edge of eye. Upper jaw teeth, males 3+2; females 2-3+1-2. Lower jaw teeth, males 4+2; females 4+1-2.

Color in preservation: Body background yellowish or brownish; three large slightly crescentic blackish bars between second dorsal and anal fins, two similar blackish bars

Figure 9 *Stenogobius kenyae* J.L.B. Smith, RUSI 878, PARATYPE, male (83.6) Kenya.

below first dorsal fin. First dorsal fin with four to six evenly spaced black marks along anterior edge of first spine, a black band along fin base, pronounced on posterior edge of membrane separating spines, a medial black band extending from first spine to upper edge of fin at sixth spine, both separated by translucent band, distal half of fin dusky; second dorsal fin with two to four rows of dusky streaks on membrane forming distinct bands on basal half of fin, distal half slightly dusky; upper third of caudal fin with blackish spotting and streaks, rest of fin dusky; anal fin dusky, darkest along margin; pelvic disk dusky on males, translucent on females; pectoral fin translucent.

Remarks

Distribution: Specimens examined reported from Somalia to South Africa in waters entering the Indian Ocean.

Ecology: Reported from fresh water to marine conditions in lowland rivers and bays.

Stenogobius (Stenogobius) macropterus (Duncker 1912)
(Figure 10)

Awaous macropterus Duncker, 1912: 252 (type locality: Ginganga near Vakvella, Ceylon)

Stenogobius malabaricus. — Munro, 1955: 236 (in part)

Stenogobius malabaricus. — Jayaram, 1981: 351 (in part)

Material examined

Four specimens from Sri Lanka, totalling three males, one female; size range 48.2 to 73.1, largest male 71.0, largest female 73.1, no gravid material.

Lectotype

ZMH 413, male (71.0), Ginganga near Vakvella, Ceylon, September 1909, G. Duncker.

Paralectotype

ZMH 413, male (52.4), same collection data as lectotype.

Additional material

CAS-SU 30139, female (73.1), Colombo, Ceylon, 4 April 1934, A.W.C.T. Herre; USNM 270374, male (48.2), fresh water tributary to Bentota Ganga, 2.7 miles south of Pitigata on road to Talgaswela, Bentara-Elipiya District, Sri Lanka, 7 July 1969, W.F. Smith-Vaniz.

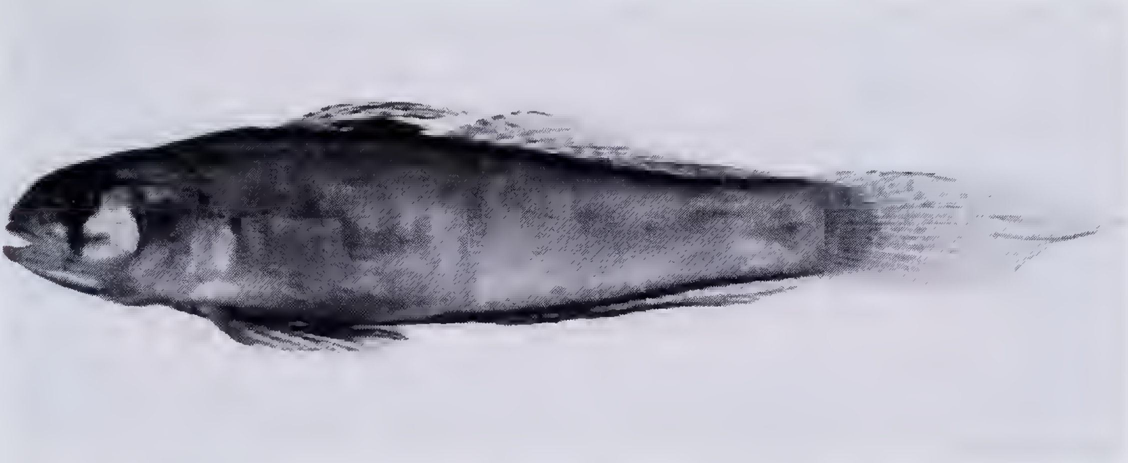

Figure 10 *Stenogobius macropterus* (Duncker), USNM 270374, male (48.2), Sri Lanka.

Diagnosis

Opercle naked; cheek naked; pectoral base usually naked; belly anteriorly usually naked; breast naked; predorsal midline naked or with few scales near first dorsal fin; first dorsal fin with crescentic to slightly tear-shaped blackish mark near posterior base of fin, most pronounced after fourth spine; pectoral fin with 14 to 15 rays, usually 15.

Relationship

Stenogobius macropterus is most closely related to *S. gymnopomus,* it can be distinguished by the presence of 15 pectoral rays, 16 in *S. gymnopomus.*

Description

D VI-I,10; A I,10; P 14 to 15, usually 15. LS 49 to 51; TRB 11 to 12; PD usually naked; cheek naked; opercle naked; pectoral base usually naked; belly anteriorly naked or with few embedded scales near pelvic base; breast naked. Jaw extending under anterior edge of eye. Upper jaw teeth, males 3+2; female 3+2. Lower jaw teeth, males 3+2; female 3+2.

Color in preservation: Body background brownish yellow; three faded brown crescentic bars between second dorsal and anal fins. First dorsal fin with black crescentic mark between fourth and sixth spines, medially a black band extending length of fin, both marks separated by a translucent band, distal half of fin dusky; second dorsal fin with translucent band along base, distally fin dusky; anal and caudal fins dusky; pelvic disk dusky on males, translucent on females; pectoral fin translucent.

Color in life: Color is based on Duncker's original description. Three faded brownish-yellow bars between second dorsal and anal fin, which are slightly convex; ctenii on edge of each scale blackish; dark-brown spot on upper pectoral base; first dorsal fin with large dark spot, small white spot medially, between the fourth and sixth spine, dark band runs entire length of fin, remainder of first dorsal fin dusky; second dorsal fin with clear stripe along its base, remainder of fin darkened on male; pelvic fin with medial region darkened; dorsal surface with dark pigmentation, ventrally not dark, male with row of spots on the bases of fins; caudal fin on male clear distally with dark border ventrally, middle with reddish oblique band, paralectotype with eight darkish transverse bands, remainder of fin dusky; pectoral fin pigmented as is pelvic fin.

Duncker does not equate dark to a particular color.

Remarks

Distribution: Sri Lanka.

Ecology: Reported from brackish and fresh water streams.

Note: This species may be synonymous with *Stenogobius malabaricus* (Day 1865: 27), but until material can be examined from the type locality it cannot be placed there with certainty. The putative type, BMNH 1889.2.1:4303, is a dried half-skin (A.C. Wheeler, pers. comm.). Unfortunately, in this condition it is impossible to evaluate diagnostic characteristics.

Stenogobius (Stenogobius) mekongensis, sp. nov.

(Figures 11a & 11b)

Stenogobius (Stenogobius) mekongensis, sp. nov. (type locality: Bassac River, Chau-Doc, upper Mekong River Delta, Vietnam).

Chonophorus lachrymosus. — Kawamota *et al*, 1975: 45

Material examined

Seven specimens from the Mekong River Delta, Vietnam totalling four males, three females; size range 49.2 to 69.1, largest male 69.1, largest female 68.4, no gravid material.

Holotype

NSMT P.23911, male (59.8), Bassac River at Chau-Doc, upper Mekong River Delta, Vietnam, 25 July 1971.

Paratypes

LIAIP 1971268, two females (67.7-68.4), Cantho River, Vietnam, 26 December 1971; LIAIP 1972382, two males (60.8-69.1), Cantho Province, Vietnam, 14 June 1972; NSMT P.23912, female (67.0), same collection data as holotype; USNM 272584, male (49.2), same collection data as holotype.

Diagnosis

Predorsal midline always scaled, ranging from few close to dorsal fin to entirely scaled with small scales; opercle usually naked; cheek naked; pectoral base scaled; belly anteriorly usually scaled next to pelvic base; breast with embedded scales; posterior nostril on line even or below lower margin of pupil; basal half of first dorsal fin with paired black bands; weak banding on distal half.

Relationship

Stenogobius mekongensis appears most closely related to *S. ingeri*. It is much more robust than that species appearing more like *Stenogobius gymnopomus* in this respect, it differs from that species by having more scales on pectoral base, predorsal midline, position of the posterior nostril, and on the dorsal fin markings.

Table 3 Scale counts in species of the subgenus *Stenogobius.*

Species	Lateral series 47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62
S. gymnopomus			1	5	2	7	1									
S. ingeri			1	3	—	4	4	1								
S. kenyae	2	2	—	—	—	—	1									
S. laterisquamatus						1	—	—	1	—	6	—	2	—	1	1
S. macropterus			2	1	—	—	1									
S. mekongensis				1	—	1	—	1								
S. ophthalmoporus		1	2	6	5	2	3									
S. psilosinionus						2	1	5	4	4	5	4	3			

	Predorsal midline 0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
S. gymnopomus	8	1	5	3	—	6	—	—	1										
S. ingeri	14	2	5	2	2														
S. kenyae											1	—	4	1	3	1			
S. macropterus	3	—	1																
S. mekongensis				2	1	—	—	—	—	—	1	—	—	1	—	—	1	—	—
S. ophthalmoporus																	2	1	2
S. psilosinionus			2	5	3	1	3	2	—	1	2	1	—	—	—	2	—	2	—

	Predorsal midline (continued) 19	20	21	22	23	24	25	26	27	28	29	30	31	32
S. laterisquamatus				1	—	1	1	2	1	2	3	1	—	2
S. mekongensis	—	1												
S. ophthalmoporus	5	—	7	2	—	—	1							
S. psilosinionus	1	1	2	1	1	—	1							

Description

D VI-I,10; A I,10; P 15 to 17, usually 16. LS 50 to 54, usually 51; TRB 11 to 12; PD scales always present, but usually patchy along midline; cheek naked; opercle usually naked; pectoral base scaled; belly anteriorly usually scaled near pelvic base; breast with embedded scales. Jaw extending under and beyond the anterior edge of eye. Upper jaw teeth, males 3+1-2, females 1-2+1. Lower jaw teeth, males 4-5+2; females 3-4+2. Posterior nostril appears on a line even with, or slightly below, lower maring of orbit.

Color in preservation: Background straw-yellow, body with three faint, broad, crescentic dusky bars between second dorsal and anal fins; three faint narrow dusky bars below first dorsal fin; body ventrally without pigmentation; snout and upper jaw dusky; cheek without markings; upper opercle with two faint dusky bands; nape slightly dusky; dorsum with some dusky spotting, most distinctive posteriorly. First dorsal fin with black band along base, most pronounced posteriorly, medially another black band extending from first spine not quite reaching sixth spine, translucent band between black

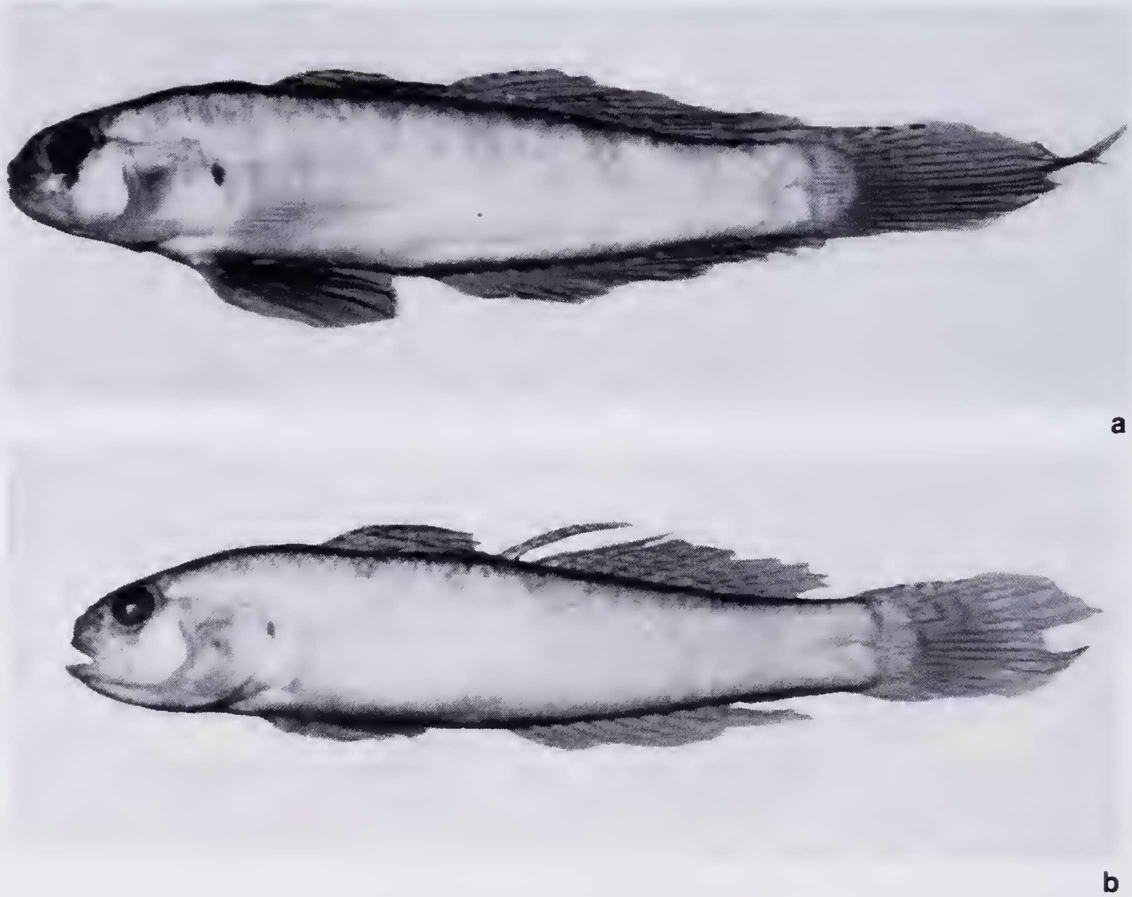

Figure 11 **a:** *Stenogobius mekongensis,* sp. nov., NSMT P.23911, HOLOTYPE, male (59.8), Chau-Doc, Vietnam; **b:** *Stenogobius mekongensis,* sp. nov., NSMT P.23912, PARATYPE, female (67.0), Chau-Doc, Vietnam.

bands, distal half of fin may have two or more faint dusky bands; second dorsal fin with three to four rows of dusky dash-like markings, most pronounced on membrane between rays forming bands entire length of fin; caudal fin with eight or so vertical bars formed by blackish pigmentation on membrane between rays on upper two-thirds of fin, most pronounced on upper anterior portion, rest of fin dusky; anal fin dusky; pelvic disk dusky on males and translucent on females; pectoral fin without notable pigmentation.

Remarks

Distribution: Known only from the Mekong River Delta region of Vietnam.

Ecology: Specimens examined were reported from fresh water rivers and streams.

Etymology: This species is named for the Mekong River Delta region from which all specimens examined were obtained.

Stenogobius (Stenogobius) ophthalmoporus species group.

(Figures 12, 13a, 13b & 13c)

This group is restricted to a narrow geographical region extending from Vietnam and the Ryukyu Islands in the north, to the islands of Sulawesi, Indonesia and eastern Papua New Guinea in the south. It is identifiable in having cheek almost always scaled; opercle always scaled; predorsal midline with scales present, usually fully scaled, mostly naked in one species; lower pectoral base always scaled, scales may cover entire base; usually four crescentic bars present between second dorsal and anal fins, variable in one species; sexual dichromatism may be well developed.

Sexual dimorphic characteristics well developed; filamentous spines of first dorsal fin normally much longer, and length of unpaired fins greater on males than females; sexual dimorphic differences not always evident on small males.

This species group currently represented by three species of which one is described as new.

Stenogobius (Stenogobius) ophthalmoporus (Bleeker 1853)

(Figures 14a & 14b)

Gobius ophthalmoporus Bleeker, 1853c: 340 (type locality: Ambon, Moluccas Islands, Dutch East Indies)

Gobius ophthalmoporus. — Gunther, 1861: 17

Gobius lacrymosus Peters, 1868: 265 (type locality: Luzon, Philippines)

Chonophorus lachrymosus. — Weber, 1894: 412 (Celebes)

Gobius ophthalmoporus. — Steindachner, 1901: 429 (Halmahera: Moluccas Islands)

Awaous lacrymosus. — Jordan & Richardson, 1910: 49 (Philippines)

Chonophorus lachrymosus. — Herre, 1927: 212 (Philippines)

Gobius ophthalmoporus. — Fowler, 1928: 405 (western Pacific)

Stenogobius genivittatus. — Koumans, 1935: 125 (in part)

?*Aparrius sabagensis* Roxas & Ablan, 1940: 165 (type locality: Luzon, Philippines)

Chonophorus lachrymosus. — Herre, 1953: 739 (Philippines)

Stenogobius genivittatus. — Koumans, 1953: 35 (in part)

Stenogobius lachrymosus. — Akihito *et al*, 1984: 271 (Japan)

Material examined

Twenty nine specimens from Indonesia, Vietnam, Taiwan and the Philippines totalling 15 males, eight females, six juveniles; size range 16.4 to 142.1, largest male 142.1, largest female 87.4, smallest gravid female 62.1.

Syntypes

RMNH 4510, two males (62.5-94.5), Ambon, Moluccas Islands, Dutch East Indies. Female (62.1) in same container not appearing to be of two specimens originally described by Bleeker is included in this study.

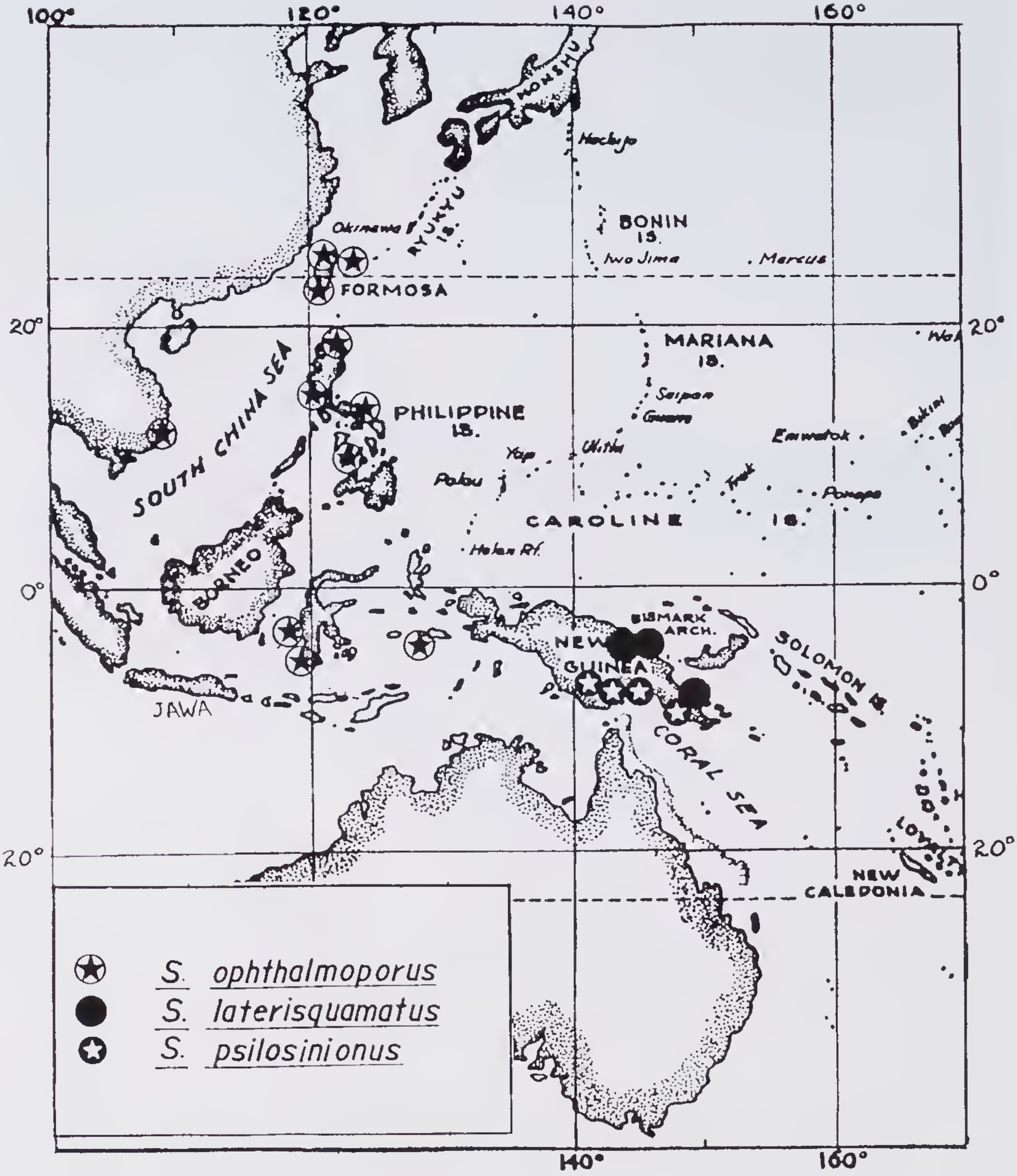

Figure 12 Distributional map of *Stenogobius ophthalmoporus* species group.

Additional material

BMNH 1870.3.29:4, female (59.5), Quingoa River, Bulacan Province, Luzon, Philippines, November 1860, W.C.H. Peters, syntype for *Gobius lacrymosus;* LIAIP 1963148, male (55.6), Aparri, Luzon, Philippines, September 1963; LIAIP 1967255, 2(65.1-76.0), one male, one female, Litse, I-lan, Taiwan, 30 October 1967; LIAIP 1974067, female (87.4), Song Cai River at Than Minh, 15 km above its mouth near Nhatrang, Vietnam, 27 September 1974; MNHN 6159, two females (59.5-69.1), same collection data as BMNH 1870.3.29:4, syntypes for *Gobius lacrymosus;* SMF 881, male (142.1), Tobelo, Halmehera, Moluccas Islands, Dutch East Indies, 17 March 1894, W. Kuchenthal; UMMZ 209051, female (83.6), Panay River, 23 km upriver from the sea at village of Salocan, Capiz Province, Panay, Philippines, 25 June 1979, J. Spielberg; USNM 135784, female (65.3), Pucot River near Mariveles, Manila Bay, Luzon, Philippines, 29 January 1909, Albatross Expedition; USNM 139342, male (39.7), Batangas River, Batangas, Luzon, Philippines, 7 June 1909, Albatross Expedition; USNM 143820, male (55.0), Cabugao River, Catanduanes Island, Philippines, 1909, Albaross Expedition; USNM 160747, male (88.9), Guimaras Island, vicinity of Buena Vista, Iloilo Province, Panay, Philippines, 14 January 1909, Albatross Expedition; USNM 160748, male (62.5), Anilao River, Passi, Iloilo Province, Panay, Philippines, 13 January 1909, Albatross Expedition; USNM 191230, male (70.3), I-lan,, Taiwan, 1960, R.E. Kuntz & W.H. Wells; USNM 257895, male (98.9), Agno River, one km south of Urbizopolo, Pangasinan, Luzon, Philippines, 16 March 1976, T.R. Roberts; USNM 260531, six juveniles (16.4-22.9), same collection data as USNM 257895; ZMA 111.557, two males (111.4-112.5), river north of Madjene, Tjenrana, Celebes, Dutch East Indies, 1888, M. Weber; ZMA 113.656, male (45.7), river near Maros, northeast of Makassar, Celebes, Dutch East Indies, 1888, M. Weber; ZMA 113.657, male (94.5), Minralang near Parepare, Celebes, Dutch East Indies, 1888, M. Weber.

Diagnosis

Predorsal midline fully scaled, usually 19 to 21; cheek almost always scaled; opercle scaled; pectoral base scaled; belly scaled anteriorly near pelvic base; breast always with exposed or embedded scales; basal half of first dorsal fin with two black bands, lower band may originate behind first or second spine; sexual dichromatism not well developed.

Relationship

This species appears most closely related to *Stenogobius psilosinionus,* but differs by slightly shorter head, shorter preanal length, fewer scales in horizontal series, and by having predorsal midline always fully scaled. It nearest relative outside the species group appears to be *Stenogobius mekongensis.*

Description

D VI-I,10; A I,9 to I,10, almost always I,10; P 15 to 16, usually 16. LS 48 to 53, usually 50 to 51; TRB 11 to 14, usually 12; PD 16 to 22, usually 19 to 21; cheek almost always scaled; opercle scaled; pectoral base scaled. Jaw reaching under anterior edge of eye. Upper jaw teeth, males 1-4+0-2; females 1-3+0-2. Lower jaw teeth, males 2-6+1-3; females 2-3+1-2. Dentition varies with size and maturation of specimens.

Color in preservation: Background grayish; trunk with zero to four grayish to blackish crescentic bars between the second dorsal and anal fins, normally four present, two faint and narrow dusky bars may be present below first dorsal fin, usually absent on larger specimens; upper half of body may have irregular blackish spotting and streaks;

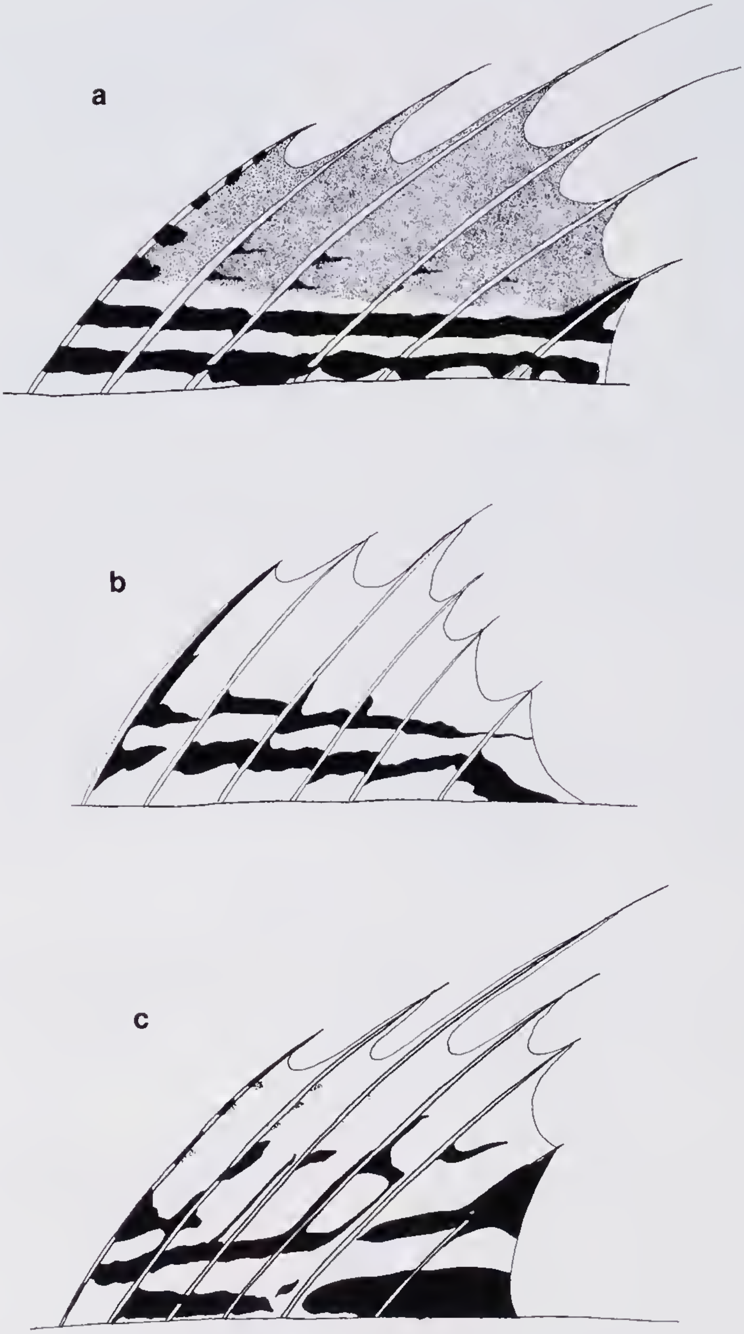

Figure 13 **a:** First dorsal fin on *Stenogobius ophthalmoporus;* **b:** First dorsal fin on *Stenogobius laterisquamatus;* **c:** First dorsal fin on *Stenogobius psilosinionus.*

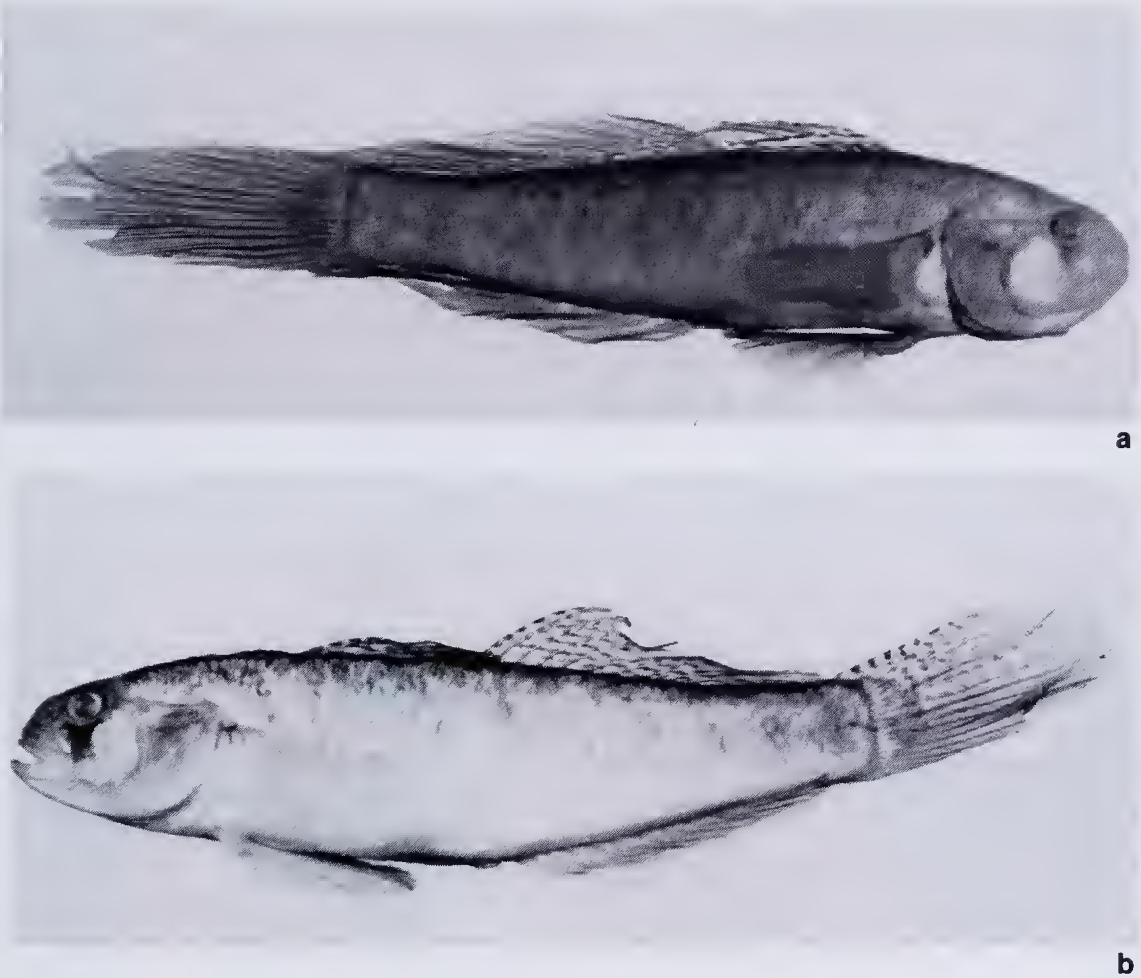

Figure 14 **a:** *Stenogobius ophthalmoporus* (Bleeker). USNM 257895, male (98.9). Luzon, Philippines. **b:** *Stenogobius ophthalmoporus* (Bleeker). LIAIP 1974067, female (87.4). Song Cai River, Vietnam.

suborbital bar short extending to or near posterior corner of jaw. First dorsal fin with black band along entire base, medially black band extending length of fin, translucent band separating both black bands, spines with black spots on distal half of fin; spine of second dorsal fin with four to six black marks, remainder of fin with four to six irregular rows of blackish pigmentation on both rays and membrane; upper unbranched and procurrent rays of caudal fin with four to seven blackish vertical streaks, upper half of fin may have dusky marks on rays forming irregular rows; membrane on pelvic disk and anal fin dusky, usually most pronounced on males, on females anal fin with light margin.

Color in life: Life colors of male based on Bleeker's original description: Body anteriorly and pectoral fin green; basal half of first dorsal fin glassy pinkish-green, above two blackish-violet longitudinal bands, outer half reddish-violet with two bands of violet; second dorsal fin pinkish-violet basally, reddish-violet in the middle and violet on the outer half; anal fin is reddish-violet with blackish-violet margin; caudal fin pinkish-violet, rays are golden, upper margin of fin reddish-violet. Life colors of female based on illustration from Akihito et al, 1984. Female background gray, belly pinkish-violet, dusky longituding streaking along midline with dusky spot on caudal fin base, near dorsal surface more longitudinal streaking; on back much dusky speckling; near isthmus the gill membrane pinkish-violet, fin markings similar to those described from preservation.

Remarks

Distribution: *Stenogobius ophthalmoporus* is known from Vietnam, Taiwan, Japan, Philippines and western Indonesia. The most widely distributed species represented in this study.

Ecology: Specimens examined were reported from estuaries in near marine conditions, to lowland rivers and streams in fresh water.

Note: *Aparrius sabagensis* is here regarded as a probable synonym based on the illustration and data given in original description. Types are no longer available having been destroyed during World War II.

In the listing of synonymies and citings for *Stenogobius ophthalmoporus* an inconsistency in spelling is noted for *lacrymosus* and *lachrymosus*. It is unclear why most previous authors failed to follow the spelling of the original description. The listing above reflects the spelling as each appears in accounts cited.

Stenogobius (Stenogobius) laterisquamatus (Weber 1908)

(Figures 15a, 15b & 15c)

Oxyurichthys laterisquamatus Weber, 1908: 261 (type locality: Moso River, tributary of Tami River, Dutch East Indies)

Paroxyurichthys laterisquamatus. — Koumans, 1953: 51

Material examined

Fourteen specimens from rivers on the northern coast of the island of New Guinea, totalling six males, six females, two juveniles; size range 38.2 to 197.1, largest males 197.1, largest female 152.4, no gravid material.

Syntypes

ZMA 116.477, two males (87.0-106.4), Moso River, tributary of Tami River, North New Guinea, Dutch East Indies, L.F. de Beaufort & M. Weber.

Additional material

AMS I.24632-001, male (97.3), Sepik River, Papua New Guinea, November 1982, D. Coates; FMNH 24604, male (149.2), Koragu, Sepik River, New Guinea, 23 May 1929, A.W.C.T. Herre; FMNH 24605,

Table 4 Pectoral ray counts in species of the subgenus *Stenogobius*.

	Pectoral rays			
	14	15	16	17
S. gymnopomus		1	18	1
S. ingeri		4	19	2
S. kenyae		5	6	
S. laterisquamatus		1	13	
S. macropterus	1	3		
S. mekongensis		2	3	2
S. ophthalmoporus		4	17	1
S. psilosinoinus		2	29	

juvenile (38.2), Marienberg, Sepik River, New Guinea, 27 May 1929, A.W.C.T. Herre; KFRS F03091, male (197.1), creek near Kapuramhembo near Embi, Papua New Guinea, 8 February 1971; KFRS F.5466-01, 4(83.3-103.3), one male, three females, Ramu River, channel between river island and eastern bank, four km south of Bunapas Mission, Madang, Papua New Guinea, 6 October 1987, G.R. Allen & L. Parenti; WAM P.27847-007, 3(44.2-75.8), two females, one juvenile, Kwatit River at confluence with Sepik River, Papua New Guinea, 28 October 1982, G.R. Allen & D. Coates; WAM P.28206-002, female (152.4), Sepik River near Pagwi, Papua New Guinea, 1 September 1983, D. Coates.

Diagnosis

Largest and most scaled *Stenogobius*; scales in horizontal series 52 to 62; cheek scaled; opercle scaled; predorsal midline 22 to 32 scales; belly anteriorly scaled; breast scaled; markings and patterns over body vary from one drainage to next; specimens retain juvenile markings to relatively large size (75.8 in this study) with sexual papilla not developed though distinguishable.

Relationship

This species most closely related to *Stenogobius psilosinionus* but differs in predorsal scales, size and body markings.

Description

D VI-I,10; A I,10; P 15 to 16, almost always 16. LS 52 to 62; TRB 14 to 16, usually 14 to 15; PD 22 to 32; cheek 22 to 104 scales; opercle 21 to 127 scales; belly anteriorly scaled next to pelvic base; breast scaled; number of scales increases with size of specimen, especially on cheek and opercle. Jaw reaching under pupil. Teeth in upper jaw, males 2-6+2-3; females 2-3+1-2. Lower jaw teeth, males 3-7+2; females 2-5+1-2.

Color in preservation: *Stenogobius laterisquamatus* most variable of all *Stenogobius* examined. Populations differ in form of color pattern from one river system to the next. Three color forms described below.

Sepik River: Background grayish; series of irregular blackish spots midlaterally; three blackish diagonal bars below second dorsal fin to midline on males, two similar bars below first dorsal fin; on females, no diagonal bars but a black spot on posterior edge of each scale on upper half of body; head grayish; nape dusky; ventral surfaces generally immaculate. First dorsal fin with translucent band along base terminating after sixth spine, black band originating at first spine terminating at or near tip of sixth spine,

Figure 15 **a:** *Stenogobius laterisquamatus* (Weber). AMS I. 24632-001, male (97.4). Sepik River, Papua New Guinea; **b:** *Stenogobius laterisquamatus* (Weber). WAM P.28206-002, female (149.2). Sepik River, Papua New Guinea; **c:** *Stenogobius laterisquamatus* (Weber), KFRS F.5466-01, male (103.3). Ramu River, Papua New Guinea.

medially another black band extending length of fin, both black bands separated by translucent band, along first spine black band extending along membrane from midlateral band to tip of spine; second dorsal fin with four rows of irregular black streaks located on membrane between rays forming bands almost entire length of fin; caudal fin with some black streaks forming irregular vertical bands limited to upper anterior half of fin; anal and pectoral fins dusky; pelvic disk dusky.

Ramu River: Background light tan; above midline all scales have dusky margin which forms a reticulated pattern, most pronounced on males; from behind pectoral base to caudal base with dusky trunk bars alternating in width and length, some appearing as blotches and others as crescentic bars, trunk bars only markings extending below midline numbering 14 in males and 11 in females. Vertical cheek bar very indistinct, appearing as short dusky bars radiating in three directions below eye; snout dusky in males. First dorsal fin similar to that described for specimens from Sepik River. Second dorsal fin in males with paired dusky streaks on membrane between rays near base of fin appearing as a continuation of bars on first dorsal fin, upper two thirds of fin with vertical dusky bars and limited to membrane between rays; females similarly marked but with three or four streaks instead of two. Anal fin dusky in males; females dusky on membrane between rays on basal half, rest of fin without pigmentation. Caudal fin in males with black spotting on upper procurrent rays, membrane between rays dusky; females with black spotting opn upper and anterior half of fin, lower two thirds of fin membrane dusky. Pelvic disk in males dusky medially to posterior edge of fin, anteriorly and laterally fin without pigmentation, pigmentation not on rays or spines; females without pigmentation. Pectoral fin translucent in both sexes.

Gogol River: Pattern based on slide of female (98 SL) provided by G.R. Allen. Specimen marked similarly to females from Ramu River. Many scales above midline have broad dusky marks which form uneven patterns as well as reticulation formed by dark scale margins. Midlateral bars not extending to lower half of body except on caudal peduncle. Fins marked similarly to those from Ramu River.

Remarks

Distribution: This species is endemic to the northern coast of the island of New Guinea.

Ecology: A river fish found in fresh water.

Note: *Stenogobius laterisquamatus* remains problematic, this is primarily due to size and pattern differences noted on specimens from different drainages without signs of intergradation. Morphometrics as well as scale counts fail to reveal data that would help distinguish between possible species. Electrophoresis may help to differentiate between species, if indeed significant differences exist. Though electrophoresis may prove helpful in resolving some of the problems in separating species of *Stenogobius*, this may not be entirely practical, specimens are often times difficult to obtain under the best of circumstances. The prospect of bringing properly chilled specimens in good condition for electrophoresis could prove almost impossible. Then there is no assurance that electrophoresis would yield revealing results. If enough evidence cannot be gathered to substantiate species, then it would seem likely that many subspecies exist.

Stenogobius (Stenogobius) psilosinionus, sp. nov.
(Figures 16a, 16b & 16c)

Stenogobius (Stenogobius) psilosinionus, sp. nov. (type locality: Fly River, Papua New Guinea)

Paroxyurichthys laterisquamatus. — Berra *et al*, 1975: 321

Stenogobius cf. *genivittatus*. — Roberts, 1978: 64

Material examined

Thirty two specimens from the southern coastal plain of New Guinea, totalling 13 males, 19 females; size range 29.2 to 96.5, largest male 96.5, largest female 94.5, no gravid material.

Holotype

USNM 217270, male (53.1), turbid fresh water creek, lower Fly River, 236 km upriver from Toro Pass, Papua New Guinea, 11 December 1975, T.R. Roberts.

Paratypes

KFRS F01876, male (96.5), Laloki River, Papua New Guinea, 9 June 1971; KFRS F03040, male (80.2), mouth of Kempwelch River, Papua New Guinea, 6 November 1970; KFRS F03449, male (80.5), Laloki River, 15 miles north of Port Moresby, Papua New Guinea, 20 June 1970, B.B. Collette; KFRS F.4314-02, female (57.8), 0.5 mile downstream from Aroa River bridge, Papua New Guinea, 18 April 1973; KFRS F.5048-03, male (96.4), Kibi Creek, Wabo damsite, Gulf Province, Papua New Guinea, 18 January 1977; USNM 217269, two females (35.3-35.8), shallow, muddy backwater open to Fly River mainstream opposite mouth of Suki Creek, 264 km upriver from Toro Pass, Papua New Guinea, 10 December 1975, T.R. Roberts; USNM 274591, three females (29.2-41.0), same collection data as holotype; USNM 279325, female (81.7), same collection data as KFRS F03449; WAM P.28201-008, 20(48.6-96.3), eight males, 12 females, Laloki River two km east of Bluff Inn Hotel, Papua New Guinea, 10 November 1982, G.R. Allen & J. Paska.

Diagnosis

Scales in lateral series 52 to 59; cheek scaled; opercle scaled; pectoral base scaled; breast scaled; belly anteriorly scaled next to pelvic base; predorsal midline usually with naked patches, seldom fully scaled; four blackish crescentic bars between second dorsal and anal fins, and two blackish crescentic bars below first dorsal fin, these markings extend to ventral surface.

Relationship

This species most closely related to *Stenogobius laterisquamatus;* it differs by having fewer scales along predorsal midline, slightly thicker caudal peduncle and smaller size.

Description

D VI-I,10; A I,10; P 15 to 16, almost always 16. LS 52 to 59, usually 54 to 58; TRB 11 to 16, usually 13 to 15; PD two to 25, usually with naked patches; cheek scaled; opercle scaled; pectoral base scaled; belly anteriorly scaled near pelvic base; breast scaled. Jaw reaching under anterior edge of eye. Upper jaw teeth, males 2-4+1-2; females 1+1. Lower jaw teeth, males 3-4+2-3; females 2-3+1-2.

Color in preservation: Background light tan on juveniles, light gray on females and dark gray on males; four blackish crescentic bars between second dorsal and anal fins, two blackish crescentic bars below first dorsal fin; nape with some blackish spotting, blackish spotting in area of first dorsal fin; snout dusky; upper opercle with some

Figure 16 **a:** *Stenogobius psilosinionus*, sp. nov., USNM 217270; HOLOTYPE, male (53.1). Fly River, Papua New Guinea; **b:** *Stenogobius psilosinionus*, sp. nov., KFRS F01876. PARATYPE, male (96.5). Laloki River, Papua New Guinea; **c:** *Stenogobius psilosinionus*, sp. nov., USNM 279325. PARATYPE, female (81.7), Laloki River, Papua New Guinea.

blackish spotting; markings not evident on small specimens; adults males much darker than females, especially at bases of dorsal and anal fins and on snout. First dorsal fin with black band at base originating either after first or second spine terminating at end of fin, translucent band above basal band originating at base of first spine, above a narrow black band extending from first spine to upper tip of fifth spine, distal half of fin dusky; second dorsal fin with some distinct black marks on spine, rest of fin with dusky streaks on membrane between rays forming irregular bands numbering three to four; upper half of caudal fin with dusky streaking forming irregular vertical bars; uppermost branches rays and procurrent rays with blackish streaking, lower half of fin dusky; anal fin dusky; pelvic disk dusky on males, translucent on females; pectoral fin translucent.

Remarks

Distribution: Known from the southern coastal plain of New Guinea.

Ecology: Known from lowland rivers and streams primarily over mud bottoms in fresh water.

Etymology: Name taken from the Greek words *psilos* (naked or bare) and *inion* (nape) in reference to the predominately naked predorsal midline.

***Insularigobius,* subgen. nov.**

(Tables 5 - 9)

Type species

Gobius genivittatus Valenciennes 1837: 64 (type locality: Tahiti).

Etymology

After the Latin word *insula* meaning island and *gobius* a name of a fish, in this case gobies; the name is in reference to the fact that all known specimens in this subgenus, including many not referred to in this paper, were reported only from island habitats, whether of continental or volcanic origin.

Description

Dorsal fin rays almost always VI-1,11; anal fin rays almost always 1,11; pectoral rays 14-16, almost always 15; first dorsal fin usually same height or shorter than second dorsal fin, spines of first dorsal usually flex posteriorly when fin is erect, spines not usually filamentous; jaw lengths usually sexually dimorphic; sensory papillae on lower preopercle in single row and may or may not have short transverse rows of papillae along lower edge of preopercle (Figures 4b & 4c); sexes are strongly dichromatic; body and fin markings tending not to differ between species; blackish mark on upper pectoral base continues anteriorly as a short bar under gill cover; two narrow blackish oblique bands from posterior edge of opercle to lower anterior edge of nape; all species have short vertical dash-like bars under most scales from midline to dorsal surface, zig-zag-like pattern formed by black margins on edges of scales along lateral midline from behind pectoral base to caudal fin base; juveniles with background of light tan to brown, laterally body covered with combination of brownish or blackish spots and bars; black oblique cheek bar prominent. Species belonging to this subgenus have close affinities with insular habitats throughout the tropical Indo-Pacific and has not been reported from continental habitats.

Insularigobius is divided into two principle groups. The *Stenogobius polyzona* species group which occurs in and peripheral to the Indian Ocean and the *S. genivittatus* species group of the western and central Pacific from French Polynesia and the Hawaiian Island to Japan and Indonesia. The *Stenogobius genivittatus* species group is further divided into three species complexes, the *S. genivittatus, S. blokzeyli* and *S. marqueti* complexes; these may or may not form a natural arrangement.

Key to species of the subgenus *Insularigobius*.

1a. Short rows of sensory papillae generally absent along lower preopercle (Figure 4b); first dorsal fin spotted in females .... 2.

1b. Short rows of sensory papillae along lower preopercle (Figure 4c); first dorsal fin in females with medial band or vertical pigmentation between spines .... 3.

2a. Eyes facing slightly upward; males without filamentous spines on first dorsal fin; jaw lengths weakly sexually dimorphic; northern New Guinea .... S. *beauforti* (Weber 1908).

2b. Eyes facing outward; adult males with filamentous spines on first dorsal fin; jaw lengths strongly sexually dimorphic; Madagascar and Reunion .... *S. polyzona* (Bleeker 1867).

3a. One or two large spots appearing on caudal peduncle of one or both sexes ...... 4.

3b. No spots appearing on caudal peduncle .... 6.

4a. Caudal peduncle length 13 to 14% of SL; Hiva Oa, Marquesas Islands .... *S. marqueti,* sp. nov.

4b. caudal peduncle length 14 to 16% of SL 5

5a. Breast almost always naked, seldom with few embedded scales; opercle almost always naked; predorsal midline usually with naked patches; Nuku Hiva, Marquesas Islands ... *S. caudimaculosus,* sp. nov.

5b. Breast almost always with few embedded scales, seldom naked; opercle usually with scales; predorsal midline almost always fully scales; Ua Pou, Marquesas Islands .... *S. squamosus,* sp. nov.

6a. Body depth in males at second dorsal origin 22 to 24% of SL; Philippines .... *S. kyphosus,* sp. nov.

6b. Body depth in males at second dorsal origin always 21% or less of SL .... 7.

7a. First dorsal fin in adult females with midlateral band and second dorsal fin with many small spots .... 10.

7b. First dorsal fin in adult females with blackish pigmentation between rays on membrane appearing as scribbles .... 8.

8a. Predorsal scales 16 to 23, usually 19 to 20; Hawaiian Islands .... *S. hawaiiensis*, sp. nov.

8b. Predorsal scales 13 to 20, usually 15 to 19 .... 9.

9a. Scales in lateral series 46 to 51, usually 48 to 49; Society Islands .... *S. genivittatus* (Valenciennes 1837).

9b. Scales in lateral series 49 to 52, usually 50 to 52; Tubuai Islands .... *S. randalli*, sp. nov.

10a. Mature males with elongate fins and no evidence of juvenile markings at less than 40 SL; trunk bars present but indistinct; New Britain, Bismarck Archipelago .... *S. alleni*, sp. nov.

10b. Mature males with elongate fins and no evidence of juvenile markings at greater than 40 SL; trunk bars generally distinct .... 11.

11a. Predorsal midline scale count highly variable and almost always with naked patches; breast naked or with few embedded scales... 12.

11b. Predorsal midline scale count not variable and almost always without naked patches; breast scaled or with numerous embedded scales ...... 13.

12a. Head and pectoral fin dusky on both sexes; trunk bars in females generally distinctive, numbering three to 10; Admiralty and Solomon Islands .... *S. hoesei*, sp. nov.

12b. Head and pectoral fin weakly dusky in males and not at all in females; trunk bars in females generally weak or absent, numbering zero to three; Irian Jaya, Indonesia .... *S. marinus*, sp. nov.

13a. First dorsal fin in large males often with filamentous spines; second dorsal fin in females with numerous spots that form two to five irregular rows; Yap and Palau Islands .... *S. fehlmanni*, sp. nov.

13b. First dorsal fin in large males without filamentous spines; second dorsal fin of females with spots that form two to three rows .... 14.

14a. Anterior teeth in one row of upper jaw of females; Lesser Sunda Islands, Indonesia .... *S. zurstrasseni* (Popta 1912).

14b. Anterior teeth in three rows on upper jaw of females; Bali .... *S. blokzeyli* (Bleeker 1861).

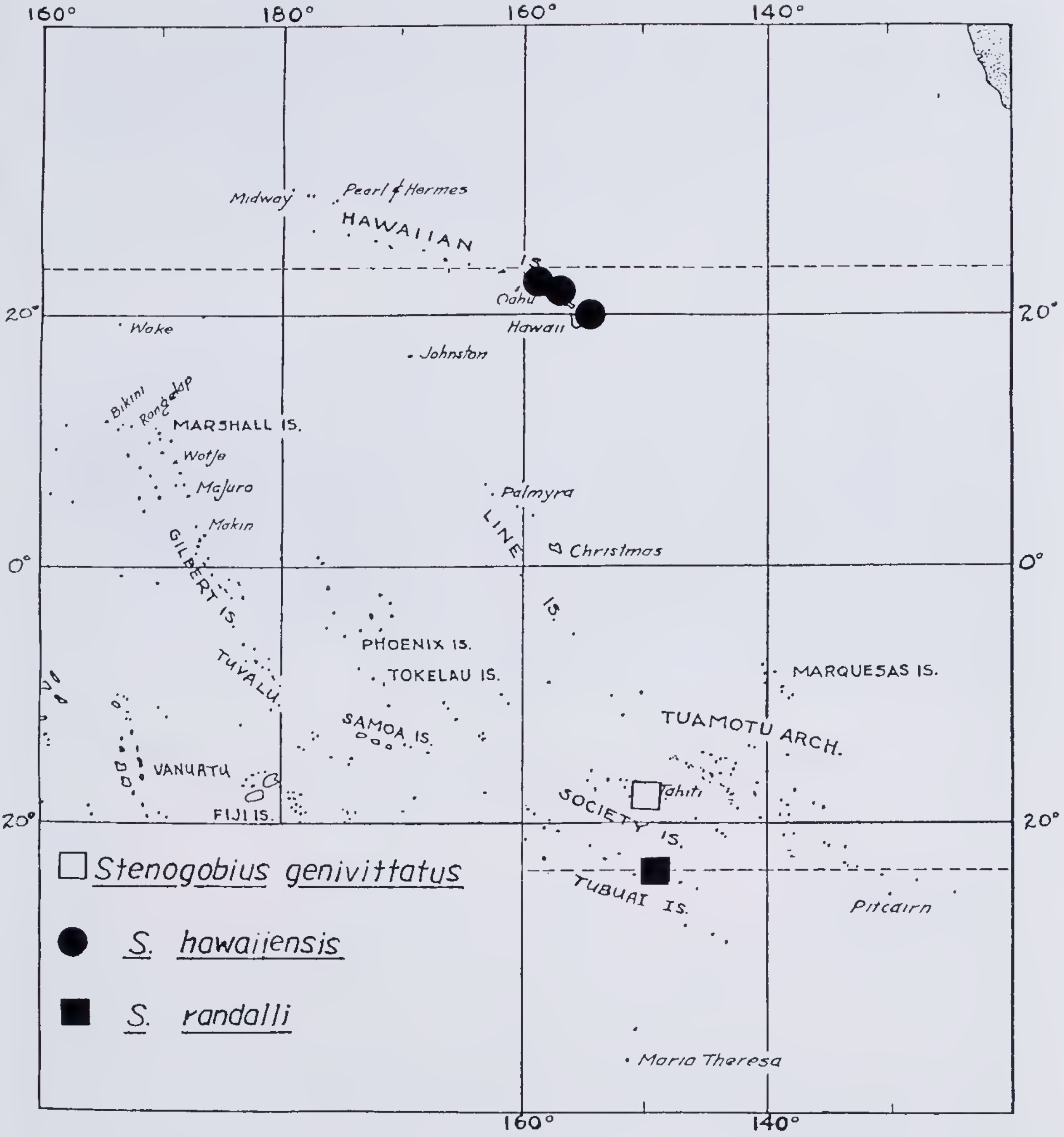

Figure 17 Distribution map of *Stenogobius genivittatus* species complex.

Stenogobius (Insularigobius) genivittatus **species group.**

Short transverse rows of papillae below lower preopercular cutaneous sensory papillae row (Figure 4c).

Sexual dimorphism well developed: Jaw lengths much greater on adult males, fins more elongate, more and larger teeth in both jaws.

Stenogobius (Insularigobius) genivittatus **species complex**

(Figure 17)

This complex is recognized in having predorsal midline almost always fully scaled, breast scaled, opercle may or may not be scaled, no spots on caudal peduncle. This complex includes three species of which two are described as new.

Stenogobius (Insularigobius) genivittatus **(Valenciennes 1837)**

(Figures 18a & 18b)

Gobius genivittatus Valenciennes, 1837: 64 (type locality: Tahiti)

Gobius genivittatus. — Gunther, 1861: 13 (in part)

Gobius genivittatus. — Gunther, 1877: 170 (in part)

Chonophorus genivittatus. — Fowler, 1928: 409 (in part)

Stenogobius genivittatus. — Koumans, 1935: 124 (in part)

Awaous genivittatus. — Fowler, 1938: 299 (in part)

Stenogobius genivittatus. — Koumans, 1953: 35 (in part)

Material examined

Fifty six specimens from the Society Island, French Polynesia, totalling 31 males, 24 females, one juvenile; size range 21.5 to 81.2, largest male 81.2, largest female 69.8, smallest gravid female 48.7.

Holotype

MNHN A.1344, male (52.0), Tahiti.

Additional material

BMNH 1873.4.3:96, female (67.3), Tahiti; BMNH 1926.10.25:6, male (43.6), Tahiti; CAS-SU 24708, male (48.8), creek, Moorea, Society Islands, 22 February 1929, A.W.C.T. Herre; FMNH 24600, female (58.4), freshwater, Tahiti, Society Islands, February 1929, A.W.C.T. Herre; FMNH 24601, male (58.1), same collection data as CAS-SU 24708; FMNH 24602, male (50.1), same collection data as CAS-SU 24708; MNHN 1927-140, male (46.9), Tahiti; MNHN 1984-804, three females (39.3-42.9), Tahiti, Society Islands, 1984, G. Marquet; MNHN 1987-926, 12(21.5-68.9), four males, seven females, one juvenile, Moorea, Society Islands, April 1986, G. Marquet; NMW 79818, male (51.1), Society Islands, 1874; USNM 270644, three males 953.9-65.9), Opunohu River, Moorea, Society Islands, March 1985, G. Marquet; USNM 278704, 20(43.4-69.3), 12 males, eight females, Moorea, Society Islands, 26 January 1986, G. Marquet; USNM 280372, 9(50.5-81.2), five males, four females, Tahiti, Society Islands, June 1986, G. Marquet.

Diagnosis

Scales on predorsal midline 13 to 20, usually 15 to 18; scales in horizontal series 46 to 51, usually 48 to 49; breast scaled; belly anteriorly with small naked patch next to pelvic base.

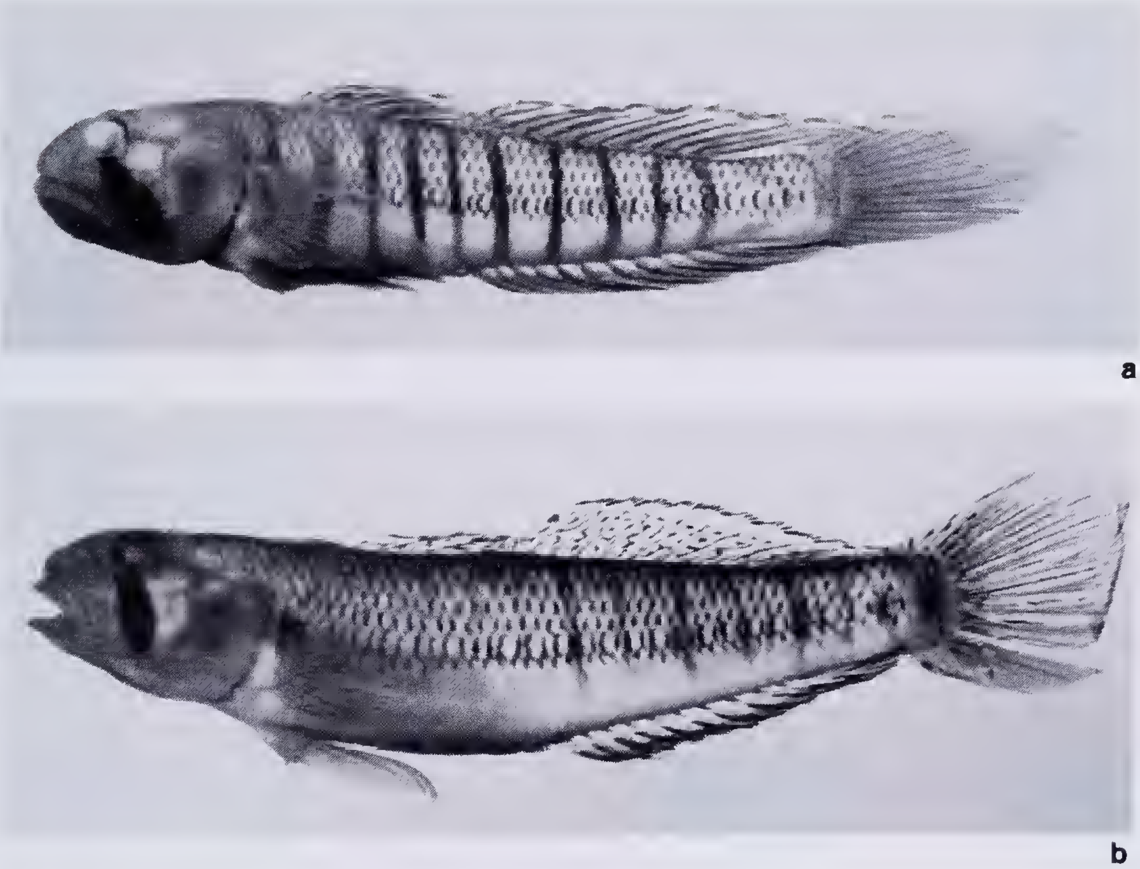

Figure 18 **a:** *Stenogobius genivittatus* (Valenciennes). USNM 278704, male (69.3), Moorea, Society Islands; **b:** *Stenogobius genivittatus* (Valenciennes). MNHN 1987-926, female (68.9). Moorea, Society Islands.

Relationship

Stenogobius genvittatus appearing most closely related to *S. randalli* differing by having fewer scales in horizontal series and fewer rows of teeth; it differs from *S. hawaiiensis* by having fewer predorsal scales, fewer teeth and usually more trunk bars in males.

Description

D VI-I,10 to VI-I,11, almost always VI-I,11; A I,10 to I,12, almost always I,11; P 15 to 16, usually 15. LS 46 to 51, usually 48 to 49; TRB 10 to 13, usually 12; PD fully scaled, 13 to 19, usually 15 to 17; cheek naked; opercle usually naked; upper pectoral base may or may not be scaled; lower pectoral base almost always naked; belly anteriorly with small naked patch posterior to pelvic base; breast scaled. Jaw reaching under posterior edge of pupil on females to beyond posterior edge of eye on males. Upper jaw teeth, males 2-5+1-2, usually 3+2; females 1-3+0-1, usually 1+0-1. Lower jaw teeth, males 3-4+1-3, usually 3+2; females 1-4+1-2, usually 1-2+1. Teeth in outer row enlarged in males.

Table 5 Morphometrics in species of the subgenus *Insularigobius* in percent of the standard length.

Species	Jaw length in males								
	8	9	10	11	12	13	14	15	16
S. alleni			1	2					
S. beauforti		2	6						
S. caudimaculosus		1	4	10	2	2			
S. fehlmanni		4	11	7	2	1	1		
S. genivittatus		8	14	6	3				
S. hawaiiensis	2	4	3	10	12	7	5	6	1
S. hoesei		1	5	6	3	2	1		
S. kyphosus				1	—	1	1		
S. marinus		1	7	14	4				
S. marqueti		3	8	5	7	1	2		
S. polyzona		4	4	6	5	3	1		
S. randalli				1	2	—	1		
S. squamosus		2	7	5	4				
S. zurstrasseni			2						

Species	Jaw length in females					
	8	9	10	11	12	13
S. alleni		4	3			
S. beauforti	2	9	8	1		
S. blokzeyli			2			
S. caudimaculosus		5	11	5		
S. fehlmanni	2	26	10	1		
S. genivittatus	2	9	10	—	1	
S. hawaiiensis	6	28	22	10	2	
S. hoesei		7	13	4		
S. kyphosus	1	2	2	3		
S. marinus		4	3	2		
S. marqueti		5	13	9		
S. polyzona	2	7				
S. randalli			1	—	2	
S. squamosus		6	8	2	3	1
S. zurstrasseni		5	3			

	Caudal peduncle depth in males				
	8	9	10	11	12
S. alleni		1	1	1	
S. beauforti		6	4		
S. caudimaculosus			13	6	
S. fehlmanni	2	16	15	3	
S. genivittatus		8	19	2	1
S. hawaiiensis	1	7	24	15	1
S. hoesei		4	12	2	1
S. kyphosus				2	2
S. marinus		9	14	3	
S. marqueti		7	18	1	
S. polyzona	1	7	4	5	
S. randalli			4		
S. squamosus		3	14	2	
S. zurstrasseni			2	1	

Table 5 (continued)

	Caudal peduncle depth in females						
	7	8	9	10	11	12	13
S. alleni			6	1			
S. beauforti		3	9	3	2		
S. blokzeyli				2			
S. caudimaculosus			2	12	7		
S. fehlmanni	1	1	28	17			
S. genivittatus			15	7	1		
S. hawaiiensis		8	10	35	5	1	1
S. hoesei			6	16	2	1	
S. kyphosus				8	1		
S. marinus			8	1			
S. marqueti			9	17	1		
S. polyzona			7	2	—		
S. randalli			2	1			
S. squamosus			7	7	5		
S. zurstrasseni			1	5	2		

	Caudal peduncle length						
	18	12	13	14	15	16	17
S. alleni		1	2	6	1		
S. beauforti		1	1	10	13	—	2
S. blokzeyli		1	1				
S. caudimaculosus			5	13	19	3	
S. fehlmanni		4	23	29	10	1	
S. genivittatus	2		3	20	23	5	
S. hawaiiensis	4	18	46	32	10	1	
S. hoesei	2	4	21	9	5		
S. kyphosus		3	7	2	1		
S. marinus		2	16	12	3	2	
S. marqueti		2	17	14	14	5	1
S. polyzona		2	2	13	7	7	1
S. randalli		4	2	1			
S. squamosus				3	20	13	2
S. zurstrasseni			6	2	2	1	

	Body depth at second dorsal fin origin on males										
	14	15	16	17	18	19	20	21	22	23	24
S. alleni				1	2						
S. beauforti				5	1	1					
S. caudimaculosus					4	9	4	2			
S. fehlmanni	1	1	5	5	8	4					
S. genivittatus			4	10	6	5	3	1			
S. hawaiiensis			4	1	6	7	5	1			
S. hoesei			2	4	6	2	1				
S. kyphosus									2	1	1
S. marinus			5	10	4	1					
S. marqueti		4	6	8	5	1					
S. polyzona		2	2	2	4	6	1				
S. randalli			1	1	1	1					
S. zurstrasseni					1	1					
S. squamosus			3	9	3	3					

Table 5 (continued)

	Head length									
	22	23	24	25	26	27	28	29	30	31
S. alleni				3	2	5				
S. beauforti			2	2	11	6	2	1	1	1
S. blokzeyli			1	1						
S. caudimaculosus					14	23	3			
S. fehlmanni			1	14	20	23	9	2		
S. genivittatus			5	9	27	11	2			
S. hawaiiensis	1	9	27	33	34	8	1			
S. hoesei				2	9	13	13	5		
S. kyphosus				3	5	5				
S. marinus					5	18	10	2		
S. marqueti				2	5	34	7	4	1	
S. polyzona				10	10	7	3	2		
S. randalli				1	2	4				
S. squamosus					11	23	4			
S. zurstrasseni				1	5	5				

	Predorsal length								
	31	32	33	34	35	36	37	38	39
S. alleni			1	5	4				
S. beauforti			3	8	5	6	4	—	1
S. blokzeyli					1	1			
S. caudimaculosus		1	7	13	14	4	1		
S. fehlmanni	2	5	12	17	18	11	3	1	
S. genivittatus		1	16	21	12	3			
S. hawaiiensis	7	13	20	34	15	6	2		
S. hoesei			2	8	15	13	3	1	
S. kyphosus			1	3	5	1	3		
S. marinus			2	15	13	4	2		
S. marqueti		2	6	13	21	11			
S. polyzona	3	4	7	9	6	2	1	1	
S. randalli		1	3	1	1	1			
S. squamosus		1	2	19	13	2			
S. zurstrasseni		1	3	2	2	2	1		

	Preanal length											
	50	51	52	53	54	55	56	57	58	59	60	61
S. alleni					2	1	4	3				
S. beauforti			1	3	8	5	8	2				
S. blokzeyli						1	—	—	—	—	—	1
S. caudimaculosus				3	8	15	9	4	1			
S. fehlmanni	3	6	9	16	16	10	6	1	2			
S. genivittatus					9	14	11	10	5	2	—	1
S. hawaiiensis	1	1	5	14	20	22	20	18	6	4	1	
S. hoesei		1	—	1	4	5	8	12	6	3	2	
S. kyphosus			1	2	—	4	3	1	2			
S. marinus				3	4	16	7	5				
S. marqueti			1	2	2	9	11	13	9	2	4	
S. polyzona			1	3	8	8	6	3	2	1		
S. randalli					1	2	2	1	—	—	—	1
S. squamosus					2	12	15	2	1	3	1	1
S. zurstrasseni		2	2	1	3	1	1	—	—	1		

Color in preservation: Basic color of body tannish or brownish to grayish; blackish trunk bars in males originate behind pectoral base extending to hypural base, extending from dorsal surface to ventral surface, usually poorly marked on caudal peduncle; in females trunk bars between second dorsal and anal fins extending to hypural base, two or three weak dusky bands may be found below first dorsal fin to midline, trunk bars in females lack intensity found in males. In both sexes membrane between spines and rays of both dorsal fins with markings appearing as irregular scribbles. outer margin in both sexes with blackish border; blackish streaking on membrane between rays of caudal fin. Pelvic disk dusky with blackish band between fifth rays in males; in females pelvic disk is colorless except dusky streak between fifth rays. Anal fin in males dusky with light margin along entire base; in females anal fin is dusky with light margin along edge of fin.

Color in life: Life color of males bases on freshly collected specimens provided by G. Marquet, represented in collection USNM 280372. Color in males similar to those described in preservation. Outer margin of both dorsal fins reddish with thin blue line along edge. Life color in females based on a slide provided by G. Marquet, of a specimen approximately 70 SL photographed at night in an estuary on Tahiti. Females do not appear to differ much from description in preservation. Outer margin of anal fin bluish; some blue flecks on head and pectoral base appears bluish.

Remarks

Distribution: *Stenogobius genivittatus* is herein considered an endemic species of the Society Islands, French Polynesia.

Ecology: All specimens were reported from fresh water in either streams or estuaries. According to G. Marquet (pers. comm.) on Tahiti this species does not leave the upper reaches of estuaries, but on Moorea it moves well inland to the bases of waterfalls.

Stenogobius (Insularigobius) hawaiiensis, sp. nov.
(Figures 19a & 19b)

Stenogobius (Insularigobius) hawaiiensis, sp. nov. (type locality: Honolulu, Oahu, Hawaiian Islands)

Awaous genivittatus. — Jenkins, 1902: 52

Awaous genivittatus. — Jordan & Evermann, 1905: 492

Awaous genivittatus. — Fowler, 1938: 299 (in part)

Chonophorus genivittatus. — Gosline & Brock, 1960: 269

Chonophorus genivittatus. — Tinker, 1978: 394

Material examined

One hundred and fifty six specimens from the Hawaiian Islands, totalling 52 males, 69 females, 35 juveniles; size range 19.7 to 114.3, largest male 114.3, largest female 93.9, smallest gravid female 47.6.

Holotype

CAS-SU 07552, male (114.3), Honolulu, Oahu, Hawaiian Islands, July 1901, A. Seale.

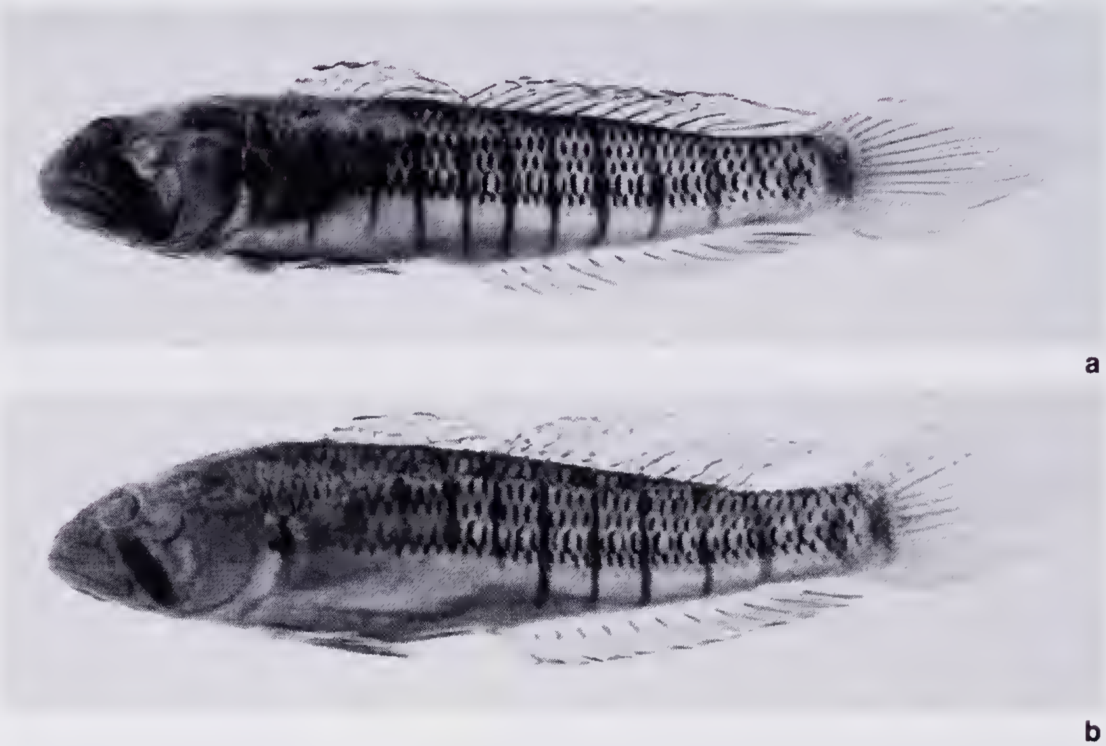

Figure 19 **a:** *Stenogobius hawaiiensis,* sp. nov., BPBM 26373, PARATYPE, male (86.9), Molokai, Hawaiian Islands; **b:** *Stenogobius hawaiiensis,* sp. nov., BPBM 26373, PARATYPE, female (79.6). Molokai, Hawaiian Islands.

Paratypes

AMNH 2349, 3(56.1-95.0), one male, two females, Hawaiian Island, 1896; ANSP 86151, 9(67.0-93.7), three males, six females, same collection data as holotype; ANSP 91401, 38(23.1-96.5), 15 males, 21 females, two juveniles, Laie Stream, Oahu, Hawaiian Islands, November 1922, C.M. Cooke et al; BPBM 26373, 4(76.1-86.9), two males, two females, Kewalo Stream, Molokai, Hawaiian Islands, 28 March 1980, R.E. Watson; BPBM 26380, 2(71.3-83.6), one male, one female, Kaipapau Stream, Oahu, Hawaiian Islands, 4 July 1980, R.E. Watson; CAS 22830, 2(39.2-71.4), one male, one female, Hanalei River, Kauai, Hawaiian Islands, 7 August 1949, P.R. Needham et al; CAS 58053, 6(72.1-110.0), three males, three females, same collection data as holotype; UAIP 1974002, 5(35.5-56.9), two males, three females, Nuuanu Stream, Honolulu, Oahu, Hawaiian Islands, 9 March 1974; USNM 55146, 11(46.8-73.7), three males, eight females, Waimea River, Kauai, Hawaiian Islands, June 1902, Albatross Expedition; USNM 55166, two males (92.9-99.5), Honolulu, Oahu, Hawaiian Islands, July 1902, Albatross Expedition; USNM 55392, 16(55.7-96.7), seven males, nine females, Hilo, Hawaii, Hawaiian Islands, 16 July 1902, Albatross Expedition; USNM 55393, 4(49.0-59.6), one male, three females, Hanapepe River, Kauai, Hawaiian Islands, June 1902, Albatross Expedition; USNM 55394, 31(19.7-81.2), five males, seven females, 19 juveniles, Hanalei River, Kauai, Hawaiian Islands, 22 June 1902, Albatross Expedition; USNM 121870, 2(33.1-55.1), one female, one juvenile, Haleiwa, Oahu, Hawaiian Islands, 10 December 1944, J.R. Simon; USNM 214000, 4(39.6-75.6), two males, two females, Kahana Stream, Oahu, Hawaiian Islands, July 1971, A. Timbol.

Additional material

CAS 22828, male (32.5), Hanalei River, Kauai, Hawaiian Islands, 31 July 1949, J.R. Needham et al;

MNHN 8909, two males (98.2-100.0), Sandwich Islands, ca. 1870, M. Ballieu; USNM 279324, 13 juveniles (20.4-38.8), same collection data as USNM 55393.

Diagnosis

Largest *Insularigobius* recorded; possesses a relatively high scale count in horizontal series, 47 to 52, usually 48 to 50; high predorsal scale count, always fully scaled, 16 to 23, usually 19 to 20; belly anteriorly almost always scaled close to pelvic base; breast always with many embedded scales; up to five rows of teeth in upper jaw and up to six in lower jaw.

Relationship

Stenogobius hawaiiensis is most closely related to *S. genivittatus*. It differs from that species by possessing a slightly deeper caudal peduncle, generally more predorsal scales, males with more teeth in upper and lower jaws, by being of much greater length, and by having slightly fewer lateral trunk bars.

Description

D VI-I,10 to VI-I,11, almost always VI-I,11; A I,10 to I,11, almost always I,11; P 14 to 16, usually 15; first dorsal fin slightly filamentous in males, most pronounced on fourth and fifth spines. LS 47 to 52, usually 48 to 50; TRB 11 to 14, usually 11 to 12; PD fully scaled, 16 to 23, usually 19 to 20; cheek almost always naked; opercle may or may not be scaled; upper pectoral base may or may not be scaled; lower pectoral base almost always naked; belly anteriorly with small naked patch adjacent to pelvic base; breast always with embedded scales. Jaw reaching under and beyond eye in males and under pupil in females. Upper jaw teeth, males 2-6+1-3, usually 3-4+1-2; females 1-4+0-2, usually 1-2+0. Lower jaw teeth, males 3-6+1-3, usually 3-6+2; females 2-5+1-2, usually 3+1.

Color in preservation: Pattern on body similar to that described for the subgenus. differences in females are small spots on upper caudal fin and two to four trunk bars below first dorsal fin; small females may have spots on membrane between spines and rays that form two to three rows, adult females never display this characteristic and have vertical pigmentation between spines and rays on membrane that appear as scirbbles.

Color in life: Life colors are based on slides of living and freshly preserved specimens as well as observations in the field by the author. In both males and females suborbital bar is edged in blue; pectoral base bluish; head and upper body greenish; outer margins of pelvic and anal fins bluish; lower margin of caudal fin bluish, upper caudal fin with two bluish-white bands. In males lower three fourths of both dorsal fins pinkish with purplish pigmentation on membrane between rays and spines; outer margin of both fins reddish. Females similarly marked, but lacks the intensity of males. It is interesting to note that the intensity of body and most fin markings in life never seemed to achieve those of freshly killed material. Observation of breeding and brooding males lacked the intensity of those after death as well. Even vertical trunk bars are more intense in preservation than in life.

Remarks

Distribution: Known only from the high islands of Hawaii.

Table 6a Fin lengths in males of species belonging to the subgenus *Insularigobius*, expressed to the nearest whole percent of the standard length.

	Second dorsal fin length																								
	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57						
S. alleni						1	—	—	—	—	—	—	—	—	1	1									
S. beauforti	1	1	—	1	—	1	—	1	—	—	—	3													
S. caudimaculosus		1	—	1	2	—	2	2	2	—	4	—	1	2	—	—	1	1							
S. fehlmanni					1	—	—	2	2	2	1	1	2	7	—	4	2	2	—	—	1	—	—	—	1
S. genivittatus						1	1	2	—	4	2	4	4	6	1	2	1	—	2						
S. hawaiiensis				2	3	2	1	1	2	1	3	2	7	3	5	4	5	3	—	1	—	1			
S. hoesei					1	1	—	2	3	1	—	2	1	1	—	2	—	2	2						
S. kyphosus																		2	—	—	1	—	—	1	
S. marinus				2	—	3	4	5	1	3	—	4	—	2	1	—	—	1							
S. marqueti	1	—	1	2	—	3	1	2	2	—	4	2	4	2	1	1	—	—	—	1					
S. polyzona					2	—	1	1	1	1	2	3	—	2	1	—	1	1	3	1	—	—	1		
S. randalli															2	1	—	1							
S. squamosus	1	—	1	2	1	4	1	1	—	1	1	2	1	—	1	—	—	1							
S. zurstrasseni							1	—	1																

	Anal fin length																	
	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56
S. alleni							1	—	—	—	1	—	1					
S. beauforti	1	2	—	—	—	1	2	2										
S. caudimaculosus			1	3	2	6	2	1	—	2	—	—	2					
S. fehlmanni	1	—	1	1	1	3	—	4	1	2	4	6	2	—	1	1		
S. genivittatus				1	—	2	1	4	6	6	2	4	2	2				
S. hawaiiensis		1	1	3	1	2	3	3	5	4	5	6	2	5	1	1	2	2
S. hoesei				3	3	3	2	1	1	1	—	1	—	2	—	1		
S. kyphosus													1	—	3			
S. marinus			1	2	2	3	5	6	4	1	1	1						
S. marqueti	1	1	—	4	2	—	3	3	6	2	1	1	1	1				
S. polyzona	1	—	2	1	1	1	—	3	4	1	1	2	3	2				
S. randalli											1	1	1	1				
S. squamosus		2	3	2	2	1	—	3	2	1	1	1						
S. zurstrasseni			1	1														

Table 6a (continued)

	Caudal fin length																								
	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42						
S. alleni						1	—	—	—	—	—	—	—	1	—	1									
S. beauforti					2	—	—	—	1	1	—	—	2												
S. caudiimaculosus		1	1	2	5	5	1	1	—	2	—	—	1												
S. fehlmanni			1	1	—	—	2	3	—	—	1	2	1	3	3	3	2	2	—	—	—	—	—	1	1
S. genivittatus					1	3	1	1	2	7	3	1	2	2	1										
S. hawaiiensis		2	3	1	—	1	3	5	3	3	4	5	4	4	3	1	2	1	1	1					
S. hoesei						1	2	2	4	1	2	1	—	3	—	1									
S. kyphosus																		1	1	—	—	—	—	1	
S. marinus			1	1	—	3	1	5	8	—	2	1	1	1											
S. marqueti	1	2	—	3	2	—	3	3	3	5	—	2	1	—	—	—	—	1							
S. polyzona				1	1	—	1	—	1	—	1	3	—	—	4	1	—	4	1	—	—	—	1		
S. randalli														1	—	3									
S. squamosus			2	4	—	—	4	—	2	1	—	1													
S. zurstrasseni				1	—	1																			

Table 6b Fin length in females of species belonging to the subgenus *Insularigobius*, expressed to the nearest whole percent of the standard length.

	Second dorsal fin length														
	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
S. alleni			1	—	5	—	—	1							
S. beauforti				4	5	3	4	—	1						
S. blokzeyli													1		
S. caudimaculosus						2	1	7	6	3	2				
S. fehlmanni		2	—	4	5	7	9	5	3	2	3	1			
S. genivittatus			1	1	2	4	3	3	4	2	3				
S. hawaiiensis					5	1	4	6	14	15	7	10	3	1	2
S. hoesei	1	—	—	—	2	1	5	4	6	4	—	1			
S. kyphosus						1	—	1		3	1	2	—	—	1
S. marinus		1		2	3	—	3								
S. marqueti			1	2	2	3	8	6	4	1					
S. polyzona			2	—	1	1	—	2	2	1					
S. randalli									1	—	1	1			
S. squamosus				3	5	1	5	2	1	2	1				
S. zurstrasseni						4	1	1	1						

	Anal fin length														
	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
S. alleni				—	2	3	1	1							
S. beauforti				2	—	8	4	3							
S. blokzeyli						1									
S. caudimaculosus							4	4	5	8					
S. fehlmanni	2	—	2	2	3	7	12	9	1	1	2				
S. genivittatus					1	1	5	5	4	4	2				
S. hawaiiensis		1	1		2	1	6	7	13	13	15	3	1	—	2
S. hoesei						4	3	7	4	6					
S. kyphosus						1	1	2	1	1	—	3			
S. marinus				3	1	2	3								
S. marqueti				1	1	4	3	10	6	—	2				
S. polyzona				1		1	1	1	1						
S. randalli								1			—	2			
S. squamosus						1	5	8	3	3					
S. zurstrasseni						1	—	2	3	1					

	Caudal fin length													
	21	22	23	24	25	26	27	28	29	30	31	32	33	34
S. alleni					1	2	3	—	1					
S. beauforti				1	1	4	4	6	1					
S. blokzeyli							1							
S. caudimaculosus					3	9	9							
S. fehlmanni					1	5	8	10	8	4	3			
S. genivittatus					2	2	6	7	2	1				
S. hawaiiensis			2	3	4	10	12	12	8	5	2	2	1	1
S. hoesei					1	—	5	4	8	3	—	2		
S. kyphosus						2	1	1	1	3				
S. marinus					1	3	1	1	3					
S. marqueti	1	—	1	1	3	8	11	1						
S. polyzona					1	—	5	1	1		1			
S. randalli									2	—	—	1		
S. squamosus					5	8	5	1	1					
S. zurstrasseni					1	3	2	—	—	1				

Ecology: Known from fresh water streams, rivers and upper reaches of estuaries always close to the coast. This species is common over fine gravel and stones in areas of riffles.

Etymology: This species is named for the Hawaiian Islands where it is an endemic.

Stenogobius (Insularigobius) randalli, sp. nov.
(Figure 20)

Stenogobius (Insularigobius) randalli, sp. nov. (type locality: Tubuai, Tubuai Islands, French Polynesia)

Material examined

Seven specimens from Tubuai, Tubuai Islands, French Polynesia, totalling four males, three females; size range 48.1 to 82.8, largest male 82.8, largest female 75.9, no gravid material.

Holotype

USNM 280371, male (80.2), fresh water stream, Tubuai, Tubuai Islands, French Polynesia, July 1986, G. Marquet.

Paratypes

USNM 292573, 6(48.1-82.8), three males, three females, same collection data as holotype.

Diagnosis

Predorsal midline fully scaled ranging 17 to 20, usually 18 to 19; scales in horizontal series 49 to 52, usually 50 to 51; TRB 12 to 13; breast scaled; upper pectoral base usually with one to three scales; opercle may or may not be scaled; first and second dorsal fins in females with pigmentation on membrane between spines and rays appearing as vertical bars, generally not appearing as scribbles.

Relationship

This species appears closest to *Stenogobius genivittatus,* but has more scales along predorsal midline, in horizontal series as well as generally more teeth in both jaws. When compared to *Stenogobius hawaiiensis* it differs by having slightly shorter caudal peduncle and smaller size; females tend to be slightly longer jawed, and have more teeth in both jaws.

Description

D VI-I,10 to VI-I,11, usually VI-I,11; A I,11 to I,12, usually I,11; P 15 to 16. LS 49 to 52, usually 50 to 51; TRB 12 to 13; PD 17 to 20, usually 18 to 19; cheek naked; opercle may or may not be scaled; upper pectoral base usually scaled; lower pectoral base usually naked; breast scaled; belly anteriorly scaled close to pelvic base. Jaw extending under posterior edge of pupil on both sexes to beyond posterior edge of eye in males. Upper jaw teeth, males 3-5+1-2, usually 3+2; females 3+1. Lower jaw teeth, males 3-4+2-3, usually 3-4+2; females 4+2. Teeth on outer row enlarged in males.

Color in preservation: In both sexes coloration and pigmentation very close to that of *Stenogobius genivittatus,* pigmentation on both dorsal fins differ in appearing as vertical bars between rays and spines instead of appearing as scribbles.

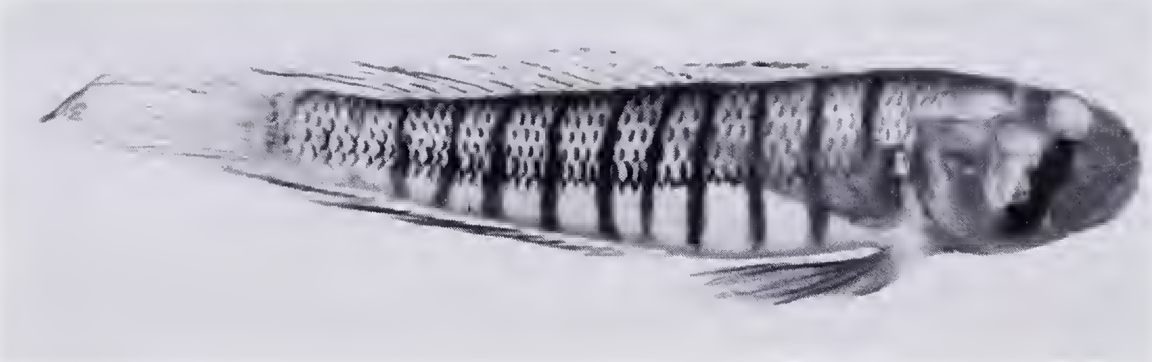

Figure 20 *Stenogobius randalli*, sp. nov., USNM 280371. HOLOTYPE, male (80.2). Tubuai, Tubuai Islands.

Color in life: Life color of both sexes based on freshly collected specimens from type lots. Color of males similar to those described for *Stenogobius genivittatus*. Outer margin of both dorsal fins reddish with thin blue line along edge. In females outer margin of anal fin bluish; some blue flecks on head; pectoral base bluish.

Remarks

Distribution: *Stenogobius randalli* is currently known only from type locality.

Etymology: This species is named in honor of John E. Randall for his many contributions to Indo-Pacific ichthyology.

Stenogobius (Insularigobius) marqueti species complex.

(Figure 21)

This species complex is limited to the Marquesas Islands of French Polynesia. The group currently includes three species, all of which are described as new, more species may exist. The species represented are *Stenogobius marqueti*, *S. caudimaculosus* and *S. squamosus*.

It is reasonable to assume as more ichthyological surveys take place in the Marquesas Islands additional new taxa will be discovered. Recent revisions of other gobioid genera, such as Hoese & Randall (1982) and Randall & Hoese (1985), have demonstrated the existence of several endemic species at this locality.

Stenogobius (Insularigobius) marqueti, sp. nov.

(Figures 22a & 22b)

Stenogobius (Insularigobius) marqueti, sp. nov. (type locality: Hiva Oa, Marquesas Islands, French Polynesia)

Material Examined

Sixty five specimens from Hiva Oa, Marquesas Islands, French Polynesia, totalling 33 males, 30 females, two juveniles; size range 24.0 to 73.9, largest male 73.9, largest female 66.6, smallest gravid female 42.8.

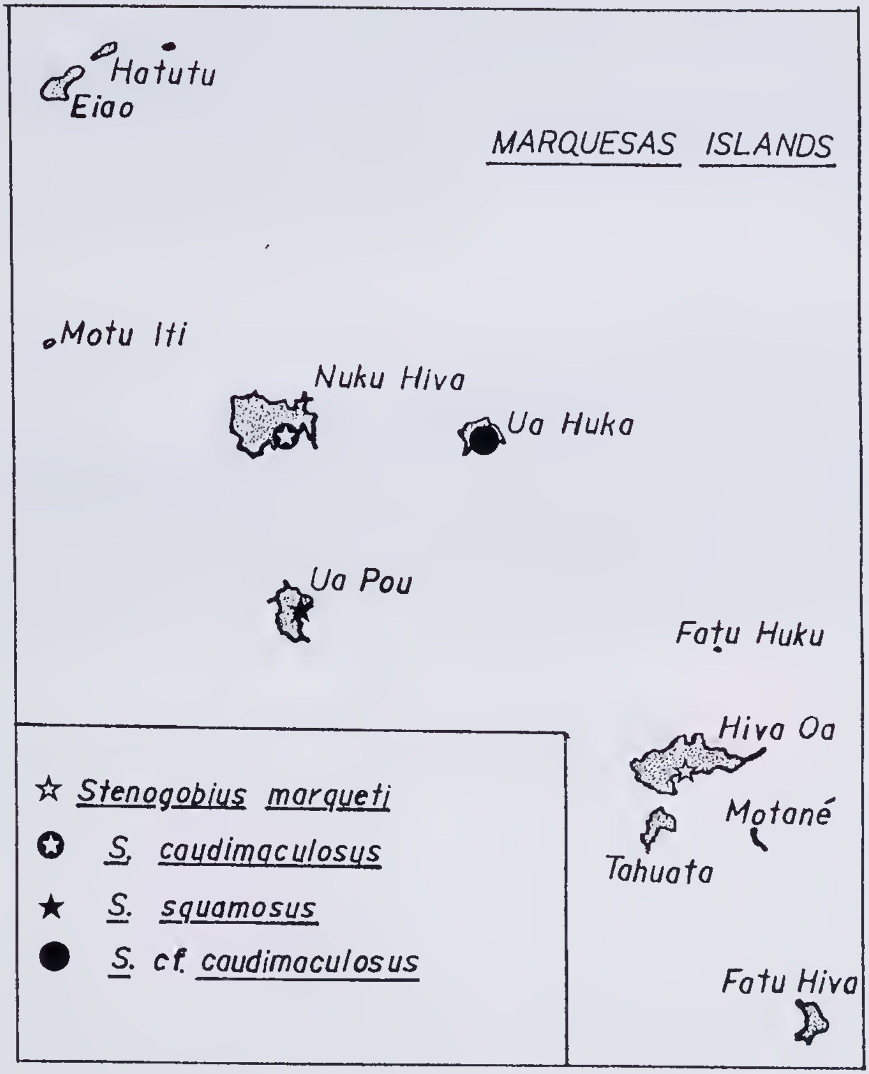

Figure 21 Distributional map of *Stenogobius marqueti* species complex.

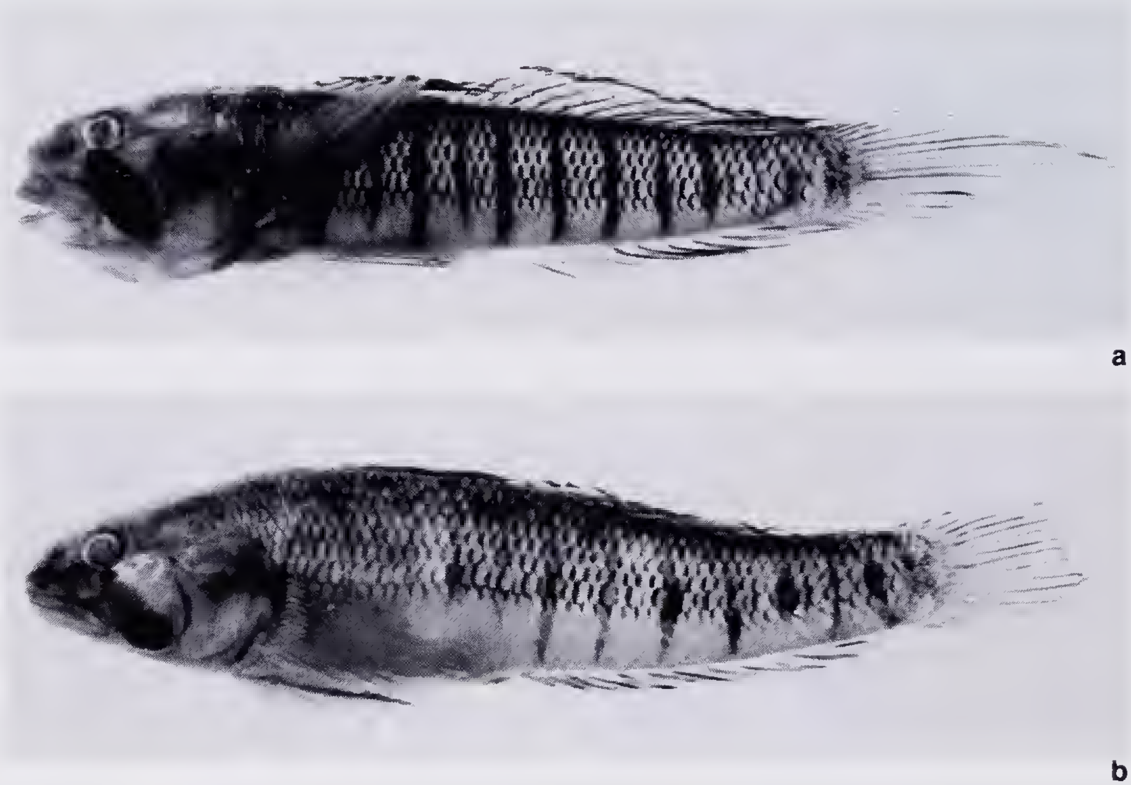

Figure 22 a: *Stenogobius marqueti*, sp. nov., MNHN 1987-930, PARATYPE, male (73.9). Hiva Oa, Marquesas Islands; b: *Stenogobius marqueti*, sp. nov., MNHN 1987-930, PARATYPE, female (63.4). Hiva Oa, Marquesas Islands.

Holotype

CAS-SU 24497, male (50.7), Hiva Oa, Marquesas Islands, French Polynesia, February 1929, A.W.C.T. Herre.

Paratypes

AMS I.26910-001, 9(33.5-61.1), three males, six females, Hiva Oa, Marquesas Islands, French Polynesia, 8 January 1987, G. Marquet; BPBM 12126, 20(24.1-67.4), 16 males, three females, one juvenile, fresh water stream entering head of Tahauku Bay, Hiva Oa, Marquesas Islands, French Polynesia, 25 April 1971, J.E. Randall et al; CAS 58054, 5(34.6-53.2), same collection data as holotype; MNHN 1987-930, 8(24.0-73.9), five males, two females, one juvenile, same collection data as AMS I.26910-001; SMF 21567, 5(45.2-61.6), two males, three females, same collection data as AMS I.26910-001; USNM 289987, 8(50.4-54.9), four males, four females, same collection data as AMS I.26910-001; WAM P.29656-001, 9(35.5-60.5), same collection data as AMS I.26910-001.

Diagnosis

Scales on predorsal midline six to 21, usually 15 to 19, sometimes with naked patches; scales in a horizontal series 48 to 51, usually 49 to 50; breast usually with one to five embedded scales, may be naked; belly anteriorly with large naked patch near pelvic base; pectoral base naked; opercle naked; females with one or two large spots on caudal peduncle.

Table 7 Scale counts in species of the subgenus *Insularigobius*.

	Lateral series								
	44	45	46	47	48	49	50	51	52
S. alleni				4	4	1			
S. beauforti		1	3	5	13	3	2		
S. caudimaculosus					2	17	12	7	1
S. fehlmanni			1	6	15	22	13	5	
S. genivittatus			1	7	14	16	8	5	
S. hawaiiensis				2	25	40	27	16	4
S. hoesei	1	2	2	11	14	7			
S. kyphosus		1	—	2	6	2	—	1	
S. marinus	2	1	2	2	8	10	1		
S. marqueti					4	17	29	5	
S. polyzona				4	13	8	2		
S. randalli						1	2	3	1
S. squamosus						5	18	15	
S. zurstrasseni				4	7	7	10	1	

Table 7 — continued

	Predorsal scales																							
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
S. alleni			1	—	—	—	—	—	—	—	—	—	—	1	—	2	1	2	3					
S. beauforti														2	1	4	6	4	6	5				
S. caudimaculosus	1	—	1	1	—	—	3	—	—	1	1	2	1	1	3	5	3	5	5	7	3			
S. fehlmanni										1	—	—	—	—	3	13	15	25	10	1				
S. genivittatus													1	2	11	17	13	7	4					
S. hawaiiensis																	3	10	16	33	23	22	7	2
S. hoesei					1	—	1	—	—	1	1	2	3	4	7	12	2	6	3					
S. kyphosus																1	1	5	3	1	1	1		
S. marinus			2	1	2	1	2	—	1	3	1	1	1	3	2	4	1	4	4	1				
S. marqueti							1	1	—	—	2	—	2	1	2	7	8	12	7	9	4	1		
S. polyzona																3	15	5	7	1				
S. randalli																			1	2	3	1		
S. squamosus																2	3	11	9	9	1	2	2	
S. zurstrasseni												1	—	—	1	3	11	6	6	3				

Relationship

Stenogobius marqueti appears more like *S. genivittatus* than its closer relatives *S. squamosus* and *S. caudimaculosus.* It differs from *Stenogobius genivittatus* by having fewer scales, being more slender, and the presence of a spot or spots on the caudal peduncle of females.

Description

D VI-I,11; A I,11; P 15 to 16, almost always 15. LS 48 to 51, usually 49 to 50; TRB 12 to 14, usually 13; PD six to 21, may have naked patches; cheek naked; opercle naked; pectoral base naked; belly anteriorly with large naked patch near pelvic base; breast usually with one to five embedded scales, never fully scaled, but may be naked. Jaw reaching under pupil to posterior edge of eye in males; in females usually under center of eye. Upper jaw teeth, males 1-4+0-2, usually 2-3+1-2; females 0-2+0-1, usually 0-1+0. Lower jaw teeth, males 2-4+1-2, usually 2-4+1-2; females 2-3+0-1, usually 2-3+1. Teeth in outer row slightly enlarged in males.

Color in preservation: In both sexes body markings similar to those described for *Insularigobius,* except females have one or two spots on caudal peduncle. In males first and second dorsal fins have dusky bars on membrane between rays and spines that tend to be adjacent to anterior edge of each spine or ray and do not appear as scribbles, but rather as bars; pectoral fins and pelvic disk dusky, pelvic disk with blackish band between the fifth rays; upper margin of caudal fin with two white bands, rest of fin almost entirely dusky, darkest on membrane between rays.

Remarks

Distribution: *Stenogobius marqueti* is known only from fresh water streams on the island of Hiva Oa, Marquesas Islands.

Etymology: This species is named in honor of Gerard Marquet in appreciation of his extensive collection efforts in fresh waters throughout French Polynesia and the discovery of four new species of *Stenogobius.*

Stenogobius (Insularigobius) caudimaculosus, sp. nov.

(Figures 23a, 23b & 23c)

Stenogobius (Insularigobius) caudimaculosus, sp. nov. (type locality: Nuku Hiva, Marquesas Islands, French Polynesia)

Material examined

Fourty three specimens from Nuku Hiva, Marquesas Islands, French Polynesia, totalling 19 males, 21 females, three juveniles; size range 24.8 to 69.9, largest male 69.9, largest female 68.5, smallest gravid female 49.4.

Holotype

MNHN 1987-929, male (69.9), fresh water stream, Nuku Hiva, Marquesas Islands, French Polynesia, 28 December 1986, G. Marquet.

Paratypes (same collection data as holotype)

AMS I.26911-001, 9(41.3-62.7), five males, four females; MNHN 1987-1843, 12(24.8-68.5), four males,

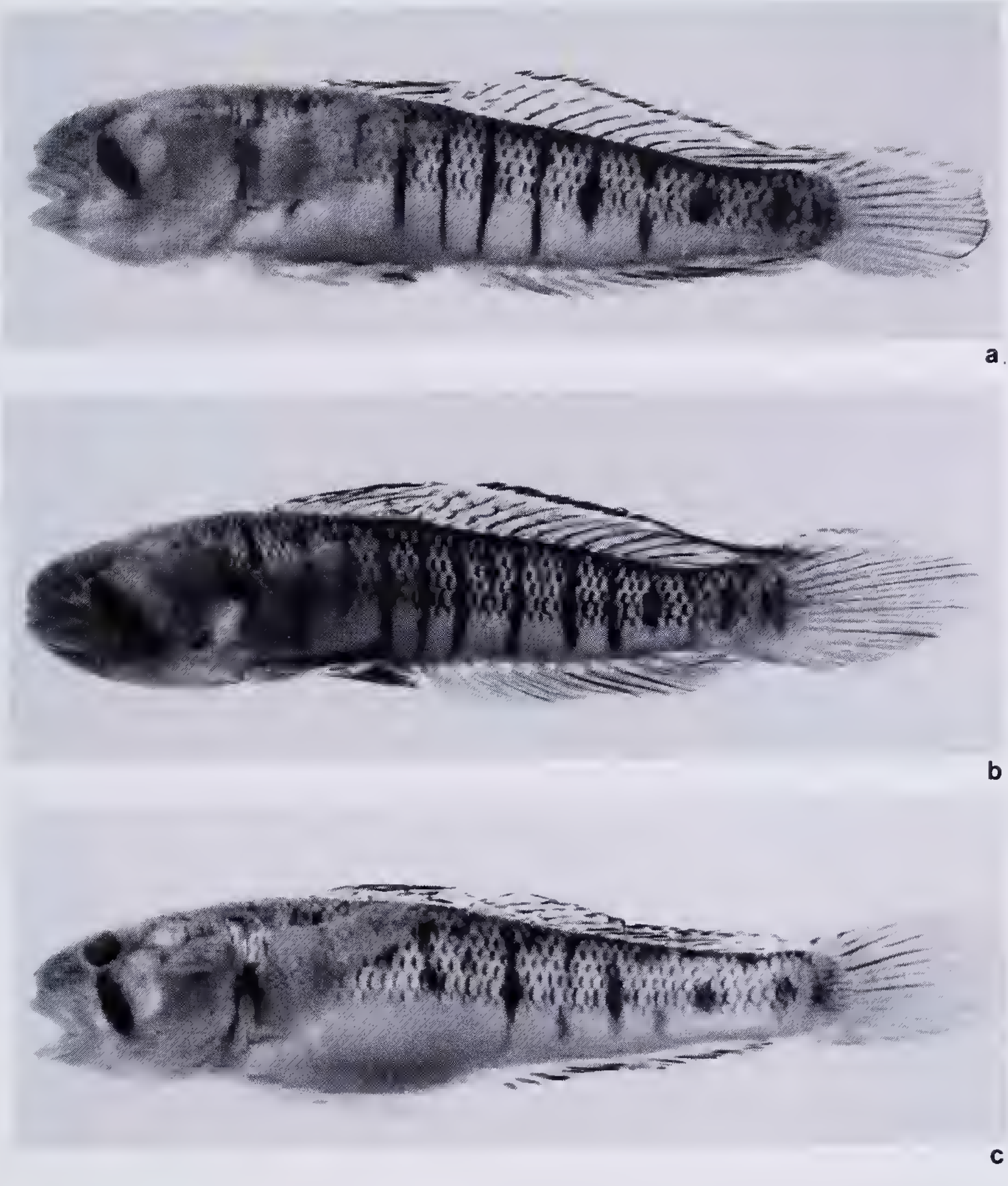

Figure 23 **a:** *Stenogobius caudimaculosus*, sp. nov., MNHN 1987-929. HOLOTYPE, male (69.9). Nuku Hiva, Marquesas Islands; **b:** *Stenogobius caudimaculosus*, sp. nov., WAM P.29317-001. PARATYPE, male (65.9), Nuku Hiva, Marquesas Islands; **c:** *Stenogobius caudimaculosus*, sp. nov. MNHN 1987-1843. PARATYPE, female (68.5), Nuku Hiva, Marquesas Islands.

five females, three juveniles; SMF 21568, 5(43.1-68.5), three males, two females; USNM 292572, 6(44.9-62.7), one male, five females; WAM P.29317-001, 10(38.9-65.9), five males, five females.

Diagnosis

Predorsal midline, usually patchy, seldom naked or fully scaled; scales in horizontal series 48 to 52, usually 49 to 50; breast almost always naked; belly anteriorly with large naked patch next to pelvic base; pectoral base naked; opercle almost always naked; cheek naked; caudal peduncle length 13 to 16% of SL, usually 14 to 15%; large spot or spots on caudal peduncle of both sexes.

Relationship

This species has an elongate caudal peduncle, when compared to all other *Insularigobius*, except *Stenogobius squamosus*. It appears very similar to *Stenogobius squamosus*, apparently its closest relative; but differs from it by having a shorter caudal peduncle and fewer scales.

Description

D VI-I,11; A I,11; P 14 to 16, almost always 15. LS 48 to 52, usually 49 to 50; TRB 12 to 14, usually 13; PD usually with naked patches; cheek naked; opercle almost always naked; pectoral base naked; breast almost always naked, but may have one to three scales present. Jaw reaching under pupil to posterior edge of eye in males, females reaching under center to posterior edge of pupil. Upper jaw teeth, males 1-3+0-2, usually 2-3+1; females 0-2+0-1, usually 1+0. Lower jaw teeth, males 3-4+1-2; females 3+1. Teeth on outer row of both jaw enlarged in males. Sexual dimorphism similar to that described for *Stenogobius genivittatus* species group, but differs by male possessing slightly shorter and broader based sexual papilla.

Color in preservation: Basic body coloration as with those described for *Insularigobius*. Trunk bars distinctive on both sexes in being broadened medially; blackish or dusky spot found on caudal peduncle with weak spot often present on hypural base. Both dorsal fins in males with dusky bars between spines and rays tending not to appear as scribbles, margin of both dorsal fins with black band and a thin translucent band along edge; second dorsal fin in females with small irregular dusky spots at base of membrane between rays, above spots dusky bars similar to those of males. In both sexes caudal fin with dusky streaks on membrane between rays, appearing darkest on upper half, in males caudal fin dusky, two blackish band near top of fin, with translucent band between, this marking appears to continue from second dorsal fin. Anal fin markings similar to those described for *Stenogobius genivittatus*. Pectoral fin dusky in both sexes, most pronounced in males. Pelvic disk dusky in males; females with dusky band on membrane between fifth rays.

Remarks

Distribution: Known only from fresh water streams on Nuku Hiva, Marquesas Islands.

Etymology: The name is derived from the Latin words *cauda* meaning tail and *maculosus* meaning spotting. This is in reference to the spot or spots that exist on the caudal peduncle of this species.

Note: This species is unique in possessing two distinctive phases of adult males. Primary males appear fully adult with elongate fins and similar to adult males of other species. Secondary males appear adolescent in having shorter fins and shorter jaw, but may reach a large size, the largest specimen examined, the holotype, was determined to be a secondary male. This has only been observed in this species of *Stenogobius*.

Stenogobius (Insularigobius) squamosus, sp. nov.

(Figures 24a & 24b)

Stenogobius (Insularigobius) squamosus, sp. nov. (type locality: Ua Pou, Marquesas Islands, French Polynesia)

Material Examined

Thirty nine specimens from Ua Pou, Marquesas Islands, French Polynesia, totalling 20 males, 19 females; size range 30.4 to 79.0, largest male 74.0, largest female 79.0, smallest gravid female 50.3.

Holotype

MNHN 1987-928, male (74.0), fresh water stream, Ua Pou, Marquesas Islands, French Polynesia, 26 December 1986, G. Marquet.

Paratypes (same collection data as holotype)

AMS I.27133-001, 9(37.6-71.8), four males, five females; MNHN 1987-1842, 10(30.4-79.0), five males, five females; SMF 21569, 5(50.3-72.7), one male, four females; USNM 289986, 5(43.1-63.1), four males, one female; WAM P.29316-001, 9(37.4-66.4), five males, four females.

Diagnosis

Species has most elongate caudal peduncle of all *Insularigobius* examined, 14 to 17% of SL, usually 15 to 16%; predorsal midline usually fully scaled, usually 17 to 19; scales in horizontal series 49 to 51, usually 50 to 51; opercle may or may not be scaled; one to two spots present on caudal peduncle.

Relationship

This species is most closely related to *Stenogobius caudimaculosus* and a yet undescribed form (MNHN 1987-927) from Ua Huka, Marquesas Islands, it differs by having more scales and longer caudal peduncle.

Description

D VI-I,11; A I,11 to I,12, almost always I,11; P 15. LS 49 to 51, usually 50 to 51; TRB 12 to 14, usually 13 to 14; PD 15 to 22, usually 17 to 21; cheek naked; opercle may or may not be scaled; pectoral base naked. Jaw reaching under pupil to posterior edge of eye in males, jaw in females reaches under center or posterior edge of pupil. Upper jaw teeth, males 2-3+1; females 0-2+0-1, usually 2+1. Lower jaw teeth, males 3-4+1-2, usually 4+2; females 2-3+1, usually 3+1. Teeth on outer row of both jaws in males enlarged. Sexual dimorphic differences similar to those described for *Stenogobius caudimaculosus*.

Color in preservation: Body pattern almost identical to *Stenogobius caudimaculosus*, only noticeable difference is the lack of intensity of spotting and trunk bars. The same conditions exist with fin markings.

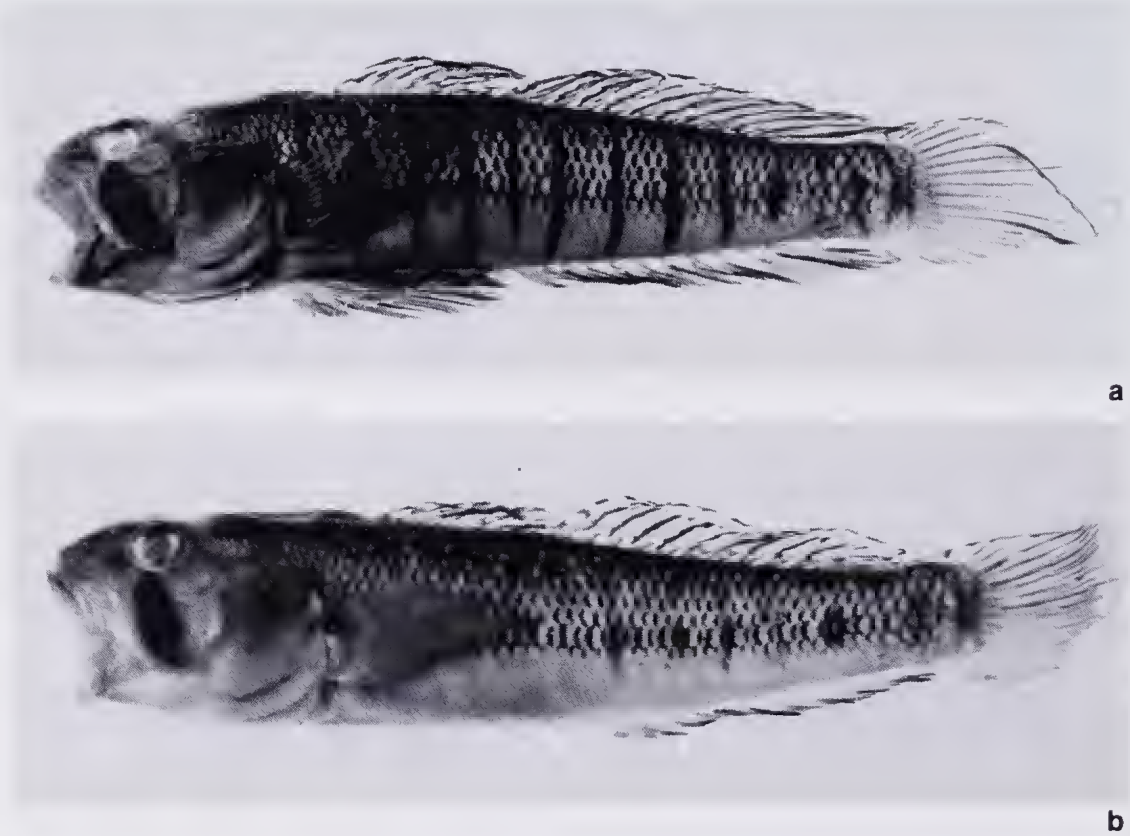

Figure 24 **a:** *Stenogobius squamosus*, sp. nov., MNHN 1987-928. HOLOTYPE, male (74.0), Ua Pou, Marquesas Islands; **b:** *Stenogobius squamosus*, sp. nov., MNHN 1987-1842. PARATYPE, female (79.0), Ua Pou, Marquesas Islands.

Remarks

Distribution: Known only from fresh water streams on the island of Ua Pou, Marquesas Islands.

Etymology: The name is taken from the Lating word *squamosus* meaning scaled. This is in reference to the fact it is the most scaled species of the *Stenogobius* examined from the Marquesas Islands.

Stenogobius (Insularigobius) blokzeyli species complex.

(Figure 25)

This group is closely related to *Stenogobius genivittatus* species complex and is most easily separated by females possessing rows of spots on the second dorsal fin and a medial band on first dorsal fin. This complex is centered along the western Pacific Ocean.

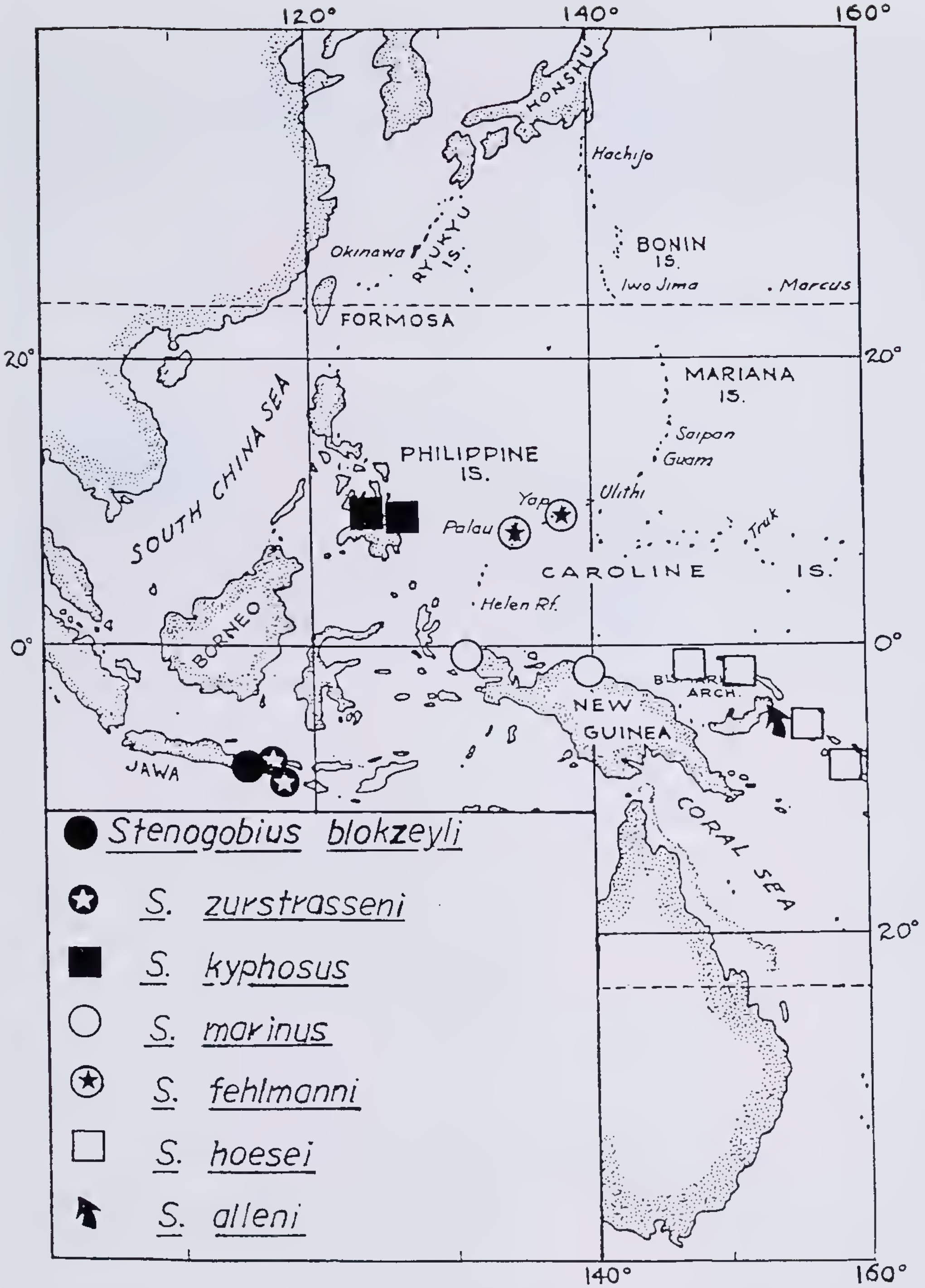

Figure 25 Distributional map of *Stenogobius blokzeyli* species complex.

Stenogobius (Insularigobius) blokzeyli (Bleeker 1861)

Gobius blokzeyli Bleeker, 1861: 240 (type locality: Bali)

Material examined

Two females from Bali, Indonesia, size range 58.8 to 70.8.

Syntypes

RMNH 4511, two females (58.8-70.8), Bali, Sunda Islands, Dutch East Indies.

Diagnosis

Upper pectoral base scaled; lower base may or may not be scaled; breast with embedded scales; belly anteriorly scaled close to pelvic base; upper jaw teeth 3+1, lower jaw teeth 3-4+1-2.

Relationship

Exact relationships cannot be ascertained until more material can be obtained from type locality.

Description

D VI-I,11; A I,11, P 15. LS, TRB and PD impossible to obtain due to poor condition of specimens; opercle scaled; cheek naked; upper pectoral base scaled; lower pectoral base may or may not be scaled; breast with embedded scales; belly scaled close to pelvic base.

Color in preservation: Background grayish brown; trunk bars vaguely visible as is the oblique cheek bar. First dorsal fin with brownish medial band; other fin markings not apparent.

Remarks

Distribution: Known only from the type locality of Bali, Sunda Islands, Indonesia.

Note: *Stenogobius blokzeyli* appears to be a valid species, however it cannot be fully evaluated at this time, as more material is needed from the type locality. The types are in very poor condition and are of one sex. It does have more teeth in both jaws than females of any other species of *Insularigobius.*

Stenogobius (Insularigobius) alleni, sp. nov.

(Figures 26a & 26b)

Stenogobius alleni, sp. nov. (type locality: New Britain, Bismarck Archipelago, Papua New Guinea)

Material examined

Ten specimens from New Britain, Bismarck Archipelago, Papua New Guinea totalling three males, seven females; size range 28.4 to 39.1, largest male 36.5, largest female 39.1, no gravid material.

Holotype

WAM P.28177-010, male (36.5), Tovarua Stream near public beach, New Britain, Bismarck Archipelago, Papua New Guinea, 10 October 1983, G.R. Allen and R.C. Steene.

Paratypes (same collection data as holotype)

AMS I.25440-001, 2(33.9-35.0), one male, one female; USNM 276274, 2(33.9-35.9), one male, one female; WAM P.28177-003, five females (28.4-39.1).

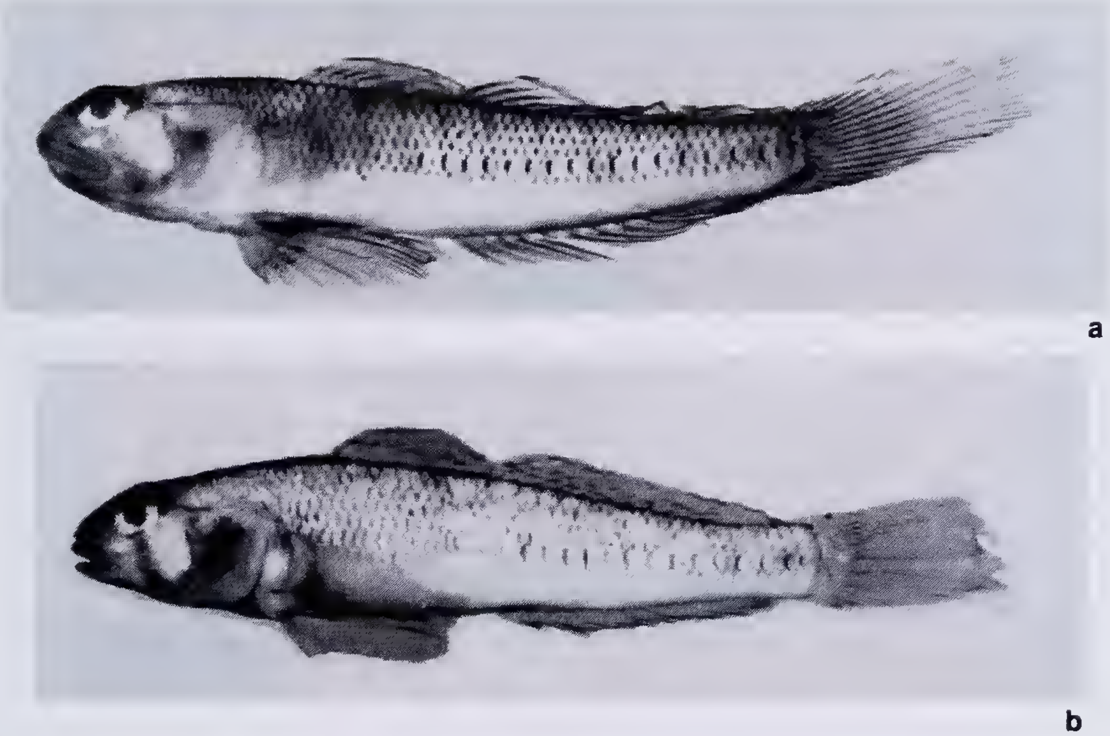

Figure 26 **a:** *Stenogobius alleni,* sp. nov., WAM P.28177-010, HOLOTYPE, male (36.5), New Britain, Papua New Guinea; **b:** *Stenogobius alleni,* sp. nov., WAM P.28177-003. PARATYPE, female (39.1), New Britain, Papua New Guinea.

Diagnosis

A small, elegant *Stenogobius;* vertical trunk bars very faint in both sexes; first dorsal fin in males with short bars on membrane that do not appear as scribbles, second dorsal fin similarly marked; first dorsal fin in females with midlateral band and dusky margin, second dorsal with dusky spots forming two rows on membrane; predorsal midline with two to 18 scales, usually fully scaled, but may be with naked patches; belly anteriorly naked close to pelvic base; breast naked. This is the smallest species of *Stenogobius* known.

Relationship

The species closest in size is *Stenogobius beauforti,* which appears to be a very distant relative. It may be most closely related to *Stenogobius fehlmanni,* but differs in lacking black pigmentation in first and second dorsal fins that appear as scribbles, by lacking filamentous dorsal spines, being slightly more slender, a shorter head, and by its small size.

Description

D VI-I,11; A I,11; P 15. LS 47 to 49, usually 47 to 48; TRB 10 to 12, usually 11; PD usually fully scaled; cheek naked; opercle usually naked; pectoral base naked; belly anteriorly naked; breast naked. Jaw extending under to anterior edge of pupil in females and to posterior edge of pupil in males. Upper jaw teeth, males 2+1-2, usually 2+2; females 1-2+0-1. Lower jaw teeth, males 3-4+2, usually 3+2; females 3+1. Teeth in outer row slightly enlarged in males.

Color in preservation: Males; first and second dorsal fins dusky, first dorsal fin with short bars medially on membrane that forms a band not appearing as scribbles, fin with a dusky margin; second dorsal fin with dusky bars between spine and rays not appearing as scribbles and fin with dusky margin; caudal fin dusky with two whitish streaks separated by dusky streak on upper margin and whitish band on lower maring of fin; anal and pectoral fins as well as pelvic disk dusky; dusky vertical trunk bars originate behind pectoral base and terminate between second dorsal and anal fins, bars somewhat crescentic and often indistinct, numbering seven to 10. Females; first dorsal fin with blackish medial band and dusky spotting above; second dorsal fin with blackish spots on membrane forming two to three rows; caudal fin with some whitish spots on upper third of fin, rest of fin translucent; anal fin with some dusky streaking and spotting, blackish band near margin with a whitish edge; pelvic disk translucent; pectoral fin slightly dusky; upper body dusky; snout dusky; vertical trunk bars very indistinct and limited to midline between second dorsal and anal fins, numbering two to five.

Remarks

Distribution: Known only from the type locality.

Ecology: Reported from a small fresh water stream.

Etymology: This species is named in honor of Gerald R. Allen for his contributions to the fresh water ichthyology of Papua New Guinea.

Stenogobius (Insularigobius) fehlmanni, sp. nov.

(Figures 27a & 27b)

Stenogobius (Insularigobius) fehlmanni, sp. nov. (type locality: Babelthuap Island, Palau Islands)

Material examined

Eighty seven specimens from the Palau Islands and Yap Island of the Caroline Islands totalling 28 males, 55 females, four juveniles; size range 14.1 to 75.1, largest male 75.1, largest female 64.1, smallest gravid female 29.7.

Holotype

CAS 51193, male (74.4), Behes Stream, Ngermelech Village, Melekeiok Municipality, Babelthuap Island, Palau Islands, 27 September 1955, H.A. Fehlmann *et al.*

Paratypes

AMS I.24812-002, female (48.7), Chimel River. 20 meters below Arai Reservior, Babelthuap Island, Palau Islands, 23 November 1983, J. June; CAS-SU 29233, female (47.7), Palau Islands, 15 October 1933, A.W.C.T. Herre; CAS 51194, female (41.4), stream at Rumu village at bridge on road to Teguren canal from bridge upstream, Yap Island. 2 September 1956, M. Brittan; CAS 57868, male (52.1), fresh water streamlet bordering north side of old Japanese airfield, Arakabesan Island, Palau Islands, 11 September 1955, H.A. Fehlmann *et al:* CAS 57869, 2(38.1-38.4), one male, one female, streamlet tributary of Gihmel River in vicinity of Ngeruluebe village, Arai Municipality, Babelthuap Island, Palau Islands, 19 September 1955, H.A. Fehlmann et al; CAS 57870, female (49.5), Didyong, fresh water streamlet draining into Komebail lagoon, Arakabesan Island, Palau Islands, 9 October 1955, H.A. Fehlmann *et al;* CAS 57871, 3 females (45.0-50.6), Ngertehiyah stream flowing through Ngerubodoru Village (Ngerbodel), Koror Island, Palau Islands, 12 October 1955, H.A. Fehlmann *et al;* CAS 57872, 2(28.9-48.3), one male, one female, Ilmaw stream, Ngetkip Village, Arai Municipality, south end of Babelthuap Island, Palau Islands, 25 October 1955, H.A. Fehlmann et al; CAS 57873, 6(35.1-45.8), three males, three females, Airisong stream, one to 1.5 miles north of Ngetkip Village, Arai Municipality, Babelthuap Island, Palau Islands, 26 October 1955, Sumang & Fehlmann; CAS 57874, female (41.5), Kyam stream south of Medorum Village, Aimeliik Municipality, Babelthuap Island, Palau Islands, 2 November 1955, H.A. Fehlmann et al; CAS 57875, 21(17.6-53.2), six males, 13 females, two juveniles, upper mangrove zone, south fork Arakitaoch stream, 1.2 miles southeast of Ngarekeai village, Airai Municipality, Babelthuap Island, Palau Islands, 15 November 1955, H.A. Fehlmann *et al;* CAS 57876, 3(14.1-41.4), one male, one female, one juvenile, channel of Arakitaoch stream through mangrove swamp about one mile southeast of Ngarekeai village, Airai Municipality, Babelthuap Island, Palau Islands, 20 September 1957, Sumang *et al;* CAS 58052, 43(21.1-75.1), 14 males, 28 females, one juvenile, same collection data as holotype.

Diagnosis

Spines of first dorsal fin in males usually filamentous, may reach seventh or eighth ray of second dorsal fin; scale count in lateral series 46 to 51, usually 48 to 50; scales in predorsal midline almost always fully scaled ranging nine to 19, usually 17; upper pectoral base usually naked; opercle may or may not be scaled; cheek almost always naked; breast always scaled.

Relationship

This species appears closest to *Stenogobius alleni.* At present no other close relative can be ascertained, a presently undescribed form from nearby Kusaie, Caroline Islands does not appear to be closely related.

Description

D VI-I,11; A I,11 to I,12, almost always I,11; P 14 to 16, usually 15; first dorsal fin often with filamentous spines in males that may reach to seventh or eighth rays of second dorsal fin. LS 46 to 51, usually 48 to 50; TRB 11 to 13, usually 12; PD nine to 19, almost always fully scaled; cheek almost always naked; opercle may or may not be scaled; lower pectoral base naked; belly scaled close to pelvic base; breast always with scales present. Jaw extending under pupil in females to beyond posterior edge of eye in males. Upper jaw teeth, males 2-3+1-2, usually 2-3+1; females 1-2+0-1, usually 1+0. Lower jaw teeth, males 3-5+2, usually 4+2; females 2-3+0-2, usually 2-3+1.

Color in preservation: Patterns of both sexes similar to those described for *Stenogobius genivittatus.* In males head slightly dusky. Females may or may not have lateral trunk bars; first dorsal fin with dusky midlateral band; second dorsal fin with many dusky spots forming irregular rows.

Remarks

Distribution: Known from the Palau Islands and Yap Island of the Caroline Islands.

Ecology: Reported from fresh and brackish water streams over sand and mud.

Etymology: This species is named for H. Adair Fehlmann for his contributions to ichthyology, as well as collecting most of the type material.

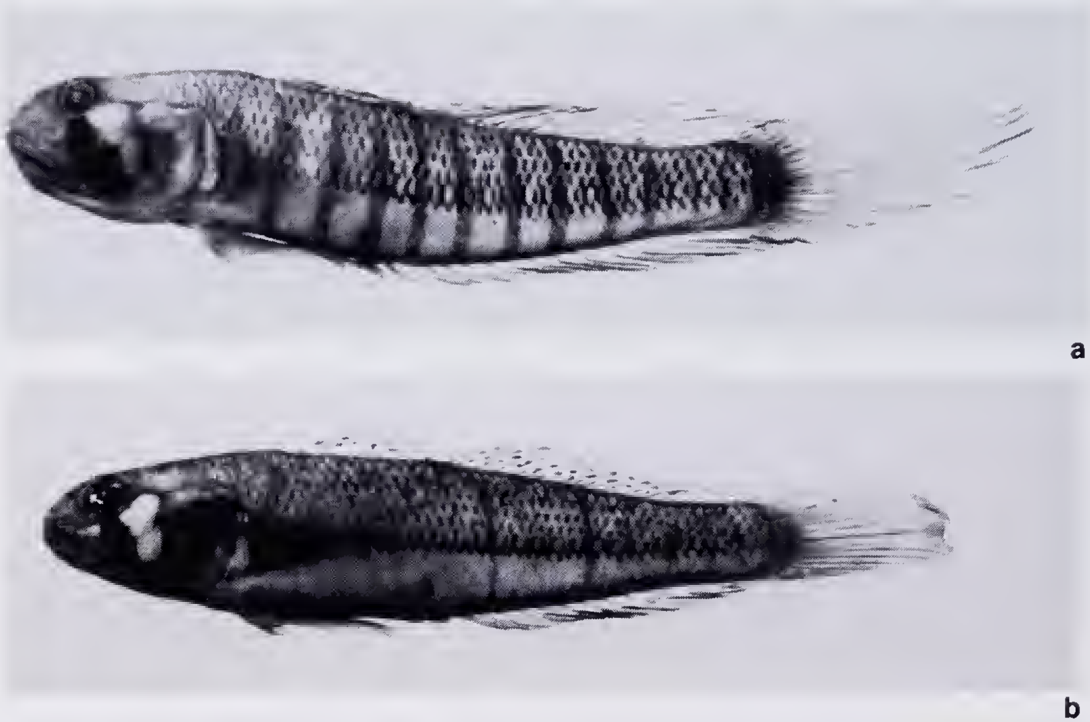

Figure 27 a: *Stenogobius fehlmanni*, sp. nov., CAS 51193, HOLOTYPE, male (74.4), Babelthuap Island, Palau Islands; b: *Stenogobius fehlmanni*, sp. nov., CAS 58052, PARATYPE, female (57.2), Babelthuap Islands, Palau Islands.

Stenogobius (Insularigobius) hoesei, sp. nov.
(Figures 28a & 28b)

Stenogobius (Insularigobius) hoesei, sp. nov. (type locality: Manus Island, Admiralty Islands, Papua New Guinea)

Material examined

Fifty eight specimens from the Admirality Islands, Solomon Islands and Bismarck Archipelago of the western Pacific, totalling 21 males, 29 females, eight juveniles; size range 18.8 to 60.8, largest male 60.8, largest female 55.6, no gravid material.

Holotype

WAM P.27829-015, male (59.6), small fresh water creek, 1.5 km southeast of Lorengau, Manus Island, Admiralty Islands, Papua New Guinea, 10 October 1982, G.R. Allen & R. Knight.

Paratypes

AMS I.25437-007, 2(47.2-50.1), one male, one female, same collection data as holotype; BPBM 30850, 2(43.6-49.6), one male, one female, near Bunia Point west of Honiara, Guadalcanal, Solomon Islands, 20 March 1965, D. Cohen; NTM S.11677-001, 2(44.9-49.7), one male, one female, same collection data as holotype; NTM S.11678-001, 2(43.6-52.2), one male, one female, same collection data as BPBM 30850; ROM 48511, 2(43.5-49.1), one male, one female, same collection data as BPBM 30580; USNM 114892, 3(23.2-36.7), one female, two juveniles, Tei River, Manus Island, Admiralty Islands, 15 January 1946, D.S. Frey; USNM 273480, 11(39.1-60.8), four males, seven females, same collection data as BPBM 30850;

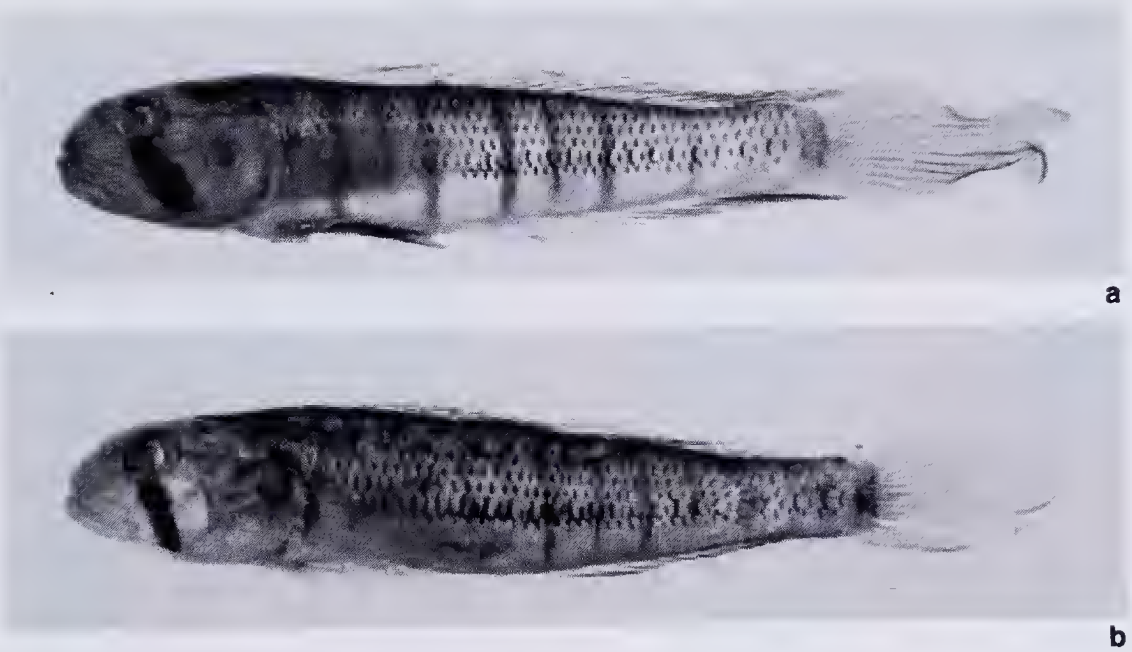

Figure 28 **a:** *Stenogobius hoesei*, sp. nov., USNM 273480, PARATYPE, male (60.8) Guadalcanal, Solomon Islands; **b:** *Stenogobius hoesei*, sp. nov., USNM 273480, PARATYPE, female (55.6) Guadalcanal, Solomon Islands.

USNM 276275, 2(47.5-52.9), one male, one female, same collection data as holotype; WAM P.27829-017, 12(22.8-46.6), three males, four females, five juveniles, same collection data as holotype; WAM P.27830-009, female (42.3), Lorengau River at base of falls, Manus Island, Admiralty Islands, Papua New Guinea, 10 October 1982, G.R. Allen & R. Knight; WAM P.28163-003, three females (28.2-34.3), small stream crossing on Arawa Road at Borora Point, Bouganville Island, Papua New Guinea, 3 October 1983, G.R. Allen & R.C. Steene; WAM P.28164-007, three females (26.5-50.1), Tekan River on road crossing west of Arigua Plantation, Bouganville Island, Papua New Guinea, 3 October 1983, G.R. Allen & R.C. Steene; WAM P.28185-015, 2(36.2-41.8), one male, one female, small creek 25 km south of Kavieng, New Ireland, Bismarck Archipelago, Papua New Guinea, 14 October 1983, G.R. Allen & R.C. Steene; WAM P.28453-001, 2(52.6-56.3), one male, one female, same collection data as BPBM 30850; ZMA 119.418, 2(42.6-48.4), one male, one female, same collection data as BPBM 30850.

Additional material

AMNH 16616, female (34.9), Los Negros Island, Admiralty Island, 1944, O. Barton; ANSP 95518, 4(31.0-57.1), three males, one female, Poha River, Guadalcanal, Solomon Islands, 11 September 1953, M. & E.A. Laird; WAM P.28162-003, juvenile (18.8), small stream three km southeast of Wakunai, Bouganville, Solomon Islands, Papua New Guinea, 3 October 1983, G.R. Allen & R.C. Steene.

Diagnosis

Predorsal midline almost always with naked patches, four to 18 scales; pectoral base almost always naked; opercle almost always naked; breast naked; third and fourth spines of first dorsal fin may be slightly filamentous on males; body anteriorly, head and pectoral fin dusky in both sexes.

Relationship

Stenogobius hoesei appears most closely related to *S. marinus*. It differs by being dusky anteriorly in both sexes, slightly longer fins, slightly shorter caudal peduncle, slightly greater predorsal length, slightly greater preanal length, slightly fewer scales in horizontal series, and by habitat preference; females possess more trunk bars and slightly thicker caudal peduncle. At present a close relationship with any other species cannot be determined.

Description

D VI-I,10 to VI-I,12, almost always VI-I,11; A I,11 to I,12, almost always I,11; P 15 to 16, almost always 15; third and fourth spines of first dorsal fin may be slightly filamentous on males. LS 44 to 49, usually 47 to 48; TRB 11 to 13, usually 11 to 12; PD usually with naked patches; cheek naked; opercle almost always naked; upper pectoral base almost always naked; lower pectoral base naked; belly anteriorly with large naked patch close to pelvic base; breast usually naked, may have few embedded scales. Jaw extending under pupil in females and beyond posterior edge of eye in males. Upper jaw teeth, males 2-4+1-2, usually 2+1-2; females 1+0-1. Lower jaw teeth, males 3-4+2-3, usually 3+2; females 2-3+1-2, usually 3+2. Teeth on outer row of upper and lower jaws enlarged in males.

Table 8 Pectoral ray counts in species of the subgenus *Insularigobius*.

	Pectoral rays			
	13	14	15	16
S. alleni			10	
S. beauforti	1	4	19	3
S. blokzeyli			2	
S. caudimaculosus		1	40	2
S. fehlmanni		3	45	10
S. genivittatus			50	5
S. hawaiiensis		5	102	14
S. hoesei			42	2
S. kyphosus		1	11	1
S. marinus		6	26	3
S. marqueti			56	1
S. polyzona		3	29	1
S. randalli			4	3
S. squamosus		1	38	
S. zurstrasseni		1	28	3

Color in preservation: Background brownish to grayish, body anteriorly and head dusky; pectoral fin dusky in both sexes. Coloration strongly sexual dichromatic and described as follows: Males; first and second dorsal fins with blackish pigmentation on membrane between rays and spines appearing as scribbles, both fins with a weak dusky margin; caudal and anal fins and pelvic disk dusky; upper fourth of caudal fin with some dusky spotting; blackish vertical trunk bars originate behind pectoral base and end near caudal fin base, these being slightly crescentic and alternate in width numbering six to 10. Females; first dorsal fin with black midlateral band and dusky margin; second dorsal fin with black spots on membrane between rays and spines that form two to three rows; vertical dusky trunk bars usually limited to area between second dorsal and anal fins, numbering three to 10.

Remarks

Distribution: Known from the Admiralty and Solomon Islands and the Bismarck Archipelago in the western Pacific.

Ecology: All specimens reported from small fresh water streams.

Etymology: This species is named in honor of Douglass F. Hoese for his contributions to gobioid systematics and for his encouragement throughout the course of this study.

Stenogobius (Insularigobius) kyphosus, sp. nov.

(Figures 29a & 29b)

Stenogobius (Insularigobius) kyphosus, sp. nov. (type locality: Camiguin Island, Philippines)

Material examined

Fourteen specimens from the Philippines totalling four males, nine females, one juvenile; size range 16.8 to 90.4, largest male 90.4, largest female 87.7, no gravid material.

Holotype

USNM 99878, male (90.4), Mahinog River, Camiguin Island, Philippines, 3 August 1909, Albatross Expedition.

Paratypes

AMS I.25439-001, 2(79.5-82.9), one male, one female, same collection data as holotype; ANSP 156992, 2(72.2-80.2), one male, one female, same collection data as holotype; ROM 48510, three females (54.2-87.7), same collection data as holotype; USNM 99929, 2(16.8-45.8), one female, one juvenile, Baganga River, Mindanao, Philippines, 13 May 1909, Albatross Expedition; USNM 99930, female (52.2), Nonucan River near Camp Overton, Iligigan Bay, Mindanao, Philippines, 6 August 1909, Albatross Expediton; USNM 120323, female (53.9), Malaga River, Leyte, Philippines, 30 July 1909, Albatross Expedition; USNM 274590, 2(80.2-83.2), one male, one female, same collection data as holotype.

Diagnosis

A very robust species, males 22 to 24% of SL at origin of second dorsal fin; steep snout; breast scaled; predorsal scales 15 to 21, usually 17 to 18, always fully scaled.

Relationship

Stenogobius kyphosus shows no close affinities with any species described or undescribed.

Description

D VI-I,11; A I,11; P 14 to 16, usually 15. LS 45 to 51, usually 48; TRB 11 to 13, usually 12; PD 15 to 21, usually 17 to 18, always fully scaled; cheek almost always naked; opercle may or may not be scaled; upper pectoral base may or may not be scaled; lower pectoral base usually naked; belly anteriorly scaled close to pelvic base; breast scaled. Jaw reaching under pupil in females and beyond posterior edge of eye in males. Upper jaw teeth, males 3-5+2, usually 3+2; females 1-2+0-1, usually 1-2+1. Lower jaw teeth, males

Figure 29 **a:** *Stenogobius kyphosus*, sp. nov., USNM 99878. HOLOTYPE, male (90.4), Camiguin, Philippines; **b:** *Stenogobius kyphosus*, sp. nov., ROM 48510, PARATYPE, female (87.7), Camiguin, Philippines.

3-5+2, usually 3+2; females 2-3+1. Teeth on outer row of both jaws enlarged in males. Body depth between origin of second dorsal fin and belly in males 22-24% of SL, greater than any other *Insularigobius* examined.

Color in preservation: Background brownish; body and head not dusky. Color sexually dichromatic: Males; first and second dorsal fins with some blackish pigmentation on membrane between spines and rays appearing as scribbles; caudal fin dusky; pectoral fin translucent; dusky vertical trunk bars originate behind pectoral base and terminate between second dorsal and anal fins, being slightly crescentic, those anterior almost vertical, these do not reach dorsal or ventral surfaces, numbering 10 to 11. Females; first and second dorsal fins with several rows of fine blackish spots on membrane; caudal fin with no detectable markings and is slightly dusky; anal fin light with a dusky margin; pelvic disk and pectoral fin translucent; vertical trunk bars usually absent or indistinct, numbering zero to eight.

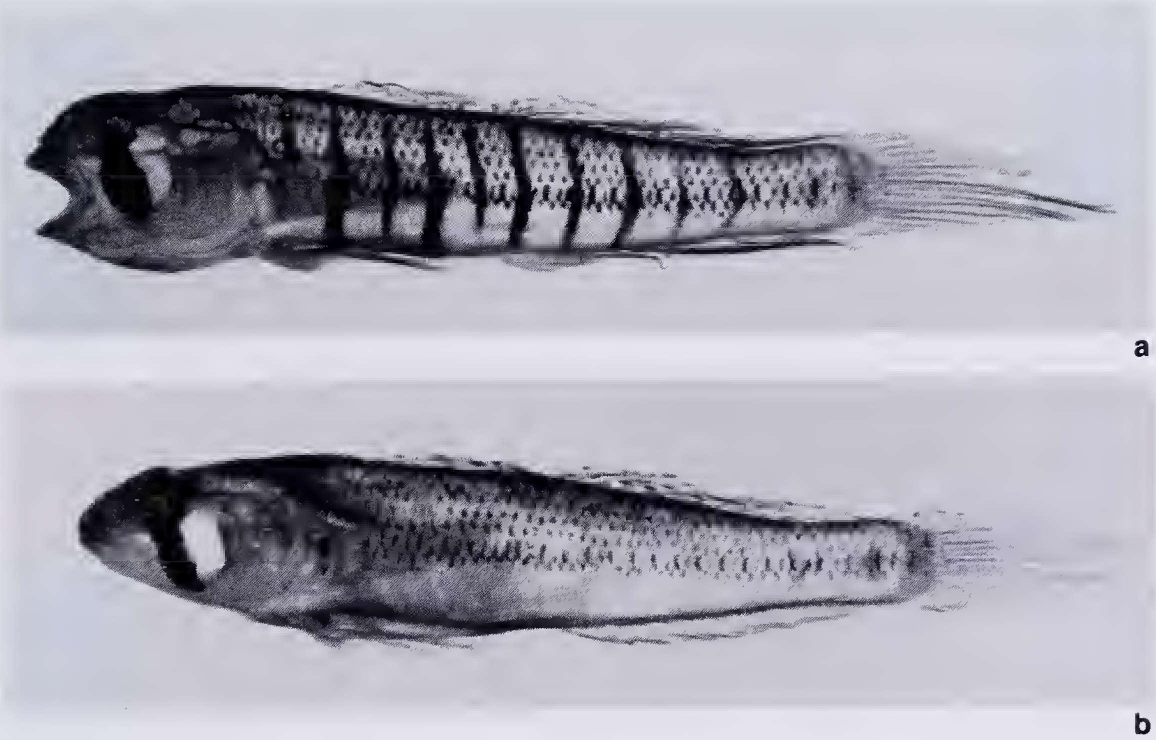

Figure 30 **a:** *Stenogobius marinus*, sp. nov., USNM 274586, HOLOTYPE, male (55.3), Irian Jaya, Indonesia; **b:** *Stenogobius marinus*, sp. nov., MZB 5649, PARATYPE, female (45.5), Irian Jaya, Indonesia.

Remarks

Distribution: Known from the rivers entering the Mindanao Sea and eastern Mindanao of the Philippines.

Ecology: Reported from rivers and estuaries over sand and mud bottoms.

Etymology: Name is taken from the Greek word *kyphos* meaning humpback, in reference to the high back of this species when compared to other species of *Insularigobius.*

Stenogobius (Insularigobius) marinus, sp. nov.
(Figures 30a & 30b)

Stenogobius (Insularigobius) marinus, sp. nov. (type locality: Irian Jaya, Indonesia)

Material examined

Thirty five specimens from Irian Jaya, Indonesia, totalling 26 males, nine females; size range 33.9 to 55.2, largest male 55.2, largest female 45.5, no gravid material.

Holotype

USNM 274586, male (55.2), between Tandjung Manganeki and Tandjung Boropen off northern Tjendrawasih, Irian Jaya, Indonesia, 1 July 1979, B.B. Collette.

Table 9 Trunk bars on species of the subgenus *Insularigobius*.

Species	Trunk bars on males																	
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
S. alleni						1	—	1	1									
S. beauforti				1	1	2	2	—	—	1	1							
S. caudimaculosus					2	1	1	2	1	7	2	2	—	1				
S. fehlmanni						1	—	2	10	9	6							
S. genivittatus								3	11	11	7	1						
S. hawaiiensis		2	—	—	1	—	3	15	22	3								
S. hoesei					3	1	—	2	12									
S. kyphosus									3	1								
S. marinus					3	3	2	6	9	2	1							
S. marqueti					1	—	1	1	8	10	6	2						
S. polyzona						1	—	2	11	6	—	2	—	—	—	—	—	1
S. randalli									1	2	—	1						
S. squamosus			1	1	—	1	—	1	6	3	5	1						
S. zurstrasseni	1	1	—	4	2	—	2	1										

	Trunk bars on females												
	0	1	2	3	4	5	6	7	8	9	10	11	12
S. alleni			2	1	3	1							
S. beauforti			1	4	4	3	6	—	—	1			
S. caudimaculosus					3	1	5	4	5	1	2		
S. fehlmanni	1	—	4	10	9	7	5	—	2	1	1		
S. genivittatus				3	3	5	6	4	3	2	1		
S. hawaiiensis	3	1	1	9	3	4	6	11	5	5	3	1	
S. hoesei				10	4	1	3	—	2	1	1		
S. kyphosus	3	—	—	—	2	1	—	1	2				
S. marinus	5	—	1	2	—	1							
S. marqueti				6	1	5	6	3	—	2	—	2	2
S. polyzona	2	1	—	2	1	1	—	2					
S. randalli						1	1	1					
S. squamosus					2	8	4	1	2	3			
S. zurstrasseni			1	3	9	2	2	1	1				

Paratypes

AMS I.25438-001, 2(37.4-50.2), one male, one female, same collection data as holotype; MZB 5649, 2(45.5-52.3), one male, one female, same collection data as holotype; USNM 274588, 28(33.9-45.3), 22 males, six females, same collection data as holotype; ZMA 113.659, 2(45.2-47.2), one male, one female, Hollandia Bay, West New Guinea, Dutch East Indies, 7 July 1911, K. Gjellerup.

Diagnosis

Predorsal midline usually with naked patches, two to 19 scales in midline; pectoral base almost always naked; opercle almost always naked; belly anteriorly naked close to pelvic base; breast naked or with few embedded scales; spines slightly filamentous on first dorsal fin in males; body anteriorly and head slightly dusky in males, not at all in females; females with few or no vertical trunk bars.

Relationship

This species is most closely related to *Stenogobius hoesei* and possibly to an undescribed form from the Maluku Islands, Indonesia. It differs by features detailed in *Stenogobius hoesei.*

Description

D VI-I,10 to VI-I,11, almost always VI-I,11; A I,10 to I,11, almost always I,11; P 14 to 16, usually 15; spines on first dorsal fin may be slightly filamentous in males. LS 44 to 50, usually 48 to 49; TRB 11 to 12; PD two to 19, almost always with naked patches; cheek naked; opercle almost always naked; upper pectoral base almost always naked; lower pectoral base naked; breast naked or with few embedded scales; belly anteriorly naked close to pelvic base. Jaw reaching under pupil in females and beyond posterior edge of eye in males. Upper jaw teeth, males 2-3+1-2, usually 2-3+1; females 1+0. Lower jaw teeth, males 3-4+2, usually 3+2; females 2+1-2, usually 2+1. Teeth on outer row of both jaws slightly enlarged in males.

Color in preservation: Background color light tan; head and body anteriorly generally not dusky. Coloration sexually dichromatic and is described as follows: Males; first and second dorsal fins with numerous blackish bars between rays and spines that appear as scribbles, small dusky spots may be present on spine of second dorsal fin; pelvic disk and pectoral fin slightly dusky; caudal fin dusky, there are few weak dusky spots on upper anterior portion of fin; dusky vertical trunk bars originate behind pectoral base and end near caudal fin base, these being slightly crescentic and tend to alternate in width, numbering six to 12. Females; first dorsal fin with blackish midlateral band and dusky margin, second dorsal fin with dusky spots on membrane forming two to three rows; caudal fin with few dusky spots on upper anterior margin of fin, rest of fin slightly dusky; anal fin light along base, dusky distally with a light margin; pectoral fin and pelvic disk translucent; dusky vertical trunk bars limited to area between second dorsal and anal fins, when present usually short, numbering zero to three.

Remarks

Distribution: Northwestern coast of the island of New Guinea.

Ecology: Brackish and near marine waters in intertidal streams and estuaries.

Etymology: The name of this species comes from the Latin word *marinus* which means the sea, this is in reference to this species apparent habitat preference.

Stenogobius (Insularigobius) zurstrasseni (Popta 1912)

(Figure 31)

Gobius zurstrasseni Popta, 1912: 15 (type locality: Lombok)

Material examined

Thirty five specimens from the Lesser Sunda Islands, Indonesia, totalling 11 males, 18 females, six juveniles; size range 16.5 to 53.3, largest male 36.8, largest female 53.3, no gravid material.

Figure 31 *Stenogobius zurstrasseni* (Popta), UF 40846, female (50.3), Flores Islands, Indonesia.

Holotype

SMF 17481, female (32.4), Sembalun, Lombok, Sunda Islands, Dutch East Indies, 24 May 1909, J. Elbert.

Additional material

SMF 21386, female (53.3), same collection data as holotype; UF 40846, female (50.3), oxbow lake, Kali Pesi, four km south of Reo, Flores, Lesser Sunda Islands, Indonesia, 24 July 1971, F.G. Thompson; UF 40861, 8(16.5-36.7), one male, three females, four juveniles, oxbow lake, Wai Mokel, five km west northwest of Aimere, Flores, Lesser Sunda Islands, Indonesia, 2 August 1971, F.G. Thompson; UF 44277, 24(18.2-41.1), 10 males, 12 females, two juveniles, oxbow lake, Nanga Boa at Nangaboa, Flores, Lesser Sunda Islands, Indonesia, 3 August 1971, F.G. Thompson.

Diagnosis

Scales in horizontal series 47 to 51, usually 48 to 50; opercle may or may not be scaled; pectoral base usually naked; scales in predorsal midline 11 to 19, usually 16.

Relationship

This species may be synonymous with *Stenogobius blokzeyli*. At present it differs by having fewer teeth in both jaws, but this may be due to most specimens being small and immature.

Description

D VI-I,10 to VI-I,11, almost always VI-I,11; A I,10 to I,11, almost always I,11; P 14 to 16, almost always 15. LS 47 to 51, usually 48 to 50; TRB 12 to 13, usually 12; PD 11 to 19, usually 16 to 18, fully scaled; cheek naked; opercle may or may not be scaled; upper pectoral base almost always naked; lower pectoral base naked; belly anteriorly naked close to pelvic base; breast with few embedded scales. Jaw length not greatly pronounced in sexes. Upper jaw teeth, males 1-2+0-1; females 1+0. Lower jaw teeth, males 3+1-2; females 3+1.

Color in preservation: Background coloration tan; head does not appear dusky. Males with vertical trunk bars beginning behind pectoral base continuing onto caudal

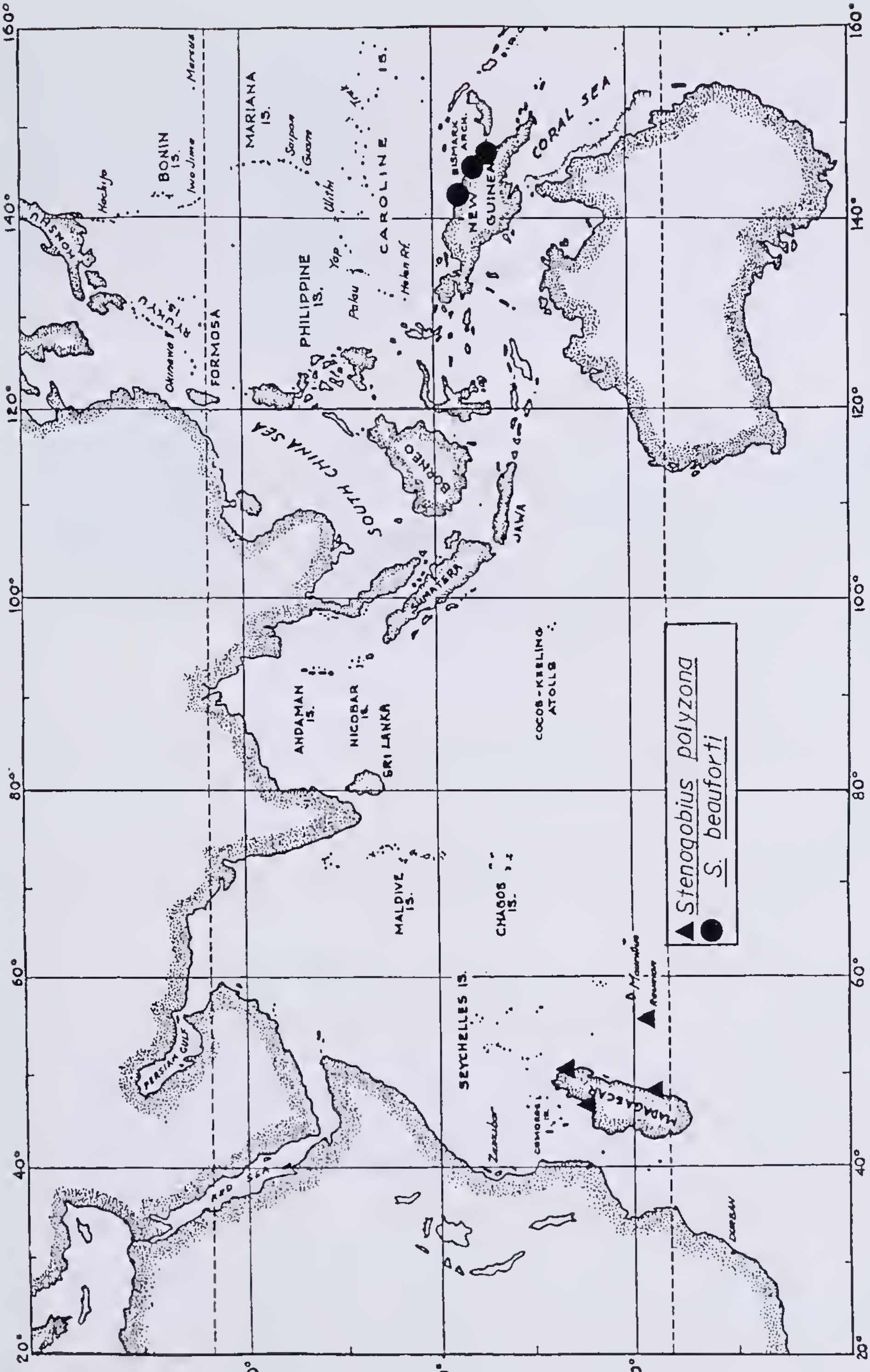

Figure 32 Distributional map of *Stenogobius polyzona species group.*

peduncle; first and second dorsal fin with some spotting, possibly due to male specimens being young. Females with short trunk bars limited midlaterally between second dorsal and anal fins; second dorsal fin with two rows of spots on membrane between rays and spines, first dorsal fin with midlateral band.

Remarks

Distribution: Lesser Sunda Islands, Indonesia
Ecology: Reported from oxbow lakes in fresh water.

Stenogobius (Insularigobius) polyzona species group.

(Figure 32)

This group is known from the western Indian Ocean and northern coastal streams on the island of New Guinea. It is identifiable by almost always lacking short transverse rows of sensory papillae below lower preopercular cutaneous sensory papillae row (Figure 4b). Females with first dorsal fin spotted.

Stenogobius (Insularigobius) polyzona (Bleeker 1867)

(Figures 33a & 33b)

Gobius polyzona Bleeker, 1867: 413 (type locality: Madagascar)

Gobius polyzona. — Sauvage, 1891: 370

Gobius polyzona. — Pellegrin, 1933: 148

Stenogobius genivittatus. — Koumans, 1935: 124 (in part)

Stenogobius genivittatus. — Koumans, 1953: 35 (in part)

Material examined

Thirty three specimens from Madagascar and Reunion, totalling 24 males and nine females; size range 35.8 to 110.7, largest male 110.7, largest female 66.0, smallest gravid female 50.8.

Syntypes

RMNH 4844, two males (110.5-110.7), Samberano River, Madagascar.

Additional Material

MNHN 1933-51, male (66.2), Faraony River, Madagascar; MNHN 1960-226, female (62.4), eastern Madagascar; MNHN 1966-993, 13(35.8-79.6), nine males, four females, Bakora River six km from confluence with Maroka River near Antesemvolu, Mananjary, Fianarantsoa, Madagascar, 1 December 1962, Kiener & Therezien; MNHN 1982-127, 3(44.3-50.8), one male, two females, Reunion Island; MNHN 1984-803, 3(46.2-74.3), two males, one female, Etang Bois Range, Reunion; NHRM KAU/1912.051.3545, male (73.4), Tamatave Market, Madagascar, 29 January 1912, W. Kaudern; NHRM KAU/1912.078.3530, male (47.3), Tamatave, Madagascar, February 1912, W. Kaudern; RUSI 16820, male (96.4), Reunion, December 1975; ZMH 19306, two males (49.8-70.8), Jvoiloina River, Madagascar, October 1864, Majastre.

Diagnosis

On males first dorsal fin same height or higher than second dorsal fin with spines generally filamentous; predorsal midline scales 15 to 19, always fully scaled; caudal peduncle elongate when compared to species of *Stenogobius genivittatus* and *S.*

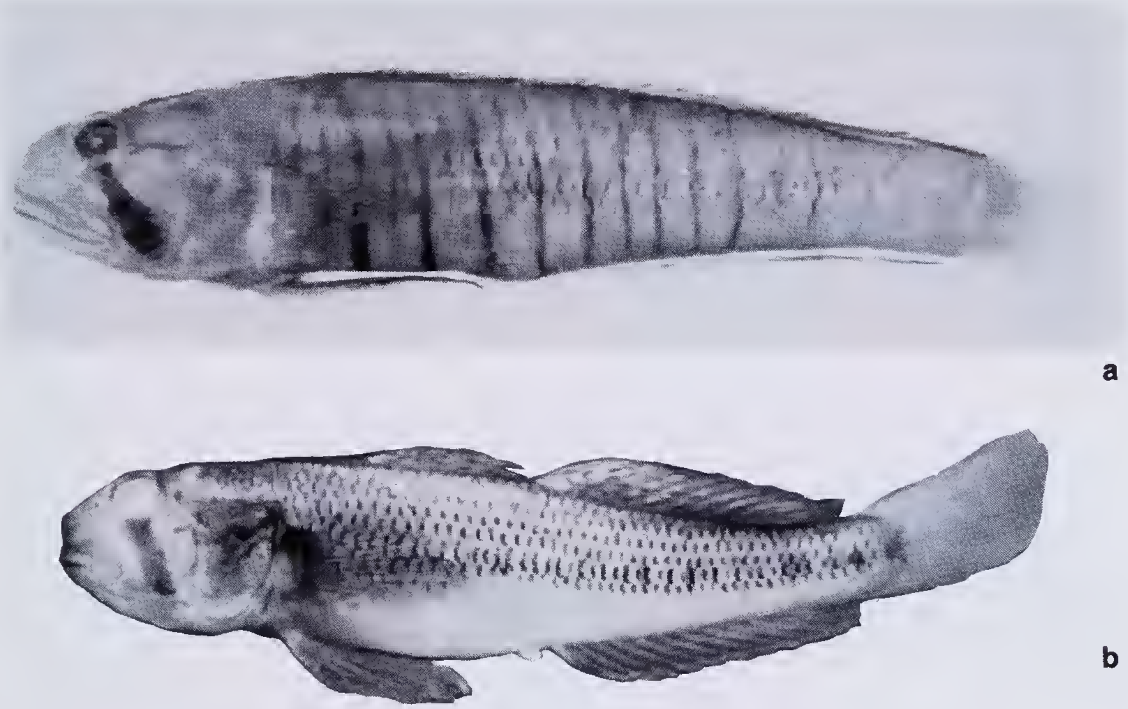

Figure 33 **a:** *Stenogobius polyzona* (Bleeker), RUSI 16820, male (96.4), Reunion Island; **b:** *Stenogobius polyzona* (Bleeker), MNHN 1982-127, female (50.8), Reunion Island.

blokzeyli species complexes; in females first and second dorsal fins with dusky spotting forming two to three rows.

Relationship

This species most closely related to *Stenogobius beauforti*. It differs by the first dorsal fin of male, by having eyes facing outward, and having sexually dimorphic jaw lengths.

Description

D VI-I,10 to VI-I,11, almost always VI-I,11; A I,11; P 14 to 16, almost always 15; first dorsal fin may be higher than second dorsal fin on males, spines may be filamentous and can extend beyond hypural base. LS 47 to 50, usually 48 to 49; TRB 11 to 14, usually 12; PD 15 to 19, usually 16, always fully scaled; cheek naked; opercle usually naked; upper pectoral base usually naked; lower pectoral base almost always naked; belly anteriorly naked close to pelvic base; breast scaled. Jaw extending under pupil in females and beyond posterior edge of eye in males. Upper jaw teeth, males 1-4+1-2, usually 3+1; females 0-2+0, usually 1+0. Lower jaw teeth, males 2-5+1-2, usually 3+2; females 2-3+1, usually 2+1. Teeth on outer row in both jaws enlarged in males.

Color in preservation: Background brownish; body and head not dusky. Color sexually dichromatic: Males; first and second dorsal fins with some blackish vertical streaking that may appear like scribbles on membrane between rays and spines; caudal fin with some dusky spotting on upper anterior portion of fin; pelvic disk dusky; pectoral fin translucent; blackish vertical trunk bars originate behind pectoral base and terminate near caudal fin base, all bars more or less vertical, nearly touching dorsal surface, but do not cross belly, numbering seven to 19. Females; first and second dorsal fins with dusky spotting forming several rows on both fins; dusky trunk bars short, when present, limited to medial region between second dorsal and anal fins, numbering zero to seven.

Remarks

Distribution: Known from fresh water streams and rivers of Madagascar and Reunion of the western Indian Ocean.

Note: The syntypes are unique in having all spines filamentous, including those on pelvic disk. More than one species appears to be represented in the above account. It is clear more material is needed in order to better isolate possible differences.

The status of *Stenogobius (Insularigobius) polyzona* may never be resolved as habitat alteration on Madagascar continues to occur at an ever increasing rate.

Stenogobius (Insularigobius) beauforti (Weber 1908)

(Figures 34a & 34b)

Gobius beauforti Weber, 1908: 261 (type locality: West New Guinea, Dutch East Indies)

Chonophorus beauforti. — Fowler, 1928: 410

Stenogobius genivittatus. — Munro, 1967: 501

Material examined

Thirty specimens from the northeastern coastal region of the island of New Guinea, totalling eight males, 20 females, two juveniles; size range 15.0 to 49.8, largest male 48.2, largest female 49.8, smallest gravid female 35.6.

Syntypes

ZMA 110.943, female (24.6), Klipong (Klifon) River on the east of the Tanah-Merah Creek mouth, West New Guinea, Dutch East Indies, 9 July 1903, L.F. de Beaufort & H.A. Lorentz; ZMA 110.944, two females (35.4-38.1), Mampira Creek, a small brook near the Utuwa River outflow east of Wendesi (?Beek.), West New Guinea, Dutch East Indies, 29/30 July 1903, L.F. de Beaufort & H.A. Lorentz.

Additional material

AMS I.16668-013, 14(35.6-49.8), four males, 10 females, stream at North Coastal Road three miles north of Maiwara, Papua New Guinea, 20 July 1969, F. Talbot; AMS I.17084-013, female (41.7), backwater and tributary streams of Murnass River downstream from bridge at North Coastal Road 25 miles north of Madang, Papua New Guinea, 24 May 1970, B.B. Collette; BMNH 1974.5.24:3543-45, 4(15.0-45.4), one male, two females, one juvenile, same collection data as AMS I.17084-013; KFRS F02511, female (39.9), same collection data as AMS I.17084-013; USNM 270671, 2 males (36.6-40.2), same collection data as AMS I.17084-013; WAM P.27833-010, male (34.7), Mandi Stream, 15 km southeast of Wewak, Papua New Guinea, 16 October 1982, G.R. Allen & D. Coates; WAM P.29613-013, 2(23.1-38.8), one female, one

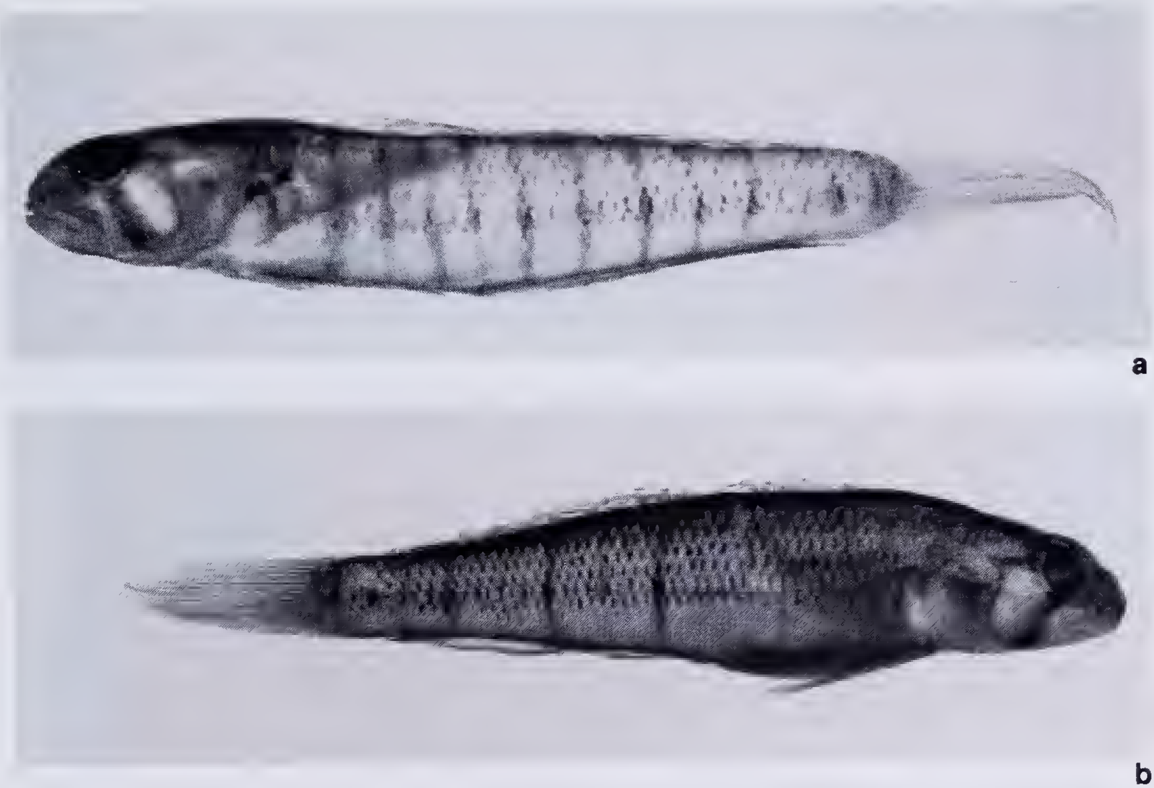

Figure 34 **a:** *Stenogobius beauforti* (Weber), AMS I. 16668-013, male (48.2), Maiwara, Papua New Guinea; **b:** *Stenogobius beauforti* (Weber), AMSI. 16668-013, female (49.8), Maiwara, Papua New Guinea.

juvenile, coastal stream near Bogia, Papua New Guinea, 19 October 1987, G.R. Allen & L. Parenti; ZMA 119.417, 2(45.2-46.0), one male, one female, same collection data as AMS I.16668-013.

Diagnosis

A small species; eyes appear to face slightly upward; jaw length only slightly sexually dimorphic; predorsal midline fully scaled, 13 to 19.

Relationship

This species appears to have no known relatives in the western Pacific or eastern Indian Ocean regions. Its closest relative is *Stenogobius polyzona,* but differs by being much smaller, lacking filamentous spines, and by having eyes appearing to face slightly upward.

Description

D VI-I,11; A I,11; P 14 to 16, usually 15. LS 45 to 50, usually 48; TRB 11 to 13, usually 12; PD 13 to 19, always fully scaled; cheek naked; opercle may or may not be scaled; upper pectoral base almost always naked; lower pectoral base almost always naked; belly anteriorly naked close to pelvic base; breast naked or with few embedded scales.

Jaw reaching under pupil in both sexes. Upper jaw teeth, males 1-3+1-2, usually 2+1-2; females 1-2+0-1, usually 1+0-1. Lower jaw teeth, males 3-4+2, usually 3+2; females 2-3+1-2, usually 2+2. Teeth in outer row on both jaws slightly enlarged in males. Sexual dimorphic characteristics most poorly devloped of all *Insularigobius* species studied. Fins slightly longer in males; jaw lengths only slighly greater in males.

Color in preservation: Background grayish; head dusky dorsally and light ventrally. Coloration sexually dichromatic and described as follows: Males; first and second dorsal fins with some vertical dusky pigmentation between rays and spines appearing as scribbles, both fins slightly dusky on margin; upper caudal fin with very few small dusky spots or streaks; pelvic disk dusky; anal fin dusky with whitish margin; dusky vertical trunk bars originate behind the pectoral base and end near caudal fin base, bars slightly crescentic between second dorsal and anal fins, anterior bars slightly oblique numbering five to 12. Females; first and second dorsal fins with dusky spotting tending to form two rows on fins; caudal fin with one or two dusky spots near upper margin, rest of fin slightly dusky; anal fin whitish basally with dark band distally and whitish margin; dusky vertical trunk bars short and restricted to midline numbering three to nine.

Color in life: Life color of female based on a color transparency provided by G.R. Allen of a specimen 38.8 SL (WAM P.29613-013). Life color similar to those described in preservation. Margins of both dorsal fins pinkish; belly pinkish; branchiostegal region pinkish; iris of eye golden.

Remarks

Distribution: Known from the northern coast of the island of New Guinea east of Djajapura, Irian Jaya, Indonesa.

Ecology: Appears to be limited to small streams close to the coast in fresh and brackish waters.

Conclusion

Though this study expands greatly the knowledge of *Stenogobius* it is by no means conclusive. The status of species from the western Pacific, Japan, Taiwan, the Philippines and Indonesia cannot be fully evaluated until the problem with *Stenogobius (Insularigobius) blokzeyli* can be resolved. There are also considerable gaps in collections with wide areas occurring in the Indo-Pacific where little or no collection efforts have taken place in fresh water.

Gobius gatum Hamilton (1822: 366), usually regarded as *Glossogobius* in most literature accounts, may actually belong to *Stenogobius* or *Awaous* (D.F. Hoese, pers. comm.). This further adds to nomenclatural problems that persist with *Stenogobius*.

It is not clear why *Stenogobius* is well represented on the island of New Guinea, yet has never been reported from Australia. Australia has many suitable habitats where it could occur, apparently some unknown factor is responsible for its absence. It must be pointed out that other widely distributed genera are also absent. *Eleotris* with a circumtropical fresh water distribution is unknown from Australia, as are the tropical Indo-Pacific genera *Papenua, Sicyopterus, Sicyopus* and *Stiphodon*. The genera of freshwater gobioid fishes with tropical Indo-Pacific or wider distribution known from Australia are *Awaous, Glossogobius. Hypseleotris, Ophieleotris, Ophiocara, Oxyeleotris, Pseudogobius* and *Redigobius.* Only seven species of genera with wide Indo-Pacific or circumtropical distribution are not endemic to Australia or share distributions with New Guinea, these being *Butis butis, Glossogobius aureua, G. giuris, Ophieleotris aporos, Ophiocara, porocephala and Redigobius bikolanus.* Note the Australian species of *Awaous* is actually undescribed and has a distribution limited to northeastern Queensland and southern New Guinea. Australia has a number of genera that are endemic or narrowly shared with other locations. *Gobiomorphus* is shared with New Zealand and *Mogurnda* is shared with New Guinea. The remaining genera appear endemic, these being *Chlamydogobius, Kimberleyeleotris, Milyeringa, Philypnodon* and *Tasmanogobius.* The distributional and colonial patterns of freshwater gobioid fishes are poorly known as well as poorly studied, but it is clear some mechanism exists that limits colonization of Australia. It is interesting to note that the wide ranging genus *Hypseleotris,* ranging from the Pacific coast of Central and South America to eastern Africa, has its greatest radiation in Australia being represented by seven nominal species and at least three undescribed, of these only one is not an endemic, *H. compressa* also occurs on New Guinea. The Australian *Hypseleotris* differ from all others of the genus by lacking any cephalic sensory pores on the head. More will likely be learned as genera go through systematic revisions, most genera of freshwater gobioid fishes are currently very poorly known.

One conclusion that can be deduced is *Stenogobius,* as a genus, is wide ranging in the tropical Indo-Pacific. However, the mechanism for wide geographic dispersion among species apparently no longer exists, as is evidenced by the high degree of endemism. There are no species occupying all or large areas of the Pacific or Indian Ocean basins.

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Description of three new species of gobiesocid fishes from southern Australia, with a key to the species of *Cochleoceps*

J.Barry Hutchins*

Abstract

Three new species of clingfishes are described: *Cochleoceps viridis* from Western Australia, *C. bicolor* from Victoria, South Australia, and Western Australia, and *C. orientalis* from New South Wales. *Cochleoceps viridis* closely resembles *C. spatula* (Günther), from South Australia and Western Australia, differing mainly in the shape of the snout and dentition. Although the other two new species are similar in appearance to each other, they can easily be distinguished by differences in colouration and snout shape. Both can be separated from *C. bassensis* Hutchins on the basis of differences in colouration, maximum size, and head shape.

Introduction

The clingfish genus *Cochleoceps* consists of small fishes (to 60 mm SL) which inhabit shallow reef and weed areas along the coastline of Australia's southern half. Hutchins (1983) stated that the genus appeared to consist of five species which could be divided into three groups on the basis of body shape and configuration of the cephalic pores. Only two of these species are currently described, *Cochleoceps spatula* (Günther, 1861) and *C. bassensis* Hutchins, 1983. The purpose of this paper, therefore, is to provide descriptions for the remaining species. A key to the genus is also included.

The methods used follow Hutchins (1983). The material examined is housed at the following institutions: Australian Museum, Sydney (AMS), Museum of Victoria, Melbourne (NMV), Natural History Museum, London (BMNH), South Australian Museum, Adelaide (SAM), and Western Australian Museum, Perth (WAM).

Systematics

Key to the species of Cochleoceps

1a. Body slender, width between pectoral bases 6 or more in SL (Figure 1); 6 preoperculomandibular pores (Figure 2); head and body without red spotting in life 2

1b. Body more robust, width 5 or less in SL; 4-5 preoperculomandibular pores; head and body covered with many moderately sized to very small red spots in life 3

2a. Snout long, generally longer than wide, length 2.8-3.1 in head length; posterior nostril positioned anterior to eye; lower jaw without large forward-projecting incisors .... *C. spatula* (Günther, 1861)

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2b. Snout relatively short, wider than long (Figure 2), length 3.3-3.5 in head length; posterior nostril behind anterior margin of eye (Figure 2); lower jaw with 4-6 large forward-projecting incisors .... *C. viridis* sp. nov.

3a. Head large, length 2.4-2.5 in SL, with prominent triangular-shaped snout; 5 preoperculomandibular pores; head and body covered with moderate-sized red spots in life, those on dorsal surface more oval shaped; dorsal surface without blue cross bars; maximum length 60 mm .... *C. bassensis* Hutchins, 1983.

3b. Head relatively smaller, length 2.7-3.6 in SL, snout small (Figure 5); 4 preoperculomandibular pores (Figure 6); head and body in life covered with small, close-packed red spots, never oval in shape, with numerous blue to purplish cross bars on dorsal surface; maximum length 30 mm SL 4

4a. Dorsal surface with about 12 narrow blue cross bars, those on body continued down sides (Figure 5); snout relatively wide and long, length 3.2-3.6 in head length; anal fin base relatively long, length 5.6-7.0 in SL .... *C. bicolor* sp. nov.

4b. Dorsal surface with numerous blue to purplish markings, tending to form short, rather irregular and often poorly-defined cross bars (Figure 8), those on body not continued down sides; snout relatively narrow and short, length 3.7-4.1 in head length; anal fin base relatively short, length 6.8-8.4 in SL .... *C. orientalis* sp. nov.

Cochleoceps viridis sp. nov.

Figures 1-3, 4a; Table 1

Cochleoceps species 1 — Hutchins, 1983: 37, 40, and 45.

Holotype

WAM P.26604-015, 39 mm SL, Emu Point, King George Sound, Western Australia, trawled from *Posidonia* beds in 2-3 m, J.B. Hutchins *et al.*, 15 April 1980.

Paratypes

32 specimens from Western Australia, 14-40 mm SL (unless otherwise designated, all specimens at WAM): P.26604-009, 6 specimens, 30-36 mm SL (35 mm specimen cleared and stained), taken with holotype; P.26622-004, 5 specimens, 29-33 mm SL, Rottnest Island, trawled at 0.5-2 m, J.B. Hutchins, 16 June 1980; P.26455-011, 5 specimens, 14-21 mm SL, Geographe Bay, J. Scott, 25 December 1977; P.28267-003, 7 specimens, 23-27 mm SL, Carnac Island, trawled at 3-4 m, J.B. Hutchins and N.O. Sinclair, 10 February 1984; P.28280-004, 2 specimens, 33 mm SL, Israelite Bay, trawled in 0.5-2 m, J.B. Hutchins, 1 April 1984; P.28288-003, 39 mm SL, Israelite Bay, trawled at 1-2.5 m, J.B. Hutchins, 6 April 1984; AMS I.31830-001, 2 specimens, 24-27 mm SL, Rottnest Island, trawled in 1-2 m, J.B. Hutchins, 6 April 1991; BMNH 1991.9.12:9-10, 2 specimens, 26-27 mm SL, same data as for previous entry; NMV 9559, 2 specimens, 26-30 mm SL, same data as for previous entry.

Table 1. Measurements (mm) and counts of the holotype and selected paratypes of *Cochleoceps viridis*

	Holotype WAM P.26604-015	Paratypes WAM P.26604-009	WAM P.26622-004	WAM P.26604-009	WAM P.26622-004	WAM P.28267-003	WAM P.26455-011
Standard length	39	36	33	30	28	23	19
Head length	12	11	11	10	9.1	8.1	6.9
Head width	6.9	5.9	6.3	5.7	5.4	5	4.6
Body depth	3.9	3.1	3.6	2.8	3	2.4	2
Body width	5.6	5.1	5.2	4.2	4.2	3.8	2.9
Snout length	3.6	3.3	3.2	2.9	2.7	2.3	2
Eye diameter	2.3	2.2	2.1	1.9	1.9	1.7	1.4
Interorbital width	2.6	2.4	2.3	2.3	2	1.7	1.4
Snout to origin of dorsal fin	30	28	25	22	22	18	14
Snout to anus	28	24	23	20	19	16	13
Caudal peduncle length	4.2	3.3	4	2.9	3.4	3.1	2.5
Caudal peduncle depth	1.6	1.6	1.5	1.4	1.3	1	0.8
Caudal fin length	6.4	6.7	6.5	6.1	5.3	4.5	3.4
Ventral disc length	7.9	7.5	6.7	6	5.3	4.7	3.4
Ventral disc width	4.9	5	5.1	4.1	4.3	3.3	2.7
Dorsal base length	5.4	3.7	3.7	3.9	3.3	2.2	1.7
Anal base length	5	5.6	4.4	4.4	4	2.4	2
Dorsal fin ray count	6	4	4	4	4	3	4
Anal fin ray count	5	5	5	5	6	4	5
Pectoral fin ray count	17	18	18	17	19	19	19

Figure 1. *Cochleoceps viridis* sp. nov., paratype, WAM P28288-003, 39 mm SL, dorsal view (photographed just after capture).

Diagnosis

This species is distinguished from all other Australian gobiesocids by the combination of its slender form, ventral disc with papillae on all four regions, subopercular spine absent, six preoperculomandibular pores, and greatly enlarged forward-projecting incisorlike teeth in the lower jaw. *Cochleoceps viridis* closely resembles *C. spatula*, the two easily being separated by differences in snout shape, position of the nostrils, and dentition (see Key to Species above).

Description

Measurements and counts of the holotype and selected paratypes are presented in Table 1. The following counts and proportions in parentheses represent the ranges for the paratypes when they differ from those of the holotype.

Dorsal fin rays 6 (3-6, average 4); anal fin rays 5 (4-6, average 5); pectoral fin rays 17 (17-19); pelvic fin rays I, 4; segmented caudal fin rays 9-11 (from cleared and stained material); vertebrae 32-33 (from cleared and stained paratypes); branchiostegals 6.

Body elongate, subcylindrical (moderately depressed anteriorly, tapering to a compressed caudal peduncle), depth 10 (9.2-11.6) and width 7.0 (6.1-7.1), both in SL; caudal peduncle moderately long, depth 2.6 (2.1-3.1) in its length; head flat, depressed, length 3.3 (2.8-3.3) in SL and head width 1.7 (1.5-1.9) in its length; snout moderately long and wide (wider than long), somewhat truncate in dorsal view, rounded anteriorly, length 3.3 (3.3-3.5) in head length; nostrils moderate in size, tubular, posterior one much shorter than anterior one; posterior nostril on or behind line joining anterior margins of eyes; anterior nostril with simple narrow triangular flap on posterior portion of rim, flap reaching about half way to posterior nostril when folded rearwards; eye moderately large with prominent clear cornea, diameter 5.2 (4.8-5.3) in head length, equal to or slightly smaller than bony interorbital width (4.6 [4.3-4.9] in head length).

Skin smooth and scaleless, usually covered by thick mucus layer; lateral line sensory system consists of moderately sized open pores and minute papillae, former found only on head (Figure 2); each pore has short tubular opening slightly longer than thickness of

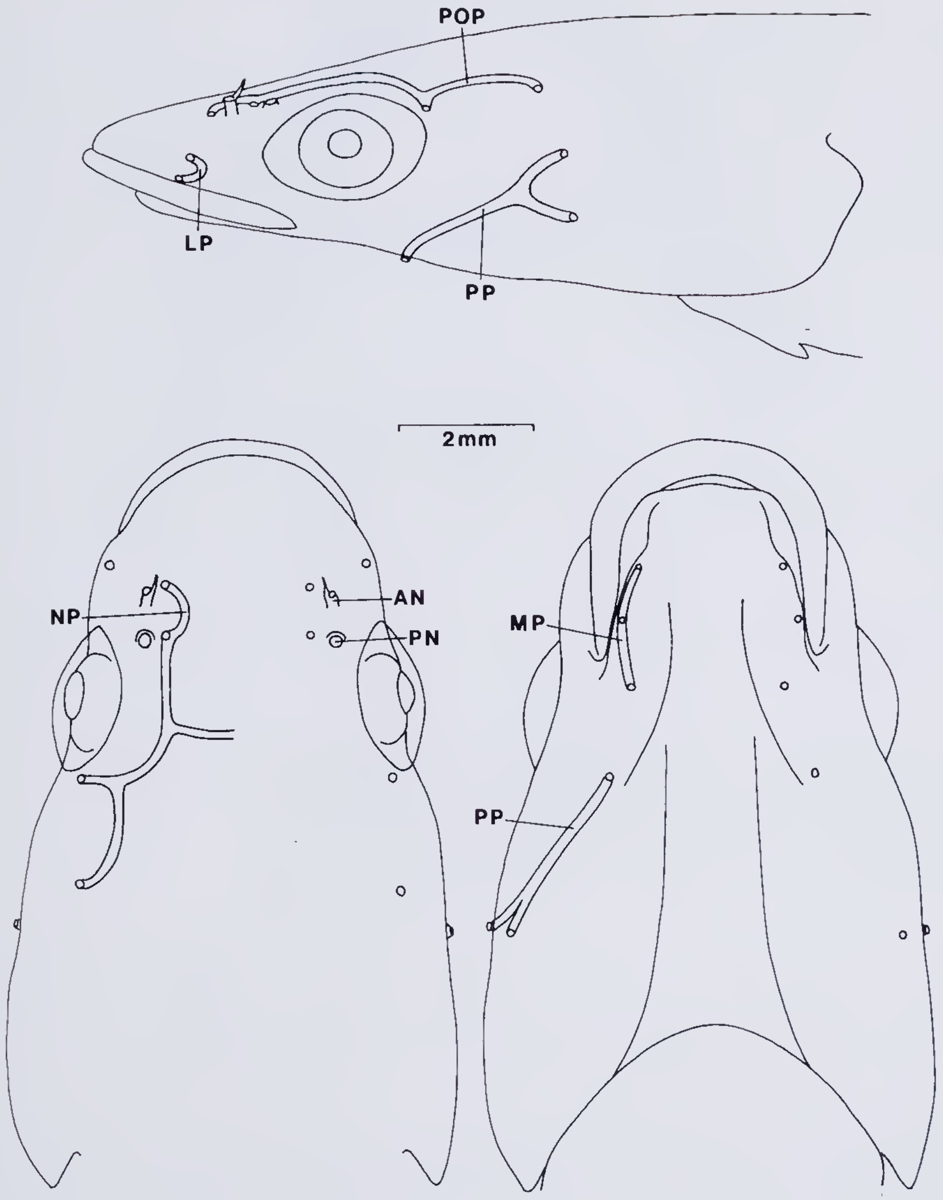

Figure 2. Diagram of the cephalic pore system of *Cochleoceps viridis* sp. nov., WAM P.26604-009, 36 mm SL (pores represented by open circles, the underlying canals on one side outlined by solid lines), lateral, dorsal and ventral views. (Abbreviations: AN, anterior nostril; LP, lacrymal pore canal; MP, mandibular pore canal; NP, nasal pore canal; PP, preopercular pore canal; PN, posterior nostril; POP, postocular pore canal).

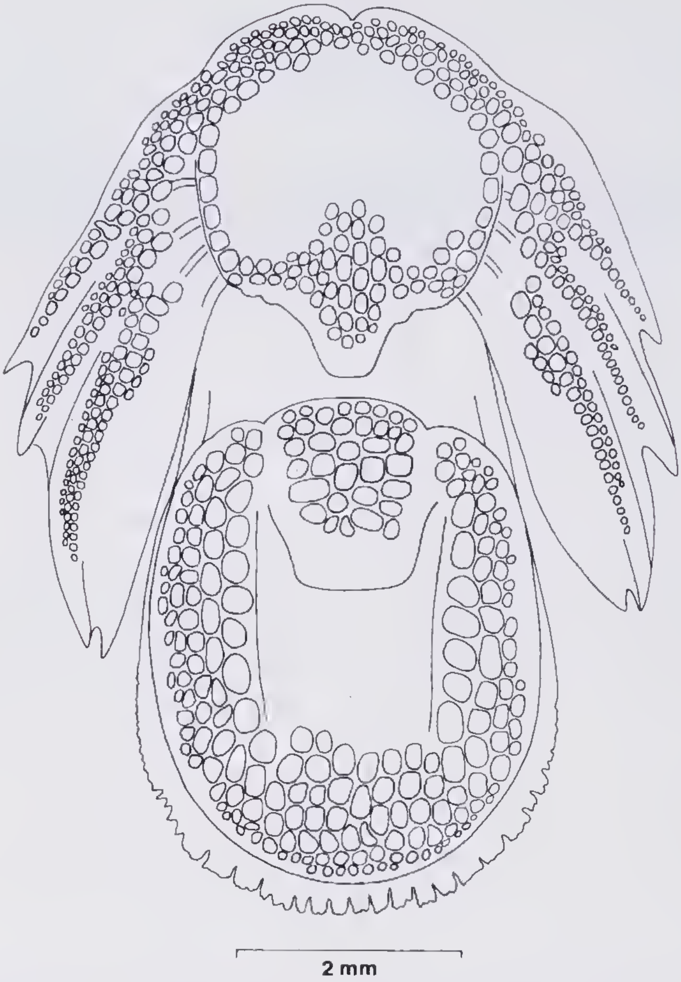

Figure 3. Ventral sucking disc of *Cochleoceps viridis* sp. nov., WAM P.28288-003, 39 mm SL, showing arrangement of papillae (ventral view, anterior end facing top of page).

mucus layer, and associated with canal in underlying bone (outlines of canals indicated in Figure 2); total of 12 pores on each side of head consisting of two lacrymal pores, two nasal pores, two postocular pores, and six preoperculomandibular pores (three pores associated with preopercle and three with mandible); papillae arranged in longitudinal series laterally on body, others scattered on head (all papillae difficult to detect).

Gill opening wide, membranes joined across isthmus, but not attached to it; upper attachment of gill membrane opposite first or second pectoral fin ray; upper attachment of pelvic fin membrane opposite 11th (10th-13th) pectoral fin ray; upper attachment of axial dermal flap opposite ninth (eighth-ninth) pectoral fin ray; ventral disc double, moderate in size, length 4.9 (4.8-5.6) and width 8.0 (6.5-8.0), both in SL; papillae on all four regions of disc, arranged as in Figure 3 (some papillae missing in holotype, particularly in region B).

Mouth inferior, upper lip projecting well forwards of lower lip; rear corner of mouth below anterior quarter of eye; lip fold on lower jaw not continued across symphysis; teeth in upper jaw small, conical, lateral teeth uniserial, expanding to 4-5 series anteriorly to form a tooth patch on either side of symphysis; teeth in lower jaw similar, except three anterior teeth on each side of symphysis greatly enlarged, incisor-like, projecting forwards horizontally; palatine and vomerine teeth absent; gill filaments on first three gill arches, absent on fourth; gill rakers 4-5, short and conical.

Bases of dorsal and anal fins short, lengths 7.2 (7.2-11.2) and 7.8 (6.4-9.6) respectively, both in SL; base of dorsal fin generally shorter than and originating posterior to anal fin (specimens with more rays in dorsal fin than in anal fin may have a longer dorsal base which originates in advance of anal fin); dorsal and anal fin rays short, subequal to base of respective fin; urogenital opening located just anterior to anal fin origin, well behind rear margin of ventral disc; genital papilla prominent.

Subopercule present, forming terminal bone posteriorly on side of head, not spine-like; dorsal postcleithral bone rather narrow (Figure 4a), reaching as high as eighth pectoral fin ray; cleithral, pelvic and ventral postcleithral bones shaped as in Figure 4a.

Colour of holotype in alcohol: overall pale yellowish brown.

Colour when fresh (based on colour transparencies of live individuals underwater and freshly collected material): ground colour apple green to pale green, and more rarely a translucent white; head and body with many minute brown spots forming either irregular longitudinal lines with short, broader cross bars on midline of back or a prominent reticulate pattern; golden yellow spots and blotches usually incorporated in above pattern, but fading on death; small pale blotches occasionally on dorsal and lateral surfaces; transluscent colour form usually with some indistinct green blotching on dorsal surface and greyish brown blotching laterally; fin rays of similar colour to overall body colour; after death, and especially after preservation, all markings become more reddish pink.

Distribution

Cochleoceps viridis is known only from south-western Western Australia, from Israelite Bay (33°37′S, 123°53′E) at the western extremity of the Great Australian Bight to Rottnest Island off Perth.

Remarks

Cochleoceps viridis has been collected by bottom trawl from *Posidonia* seagrass beds at depths of 1-5 m, sometimes in association with *C. spatula*. The two are easily distinguished by the length of the snout, the snout being noticeably shorter in *C. viridis* (wider than long versus longer than wide in *C. spatula,* see Hutchins 1983, Figure 2). In addition, *C. viridis* possesses greatly enlarged, forward projecting incisors in the lower jaw, a feature lacking in *C. spatula*.

Many of the osteological features of *Cochleoceps viridis* are shared by *C. spatula,* especially regarding the shape and positioning of the pelvis, postcleithral bones, pelvic fin spine, cleithrum, maxillary, palatine, and ectopterygoid. Other members of the genus

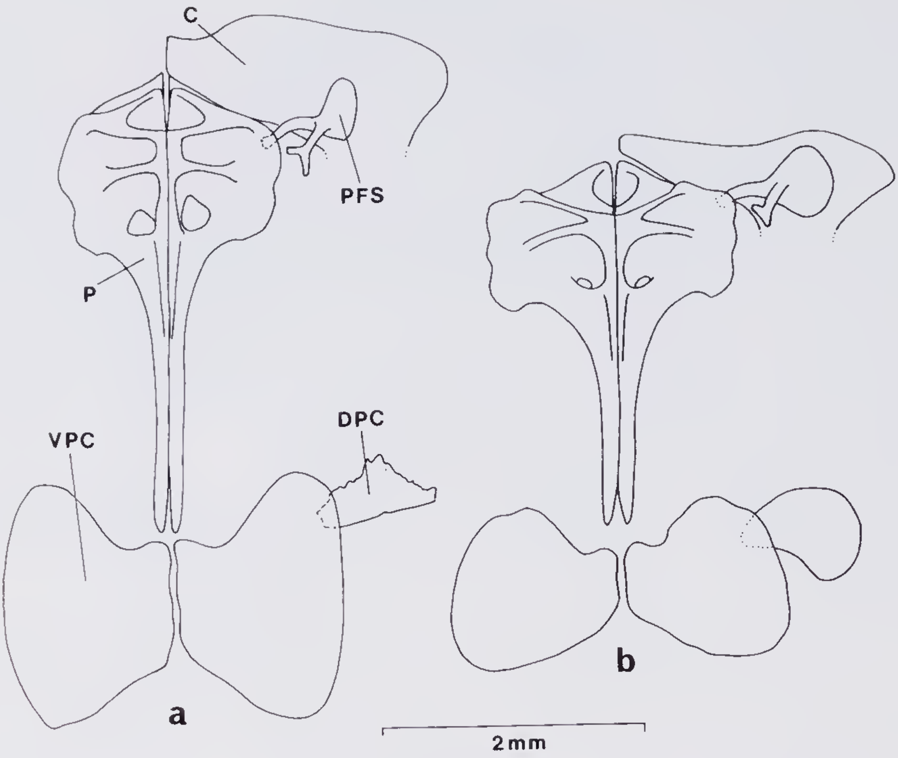

Figure 4. Pelvis and associated bones (ventral view, anterior end facing top of page) of a, *Cochleoceps viridis* sp. nov., WAM P.26604-009, 35 mm SL; and b, *C. bicolor* sp. nov., WAM P. 26608-025, 20 mm SL (for clarity, all pelvic fin rays and some bones from left side omitted from each illustration; also, anterior portion only of right cleithrum shown). (Abbreviations: C, cleithrum; DPC, dorsal postcleithrum; P, pelvis; PFS, pelvic fin spine; VPC, ventral postcleithrum).

differ considerably, particularly with respect to the last five bones. Furthermore, an undescribed species at present included in an undescribed genus tentatively referred to as Genus A (Hutchins, in press), shares many of the osteological features of *C. spatula* and *C. viridis*. However, like the other two currently undescribed members of Genus A, it possesses a prominent subopercular spine, a feature lacking in all species of *Cochleoceps*. In spite of the latter character, this new species has more in common with *C. viridis* and *C. spatula* than do any of the other present members of *Cochleoceps* (*bassensis*, *bicolor* sp. nov., and *orientalis* sp. nov.). However, the relationships between the three species considered to belong to Genus A are presently obscure due to the shortage of material. Further studies now in progress may show that a redefinition of generic limits is necessary.

This species is named *viridis* after its predominantly green colouration.

Additional material examined.

WAM P.30262-001, 9 specimens, 24-30 mm SL, Rottnest Island, Western Australia, trawled at 1-2 m, J.B. Hutchins, 6 April 1991.

Cochleoceps bicolor sp. nov.
Figures 4b, 5-7; Table 2

"Clingfish" — Hutchins, 1979: 7, Figure.; Scott *et al.*, 1980: Figure.

Cochleoceps species 2 — Hutchins, 1983: 44-46.

Cochleoceps species — Hutchins and Thompson, 1983: 20 and 76, Figure; Hutchins and Swainston, 1986: 32 and 123, Figure; Hutchins, 1991, 627, Figures.

Holotype

WAM P.28522-002, 22 mm SL, Flinders Island, off Cape Leeuwin, Western Australia, rotenone at 12-13 m, J.B. Hutchins *et al.*, 18 April 1985.

Paratypes

22 specimens, 13-30 mm SL (unless otherwise designated, all specimens from Western Australia): WAM P.25763-002, 13 mm SL, Sandy Hook Island, Archipelago of the Recherche, by hand from the ascidian *Pyura spinifera* at 27 m, J.B. Hutchins, 8 April 1977; WAM P.26608-025, 20 mm SL (cleared and stained), Cheyne Beach, rotenone at 15 m, J.B. Hutchins *et al.*, 19 April 1980; WAM P.28293-007, 4 specimens, 15-21 mm SL, Lucky Bay, east of Esperance, rotenone at 5-7 m, J.B. Hutchins, 12 April 1984; WAM P.28300-003, 4 specimens, 18-21 mm SL, Lucky Bay, east of Esperance, rotenone at 11-12 m, J.B. Hutchins, 16 April 1984; WAM P.28296-007, 7 specimens, 14-26 mm SL, Mondrain Island, Archipelago of the Recherche, rotenone at 5-6 m, J.B. Hutchins *et al.*, 13 April 1984; WAM P.28265-001, 30 mm SL, off Parker Point, Rottnest Island, by hand at 22 m, J. Keesing, 4 February 1984; AMS I.31831-001, 17 mm SL, Lucky Bay, rotenone at 10 m, J.B. Hutchins *et al.*, 11 April 1984; BMNH 1991.9.12:11, 18 mm SL, same data as previous specimen; NMV A.2829, 29 mm SL, Flinders Island, South Australia, R. Kuiter, 29 March 1982; SAM F.6986, 28 mm SL, American River, Kangaroo Island, South Australia, by hand, N. Holmes, 11 December 1985.

Diagnosis

This species is distinguished from all other Australian gobiesocids by the combination of its small size (to 30 mm SL), ventral disc with papillae on all four regions, subopercular spine absent, four preoperculomandibular pores, and unique colouration. It differs from the similarly shaped *C. orientalis* sp. nov. (see following description) by differences in colouration, snout shape, and length of the anal fin (see Key to Species above).

Description

Measurements and counts of the holotype and selected 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.

Dorsal fin rays 5 (4-6, average 6); anal fin rays 6 (5-6, average 5); pectoral fin rays 23 (21-23); pelvic fin rays I, 4; caudal fin rays 10; vertebrae 31 (from radiographs and cleared and stained material); branchiostegals 6.

Body somewhat robust, moderately depressed anteriorly, tapering to compressed caudal peduncle, depth 5.4 (4.8-6.7) and width 4.3 (3.9-4.6), both in SL; caudal peduncle short but obvious, depth 0.9 (0.9-1.2) in its length; head moderately wide, length 3.1 (2.8-3.6) in SL and head width 1.2 (1.2-1.4) in its length; snout short, somewhat triangular when viewed from above, rounded anteriorly , length 3.2 (3.2-3.6) in head

Table 2. Measurements (mm) and counts of the holotype and selected paratypes of *Cochleoceps bicolor*

	Holotype	Paratypes				
	WAM P.28522-002	WAM P.28265-001	NMV A.2829	WAM P.28296-007	WAM P.28300-003	WAM P.28300-003
Standard length	22	30	28	26	21	18
Head length	7	8.3	8.7	8.2	6.5	6.5
Head width	5.7	6.8	7.3	6.5	4.6	4.5
Body depth	4.1	4.5	4.8	5.4	3.5	3.1
Body width	5.1	6.7	6.8	6.6	4.9	3.9
Snout length	2.2	2.3	2.5	2.3	1.9	1.8
Eye diameter	1.9	2.6	2.5	2.3	2.1	1.8
Interorbital width	2.2	2.7	2.3	2.4	1.5	1.4
Snout to origin of dorsal fin	16	22	21	20	15	13
Snout to anus	13	19	17	17	13	11
Caudal peduncle length	1.8	2.2	2.5	2.3	2.1	2
Caudal peduncle depth	2.1	2.4	2.7	2.3	1.8	1.8
Caudal fin length	4.8	5.4	6.1	5.6	—	4
Ventral disc length	6.4	7.9	7.5	7.4	5.9	5.6
Ventral disc width	5.6	6	7.4	6.2	4.9	4.3
Dorsal base length	3.1	4.3	4.5	3.9	3	2.5
Anal base length	3.7	4.3	5	3.9	3.1	2.8
Dorsal fin ray count	5	5	6	5	6	6
Anal fin ray count	6	6	6	5	6	6
Pectoral fin ray count	23	23	21	22	22	21

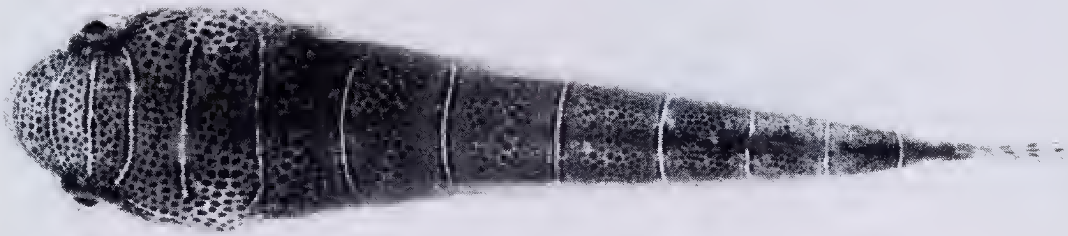

Figure 5. *Cochleoceps bicolor* sp. nov., holotype, WAM P.28522-002, 22 mm SL, dorsal view (photographed just after capture).

length; nostrils moderate in size, tubular, posterior one shorter than anterior one; posterior nostril behind anterior margin of eye, anterior nostril just in front of eye, latter with a simple narrow triangular flap on posterior portion of rim, flap reaching about one third to two-thirds to posterior nostril; eye moderately large, diameter 3.7 (3.1-3.7) in head length, almost equal to bony interorbital width (3.2 [3.1-4.6] in head length).

Skin smooth and scaleless, usually covered by thick mucus layer; lateral line sensory system consists of moderately sized open pores and minute papillae, former found only on head (Figure 6); each pore with short tubular opening slightly longer than thickness of mucus layer, associated with canal in underlying bone (outlines of canals indicated in Figure 6); 10 pores on each side of head, two lacrymal, two nasal, two postocular, and four preoperculomandibular pores (two pores associated with preopercle, two with mandible); papillae arranged in two longitudinal series laterally on body, others scattered on head (difficult to detect).

Gill opening wide, membranes joined across isthmus but not attached to it; upper attachment of gill membrane opposite first or second pectoral fin ray; upper attachment of pelvic fin membrane opposite 15th (12th-15th) pectoral fin ray; upper attachment of axial dermal flap opposite sixth (sixth-seventh) pectoral fin ray; ventral disc double, moderately large in size, length 3.4 (3.2-3.8) and width 3.9 (3.8-5.0), both in SL; papillae on all four regions of disc, arranged as in Figure 7 (some disc papillae lost in holotype and some paratypes).

Mouth inferior, upper lip projecting noticeably forwards of lower lip; rear corner of mouth below anterior margin of eye; lip fold on lower jaw not continued across symphysis; teeth in upper and lower jaws small, conical, with acute posteriorly curving tips; outermost teeth uniserial, close-packed, encompassing band of 1-3 irregular rows of somewhat smaller, more widely spaced teeth (anterior teeth in lower jaw projecting further forwards than those in upper jaw); palatine and vomerine teeth absent; gill

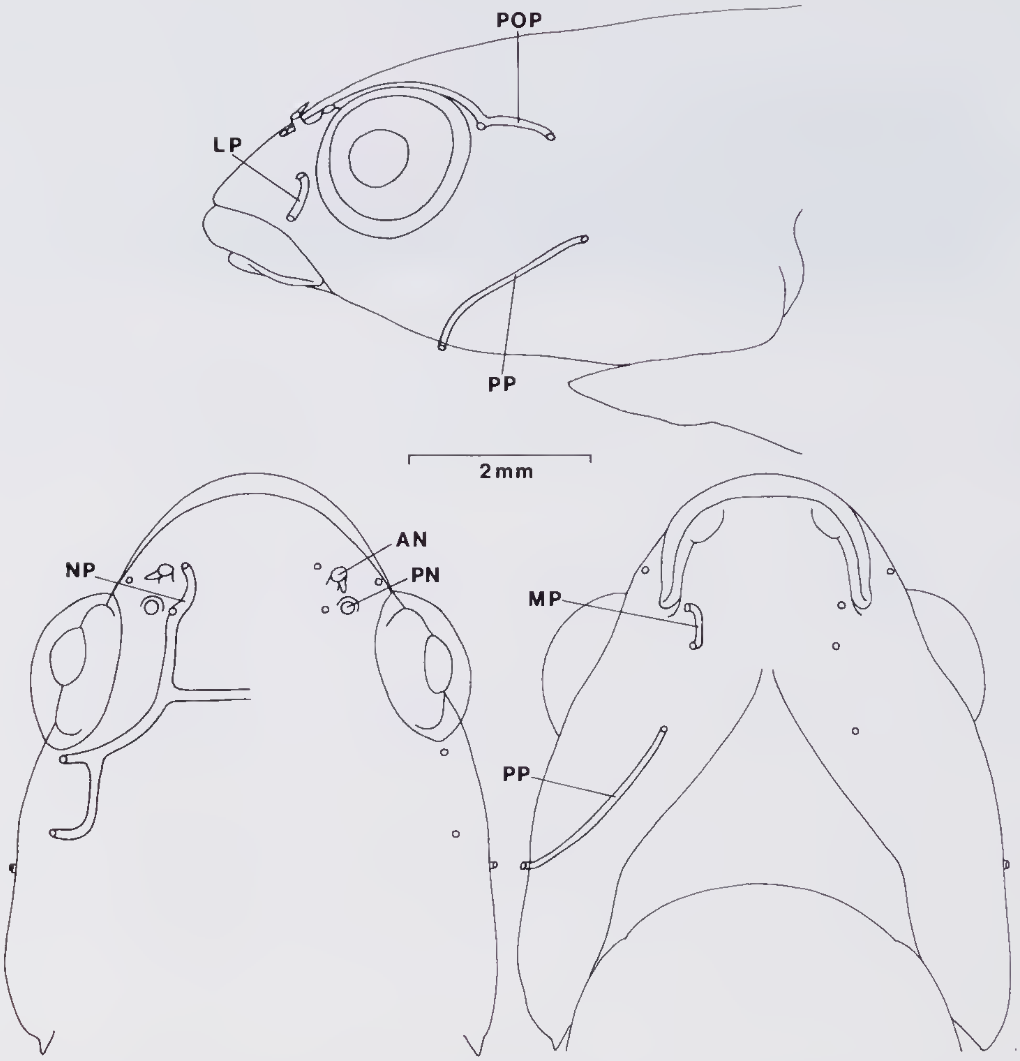

Figure 6. Diagram of the cephalic pore system of *Cochleoceps bicolor* sp. nov., holotype, WAM P.28522-002, 22 mm SL, (pores represented by open circles, the underlying canals on one side outlined by solid lines), lateral, dorsal and ventral views. (Abbreviations as for Figure 2).

filaments on first three gill arches, absent on fourth; gill rakers on second gill arch 8-9, moderately long, conical, and finely pointed.

Bases of dorsal and anal fins short, lengths 7.1 (6.2-7.2) and 5.9 (5.6-7.0) respectively, both in SL; dorsal fin generally originating above origin of anal fin; dorsal and anal fin rays moderate in length, anterior 1-2 longest, about equal to base of respective fin; urogenital opening located about one-third to midway between posterior margin of ventral disc and anal fin origin; genital papilla prominent.

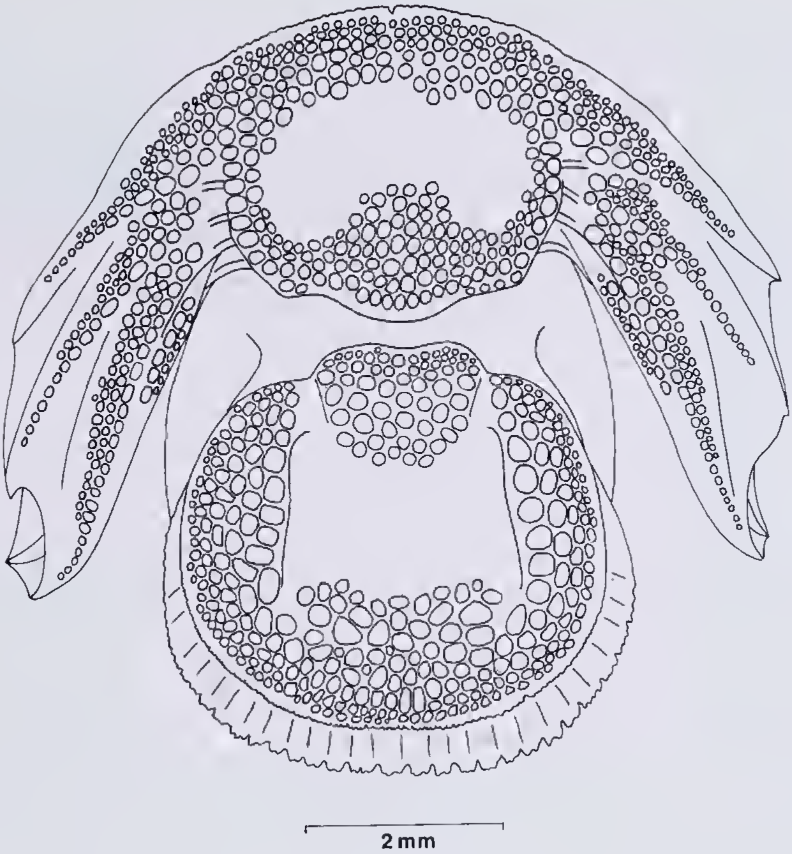

Figure 7. Ventral sucking disc of *Cochleoceps bicolor* sp. nov., NMV A.2829, 28 mm SL, showing arrangement of papillae (ventral view, anterior end facing top of page).

Subopercular element present, forming terminal bone posteriorly on side of head, not spinelike; dorsal postcleithral bone rather large, shaped as in Figure 4b, reaching as high as tenth pectoral fin ray; cleithral, pelvic and ventral postcleithral bones shaped as in Figure 4b (cleithrum without prominent forward-projecting flange near symphysis).

Colour of holotype in alcohol: overall pale yellowish brown.

Colour when fresh (based on colour transparencies of live fish underwater and freshly collected material): ground colour pale yellowish brown to pinkish brown, head and body covered with many very small to minute, closely packed reddish spots (Figure 5), those on posterior portion of body normally more dusky in colour, producing a distinctly bicoloured appearance; 12-15 narrow iridescent blue bars across dorsal surface, those on body continued down sides (1-3 additional bars radiate out posteriorly and anteriorly from margin of eye); reddish spots adjacent to blue bars usually more dusky, forming darker margins to cross bars; fins hyaline, with indications of reddish spotting, particularly on caudal where spotting forms about five distinct cross bands; iris reddish.

Distribution

Cochleoceps bicolor ranges from Port Phillip Bay in Victoria to Lancelin (31°01'S, 115°20'E) in Western Australia. Its presence in Victoria is based on a single individual photographed at Portsea Pier, Port Phillip Bay.

Remarks

Cochleoceps bicolor inhabits areas of rocky reef, usually occurring on sponges and ascidians where it sets up "cleaning stations" for the purpose of removing skin parasites from other species of fish (see Hutchins 1991 for a more detailed account of the natural history of this species). It is capable of undergoing reasonably rapid colour changes to match the colour of its substrate (by increasing or decreasing the size of the closely packed spots on its head and body).

The differences between this species and both *Cochleoceps spatula* and *C. viridis* were discussed in the previous species account. In addition, it differs from *C. bassensis* and *C. orientalis* sp. nov. (described below) by having bright blue bars almost completely encircling its body, a character lacking in the latter two species. The features separating it from *C. orientalis*, however, are only slight (differences in colouration, snout shape, and length of anal fin base [see Key to Species]). Furthermore, although the ranges of these two species are separated by Bass Strait, they share the same ecological niche (both are specialised fish cleaners, see above). This may suggest that the two are only subspecifically distinct; however, the morphological differences referred to above indicate that the two forms must have been separated for a considerable period of time (see Hutchins 1987, for information on the formation of allopatric species pairs in the Bass Strait region). Therefore, they are here afforded full specific recognition.

This species is named *bicolor* with reference to its two-tone body colouration (reddish anteriorly, dusky posteriorly).

Additional material examined.

WAM P.26005-009, 2 specimens, 12-21 mm SL, Mondrain Island, Archipelago of the Recherche, rotenone at 10-13 m, 13 March 1978; P.26616-002, 17 mm SL, Rottnest Island, Western Australia, rotenone at 8 m, 7 June 1980; P.28519-003, 15 mm SL, Cape Naturaliste, Western Australia, rotenone at 6-7 m, 13 April 1985.

***Cochleoceps orientalis* sp. nov.**

Figure 8; Table 3

Cochleoceps species 3 — Hutchins, 1983: 44-45.

Cochleoceps species — Hutchins and Swainston, 1986: 32 and 123, Figure; Hutchins, 1991: 633.

Holotype

WAM P.27103-001, 22 mm SL, Big Island, off Wollongong, collected from the ascidian *Pyura spinifera* by hand at 10 m, J.B. Hutchins, 3 February 1981.

Paratypes

5 specimens, 19-23mm SL (all specimens from New South Wales): AMS I.21975-001, 19 mm SL, The Haven, Terrigal, K. Handley, 26 February 1977; NMV A.2830, 23 mm SL, Montague Island, New South Wales, R. Kuiter, 15 September 1981; WAM P.27103-002, 3 specimens, 21-23 mm SL (one cleared and stained), collected with holotype.

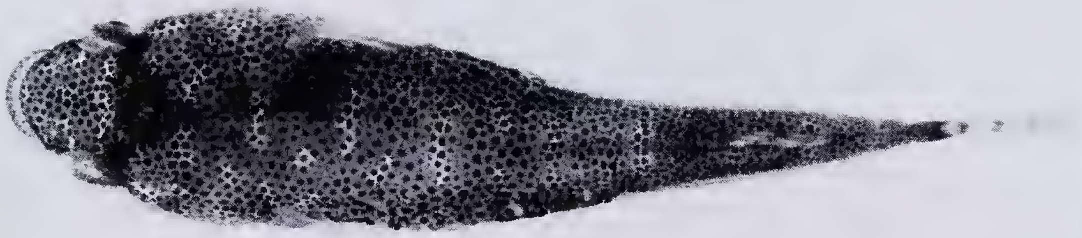

Figure 8. *Cochleoceps orientalis* sp. nov., holotype, WAM P.27103-001, 22 mm SL, dorsal view (photographed just after capture).

Diagnosis

A species of *Cochleoceps* closely resembling *C. bicolor* (described above), but differing in colouration, snout shape, and length of anal fin base (see Key to Species).

Description

Measurements and counts of the holotype and selected paratypes are presented in Table 3. The following counts and proportions in parentheses represent the ranges for the paratypes when they differ from those of the holotype.

Dorsal fin rays 5 (5-6, average 5); anal fin rays 5(4-6, average 5); pectoral fin rays 21(21-23); pelvic fin rays I,4; caudal fin rays 10; vertebrae 30-31 (from radiographs and cleared and stained material); branchiostegals 6.

Body somewhat robust, moderately depressed anteriorly, tapering to compressed caudal peduncle, body depth 5.9 (4.8-6.6) and width 4.7 (3.9-4.6), both in SL; caudal peduncle short but obvious, depth 1.1 (0.7-1.1) in its length; head moderately depressed, length 3.1 (2.7-3.1) in SL and head width 1.4 (1.2-1.4) in its length; snout short, somewhat triangular when viewed from above, rounded anteriorly, length 3.7 (3.7-4.1) in head length; nostrils moderate in size, tubular, posterior one shorter than anterior one; posterior nostril behind anterior margin of eye, anterior nostril just in front of eye, latter with simple narrow triangular flap on posterior portion of rim, flap reaching about one third to two-thirds to posterior nostril; eye moderately large, diameter 3.5 (3.4-3.7) in head length, almost equal to bony interorbital width (3.5 [3.5-4.3] in head length).

Skin smooth and scaleless, usually covered by thick mucus layer; lateral line sensory system consists of moderately sized open pores and minute papillae, former found only on head; each pore with short tubular opening slightly longer than thickness of mucus layer, associated with canal in underlying bone; 10 pores on each side of head, two lacrymal, two nasal, two postocular, and four preoperculomandibular pores as in *Cochleoceps bicolor* (see Figure 6); papillae arranged in two longitudinal series laterally on body, others scattered on head (papillae difficult to detect).

Table 3. Measurements (mm) and counts of the holotype and selected paratypes of *Cochleoceps orientalis*

	Holotype	Paratypes			
	WAM P.27103-001	NMV A.2830	WAM P.27103-002	WAM P.27103-002	AMS I.21975-001
Standard length	22	23	21	19	19
Head length	7	7.7	6.9	6.5	7.1
Head width	5.1	6.4	5.2	4.5	5.5
Body depth	3.7	4.4	3.2	3.2	4
Body width	4.7	5.9	4.8	4.1	4.7
Snout length	1.9	2	1.7	1.7	1.9
Eye diameter	2	2.2	2	1.9	1.9
Interorbital width	2	2	1.8	1.5	1.7
Snout to origin of dorsal fin	16	17	16	15	14
Snout to anus	14	14	13	12	12
Caudal peduncle length	1.9	1.9	1.8	1.8	1.3
Caudal peduncle depth	1.7	2.5	1.9	1.8	2
Caudal fin length	4.9	5.1	4.1	4	—
Ventral disc length	5.9	6.2	5.7	5.5	5.4
Ventral disc width	5.2	5.9	4.7	4.5	5
Dorsal base length	2.8	3.8	2.9	2.9	2.9
Anal base length	3	3.3	2.5	2.7	2.8
Dorsal fin ray count	5	5	5	6	5
Anal fin ray count	5	4	5	5	6
Pectoral fin ray count	21	22	23	22	23

Gill opening wide, membranes joined across isthmus but not attached to it; upper attachment of gill membrane opposite first or second pectoral fin ray; upper attachment of pelvic fin membrane opposite 13th (13th-14th) pectoral fin ray; upper attachment of axial dermal flap opposite eighth pectoral fin ray; ventral disc double, moderately large in size, length 3.7 (3.5-3.7) and width 4.2 (3.8-4.5), both in SL; papillae on all four regions of disc, arranged as in *Cochleoceps bicolor* (see Figure 7).

Mouth inferior, upper lip projecting noticeably forwards of lower lip; rear corner of mouth below anterior quarter of eye; lip fold on lower jaw not continued across symphysis; teeth in upper and lower jaws small, conical, with acute posteriorly curving tips; outermost teeth uniserial, close-packed, encompassing band of 1-3 irregular rows of somewhat smaller, more widely spaced teeth (anterior teeth in lower jaw projecting further forwards than in upper jaw); palatine and vomerine teeth absent; gill filaments on first three gill arches, absent on fourth; gill rakers on second gill arch 8-9, moderately long, conical, and finely pointed.

Bases of dorsal and anal fins short, lengths 7.9 (6.1-7.2) and 7.3 (6.8-8.4) respectively, both in SL; dorsal fin generally originating above anal fin, or slightly in advance; dorsal and anal fin rays moderate in length, anterior 1-2 longest, about equal to base of respective fin; urogenital opening located about one-third to mid way between posterior margin of ventral disc and anal fin origin; genital papilla prominent.

Subopercle present, forming terminal bone posteriorly on side of head, not spine-like; dorsal postcleithral bone shaped like those of *Cochleoceps bicolor* (Figure 4b), reaching as high as tenth pectoral fin ray; cleithral, pelvic and ventral postcleithral bones shaped like those of *C. bicolor* (see Figure 4b).

Colour of holotype in alcohol: overall pale yellowish brown.

Colour when fresh (based on colour transparencies of freshly collected material): ground colour pale yellowish brown to pinkish brown, head and body covered with many very small to minute, closely packed reddish spots (Figure 8); iridescent blue to purplish markings on head and body, tending to form short, rather irregular and often poorly-defined cross bars on back, those on body not continued down sides (one bar joins eyes across interorbital space); short wavy blue line from posterior margin of eye directed obliquely across cheek; some blue spots on dorsal surface of head and along side of body, latter sometimes forming a wavy blue line; reddish spots adjacent to blue bars occasionally somewhat darker, forming dark margins to cross bars; fins hyaline, with indications of reddish spotting, particularly on caudal where spotting forms about 3-4 distinct cross bands; iris reddish.

Distribution

Cochleoceps orientalis is found only in New South Wales, ranging from Seal Rocks (32°28′S 152°32′E) to Montague Island (36°15′S 150°14′E). It has also been reported once from Western Port in Victoria (R. Kuiter, pers. comm.) but this requires confirmation (other fish species endemic to Australia's east coast have infreqently strayed as far west as Western Port).

Remarks

Cochleoceps orientalis occurs in similar habitats to *C. bicolor*. Like the latter species, *C. orientalis* also sets up "cleaning stations" on ascidians and sponges for the purpose of removing skin parasites from other species of fish.

The similarities between *Cochleoceps orientalis* and *C. bicolor* have been discussed in the account of the latter species.

This species is named *orientalis* with respect to its geographical distribution.

Acknowledgements

Specimens were kindly provided on loan by M.F. Gomon (NMV), J. Leis (AMS), and C.J.M. Glover (SAM). Colour transparencies of clingfishes were made available by R.H. Kuiter and N. Holmes for which I am very grateful. I would also like to thank two anonymous referees for their comments on the manuscript. K. Smith (WAM) provided technical assistance.

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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 Codes 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.

Manuscripts

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 positions 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.

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The senior author is sent two sets of galley proofs (one to be retained) and one set of page proofs which must be returned promptly.

The senior author will receive fifty free offprints of the paper. Additional offprints can be ordered at page proof stage.

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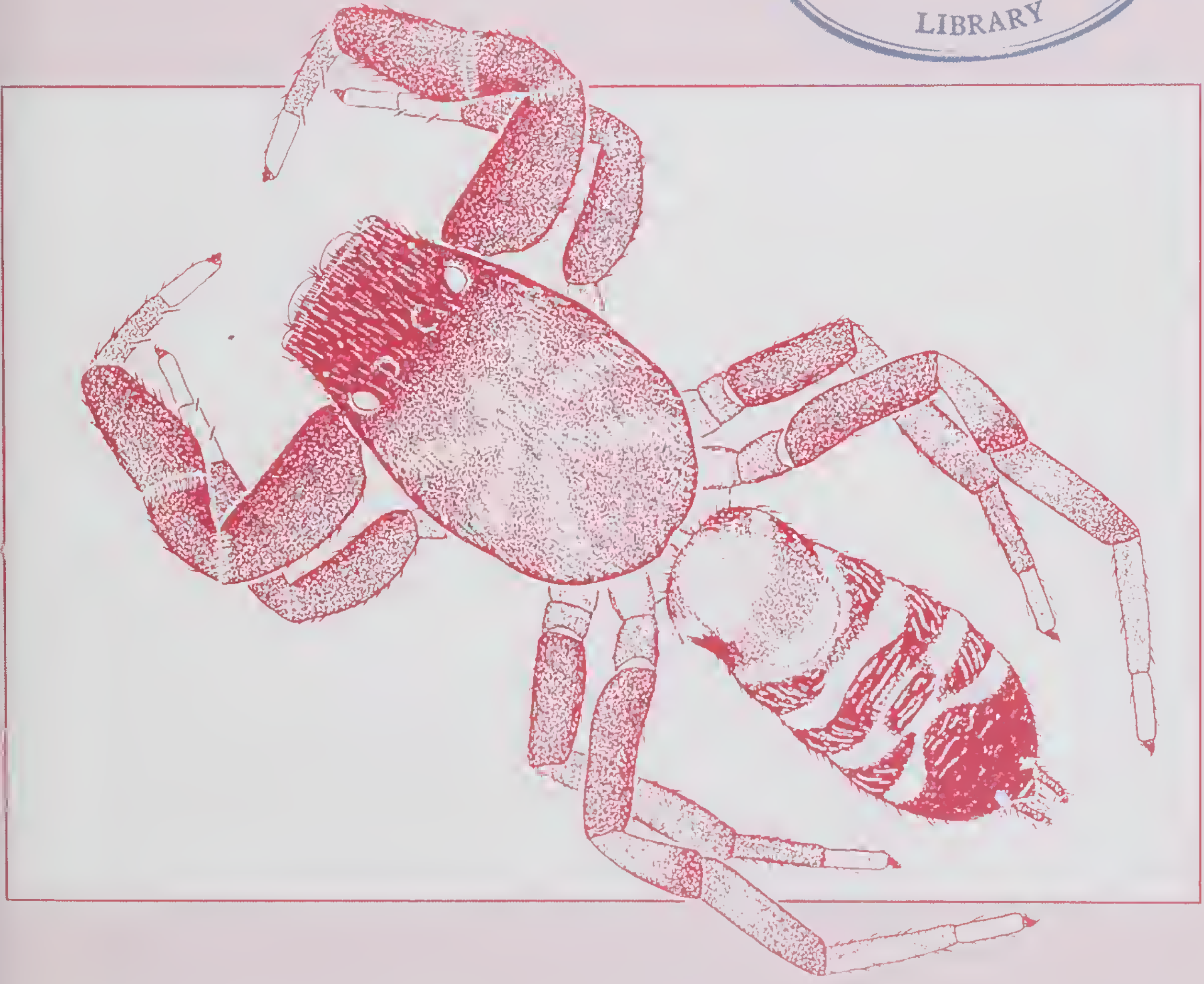
RECORDS of the Western Australian Museum

Volume 15, Part 4.
1992



RECORDS of the Western Australian Museum

Volume 15, Part 4.
1992

Cover: A new genus of spider (*Zebraplatys*) from Australia.

The *Records of the Western Australian Museum (Rec. West. Aust. Mus.)* is published irregularly with up to four parts appearing each year. A series of supplements, usually devoted to recording the basic data and results of specific Museum studies, is also produced. The journal and supplements are available for sale or exchange, the current price per part being $10.00 plus postage. All but a few back issues are available and orders and enquiries should be addressed to the Bookshop, Western Australian Museum, Francis Street, Perth, W.A. 6000, Australia.

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Salticidae (Arachnida: Araneae) of Oriental, Australian and Pacific Regions, VIII. A new genus from Australia

Marek Żabka*

Abstract

Zebraplatys gen. nov. is described. *H. fractivittata* Simon 1909 is designated the type species and redescribed — thus *H. fractivittata* Simon = *Z. fractivittata* (Simon 1909) comb. nov. *Holoplatys quinquecingulata* Simon = *Z. quinquecingulata* (Simon 1909) comb. nov. *Z. harveyi* sp. nov. and *Z. keyserlingi* sp. nov. are described and a key to the species is given.

Introduction

Holoplatys fractivittata Simon and *H. quinquecingulata* Simon were omitted from Żabka's (1991) revision of *Holoplatys* and are re-described here in *Zebraplatys*. Both species (females only) were described by Simon (1909) from Western Australia and since then have not been recorded. Recent study confirmed generic dissimilarity of Simon's species and justified erection of a new genus.

Material and Methods

The paper is based on type specimens and fresh material collected recently in New South Wales, South and Western Australia. Routine methods of specimen investigation and measurement taken were described earlier (Żabka 1990). Morphological details are presented on figures in the text.

Collections studies

AM — Australian Museum, Sydney
MNHN — Museum National d'Histoire Naturelle, Paris
SAM — South Australian Museum, Adelaide
WAM — Western Australian Museum, Perth
ZMB — Zoologisches Museum der Humboldt-Universität, Berlin

Abbreviations used:

AEW — anterior eyes width, ag — accessory gland, AL — abdomen length, cd — cephalic depressions, cf — cymbial flange, CL — cephalothorax length, co — copulatory opening, CW — cephalothorax width, da — dorsal (dorsolateral) tibial apophysis, e — embolus, EFL — eye field length, fd — fertilization duct, id — insemination duct, PEW — posterior eyes width, s — spermatheca, sc — abdominal scutum, sr — seminal reservoir, ta — retrolateral tibial apophysis, tg — tegulum.

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*Zaklad Zoologii WSR-P, 08-110, Siedlce, Poland

Systematics

Zebraplatys gen. nov.

Type species
Holoplatys fractivittata Simon, 1909.

Diagnosis

The representatives of the genus can easily be distinguished by their very flat body and zebra-like abdominal pattern.

Description

Small to medium spiders, ranging from about 3.10 to over 7 mm in length. The body slender, elongate and flat. Cephalothorax with more or less distinctive *Holoplatys*-like cephalic depressions (cd), abdomen with light and dark transverse stripes forming zebra-like pattern. Male abdomen with anterior scutum (sc). Clypeus very narrow. Chelicerae small, unident, with two promarginal teeth. First legs strongest and darkest, as in most *Holoplatys* species tibial spines reduced. Leg formula: IV-I-II-III. Palpal organ massive with distinctive retrolateral (ta) and dorsal or dorsolateral (da) tibial apophyses. Cymbium of some species with flange (cf), tegulum (tg) large, irregular in shape. Embolus (e) short and strong or thin and long, seminal reservoir (sr) not meandering. Insemination ducts (id) rather long, spermathecae (s) pear-shaped, accessory glands (ag) distinctive.

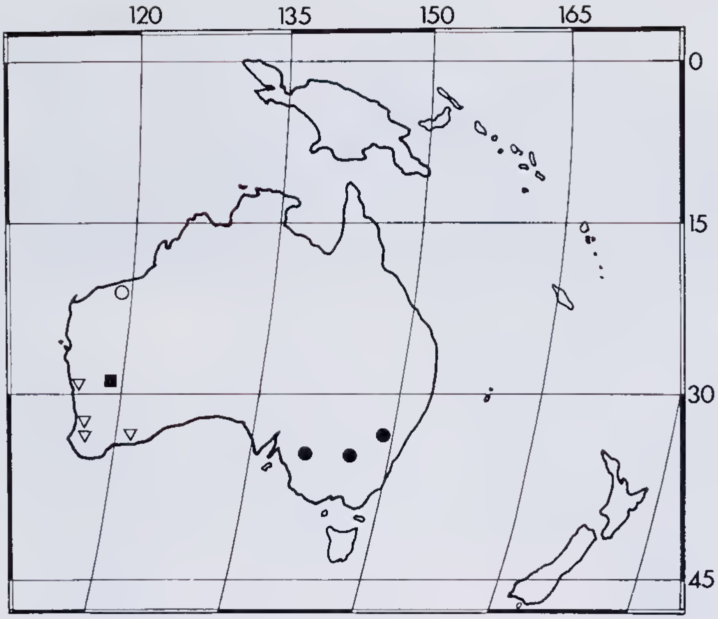
Etymology

The name refers to zebra-like colour pattern and flat body shape ("platys" = flat), and it is feminine in gender.

Relationships, biology and distribution

The genus *Zebraplatys* is a newly defined representative of a monophyletic group (subfamily) that includes *Holoplatys, Ocrisiona, Paraplatoides* and some undescribed Australian genera Żabka 1990, 1991 a-b). They are all well adapted for entering cracks and folds in bark (mostly of *Eucalyptus*) having very flat body, small vertical chelicerae and strong but poorly armed first legs. The epigyne is simple and *Holoplatys*-like. The structure of the palpal organ of *Zebraplatys* suggests that the genus is the most specialized derivate of the group and closest relative of the *grassalis* group of *Holoplatys* in which *H. lhotskyi* Żabka has similar genitalic pattern (Żabka 1991a). *Ocrisiona*, being relatively large and robust, seem to occupy the most ancestal position in the group.

The genus is widespread but rare, being found in scattered localities of Western Australia, South Australia, New South Wales and Victoria. Its distribution is given on the map below.



Distribution of *Zebraplatys:* (▽) = *Z. fractivittata* (Sim.); (■) = *Z. quinquecingulata* (Sim.); (●) = *Z. harveyi* sp. nov.; (○) = *Z. keyserlingi* sp. nov.

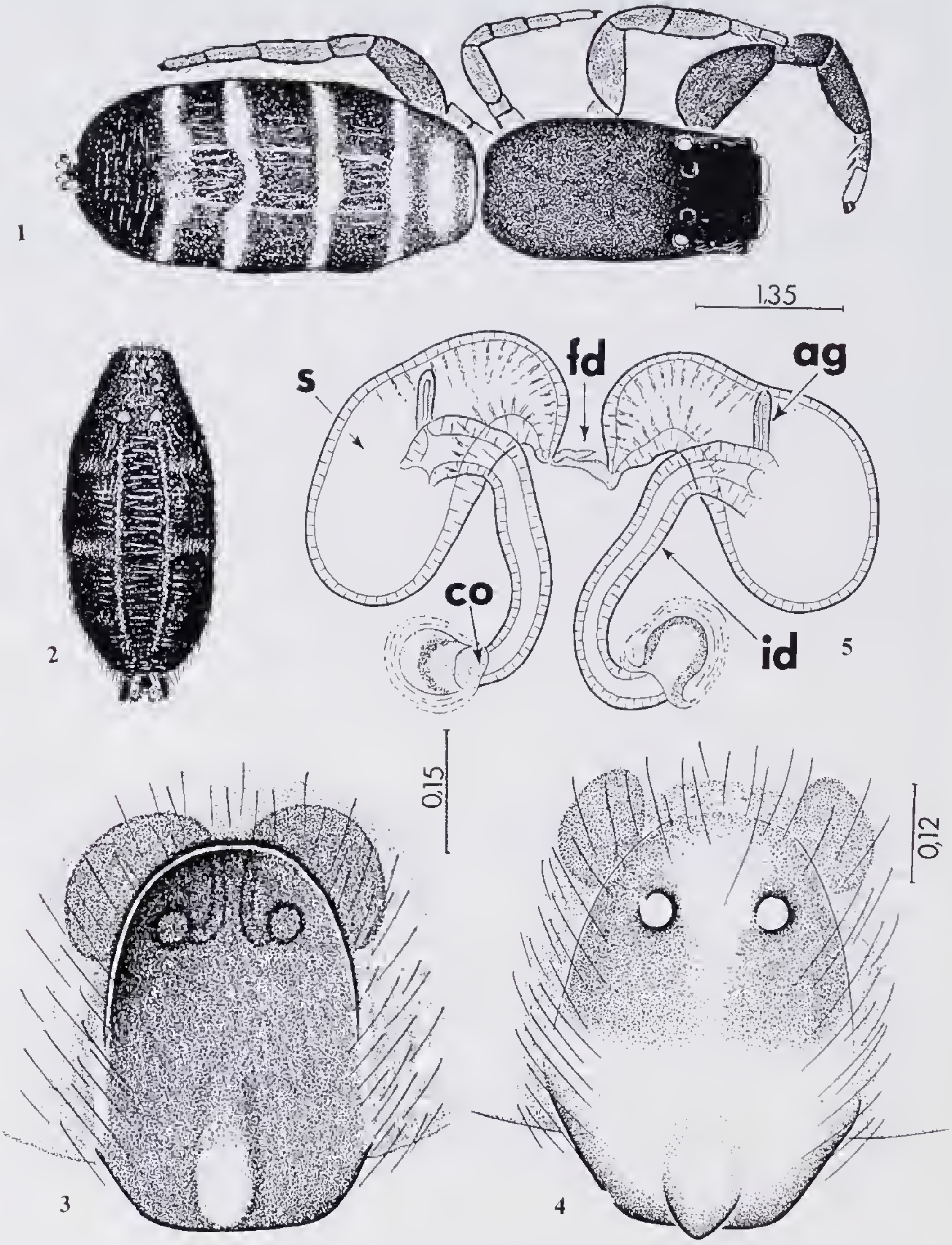
Key to the species of *Zebraplatys*

Males

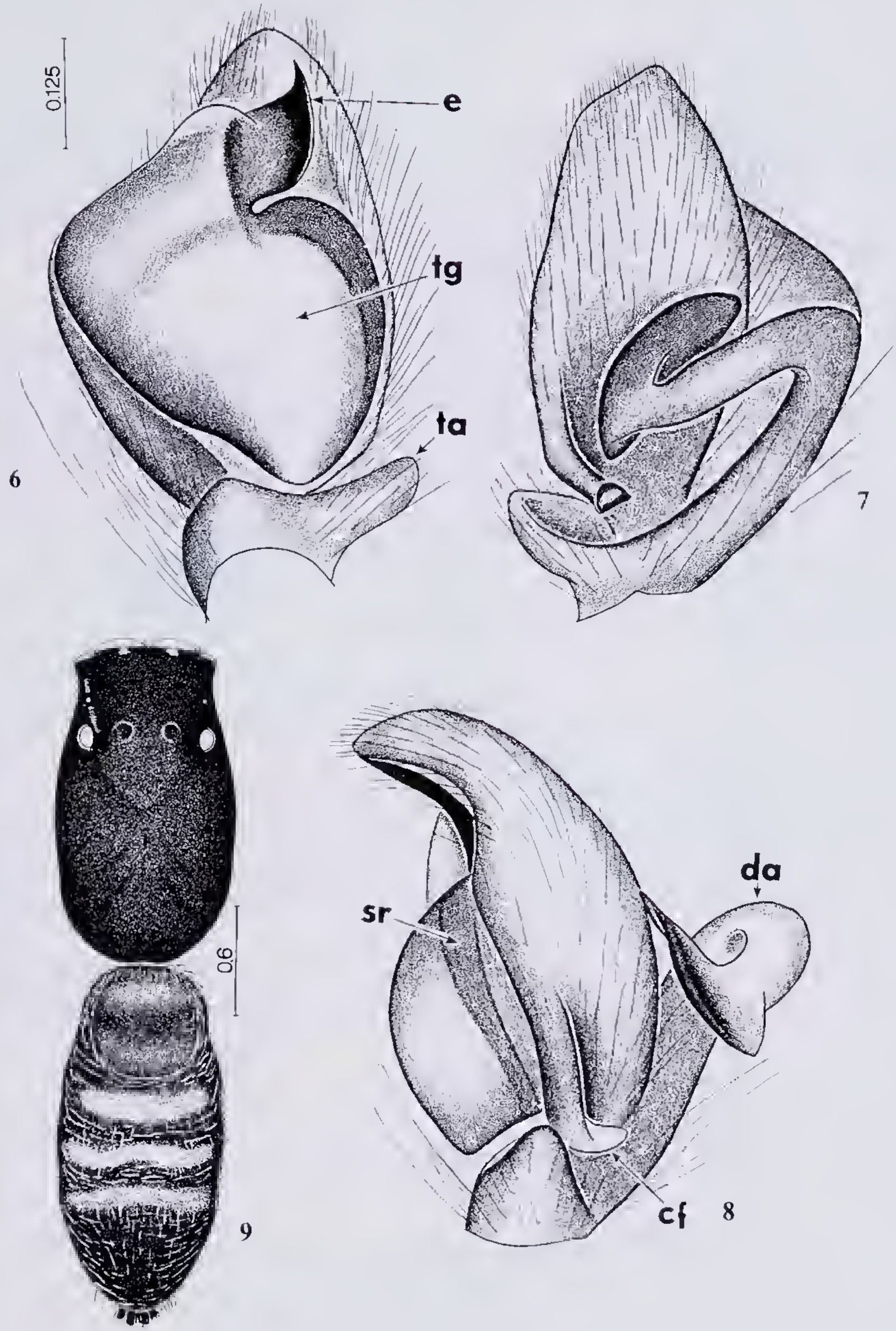
1. Embolus short and massive, dorsal tibial apophysis extremely large — *Z. fractivittata* (Simon) (Figures 6-9).
   — Embolus long and thin 2
2. First tibiae with single prolateral spines, cephalothorax rectangular in shape, tibial apophyses rather small, embolus coiled around tegulum — *Z. keyserlingi* sp. nov. (Figures 19-22).
   — Metatarsal spines missing, cephalothorax pear-shaped, tibial apophyses large, embolus different — *Z. harveyi* sp. nov. (Figures 13-15).

Females

1. Internal genitalia distant from the epigastric furrow.................................. 2
   — Internal genitalia close to the epigastric furrow, insemination ducts coiled — *Z. harveyi* sp. nov. (Figures 16-18).
2. Epigyne with posterior knob, insemination ducts "C" — shaped — *Z. fractivittata* Simon (Figures 1-5).
   — Posterior know missing, epigastric furrow with double pocket, insemination ducts "S"-shaped — *Z. quinquecingulata* (Simon) (Figures 10-12).



Figures 1-5 ♀ *Zebraplatys fractivittata* (Simon, 1909): general appearance (1), abdominal pattern (2), epigyne (3-4) and internal genitalia (5). 1, 4-5 — lectotype, ZMB 18746. 2-3 — Grass Path, WAM 88/8.



Figures 6-9 ♂ *Zebraplatys fractivittata* (Simon, 1909): palpal organ (6-8) and general appearance (9). Parmelia, WAM 89/346.

Zebraplatys fractivittata (Simom, 1909) comb. nov.

Figures 1-9

Holoplatys fractivittata Simon, 1909: 199.

Material

Western Australia: female lectotype, Stat. 82, Moonyoonooka, 13 July 1905, ZMB 18746. Female paralectotype, Austral. occid. (Michaelsen), MNHN 24346. Female, Grass Patch, 12 November 1986, A.F. Longbottom, WAM 88/8. Female, Como, 20 June 1967, B.H. Solomon, WAM 88/3. Female, Parmelia, under bark of *Eucalyptus marginata*, 14 April 1987, A.E. de Jong, WAM 88/27. Male, Parmelia, near Kwinana, 5 June 1989, A.E. de Jong, WAM 89/346.

Diagnosis

Epigyne with posterior knob, insemination ducts "C"-shaped. Dorsal tibial apophysis of palpal organ extremely large, embolus short and massive.

Female (Figure 1-2). Eye field and margins of cephalothorax black, thorax slightly lighter. Abdomen zebra-like but in some specimens almost black. Spinnerets greyish. Clypeus blackish with single dark hairs. Maxillae, labium and sternum honey-yellow, venter light-grey. Tarsi I yellow, other segments grey to brown, lighter dorso-ventrally. Other legs generally lighter, distal end of segments sometimes darker.

Epigyne as illustrated in Figures 3-5.

Leg spination. mI: p1-1, r1-1; mII: p1-1, r1-1.

Dimensions

CL 2.07-2.29 (2.20), CW 1.18-1.28 (1.24), ratio CW: CL 0.55-0.57 (0.56), EFL 0.60-0.68 (0.64), ratio EFL: CL 0.28-0.29 (0.29), AEW 0.89-0.99 (0.95), PEW 0.84-0.96 (0.92), AL 2.51-3.70 (3.05).

Male (Figure 6). Cephalothorax brown, marginally darker. Abdomen with anterior scutum and zebra-like abdominal pattern. Spinnerets black. Clypeus black with silvery-white hairs. Maxillae, labium and sternum dirty light-brown. Venter beige centrally, darker laterally. Legs I massive, dark-brown with yellow tarsi, other legs lighter — especially dorso-ventrally.

Palpal organ (Figures 7-9) with extremely large dorsal tibial apophysis, retrolateral apophysis relatively small, cymbial flange distinctive, embolus wide and short, pointed apically.

Leg spination. mI: p1-1, r1-1; mII: p1-1, r0-1.

Dimensions

CL 1.75, CW 1.05, ratio CW: CL 0.60, EFL 0.55, ratio EFL: CL 0.31, AEW 0.75, PEW 0.75, AL 1.90.

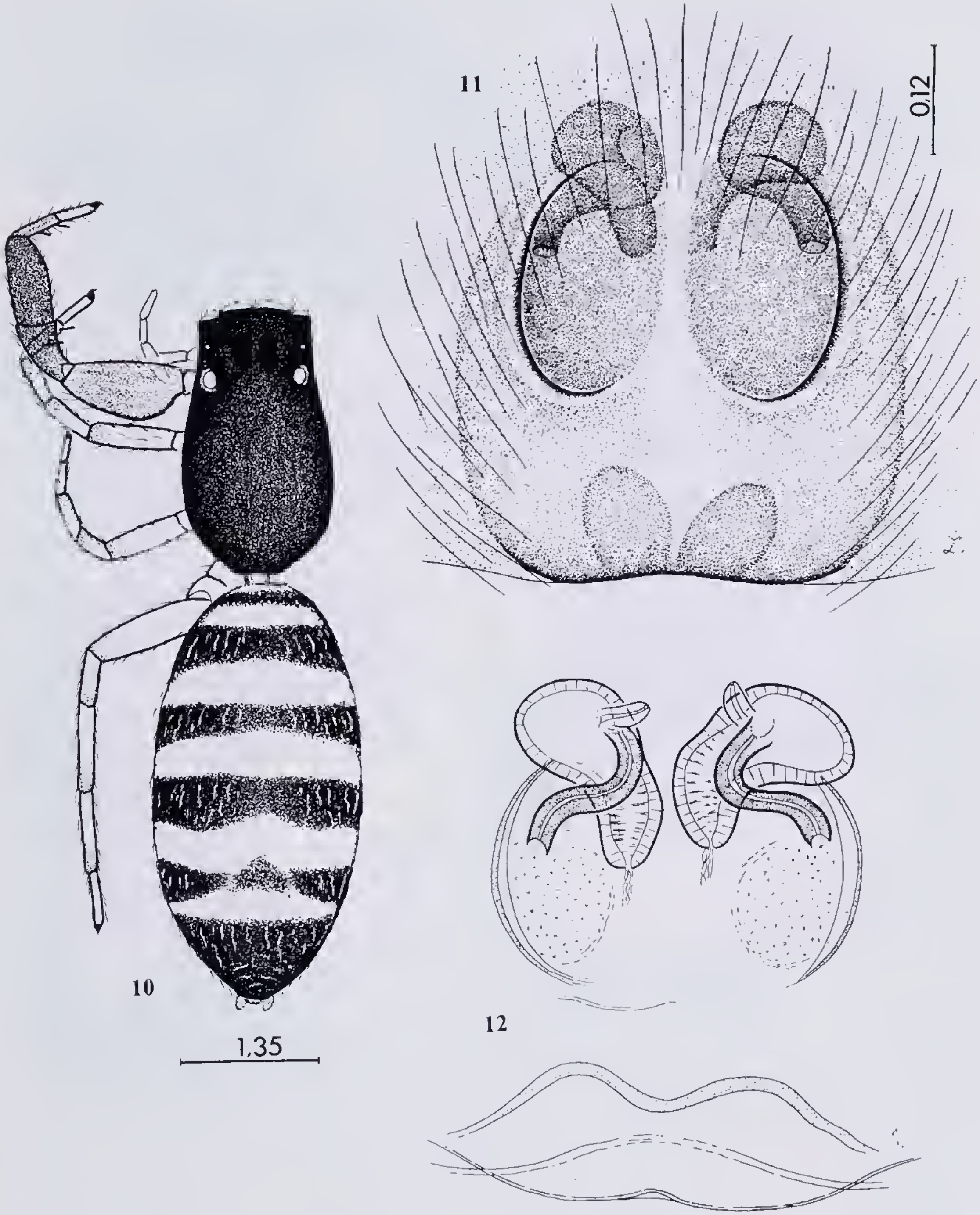
Zebraplatys quinquecingulata (Simon, 1909) comb. nov.

Figures 10-12

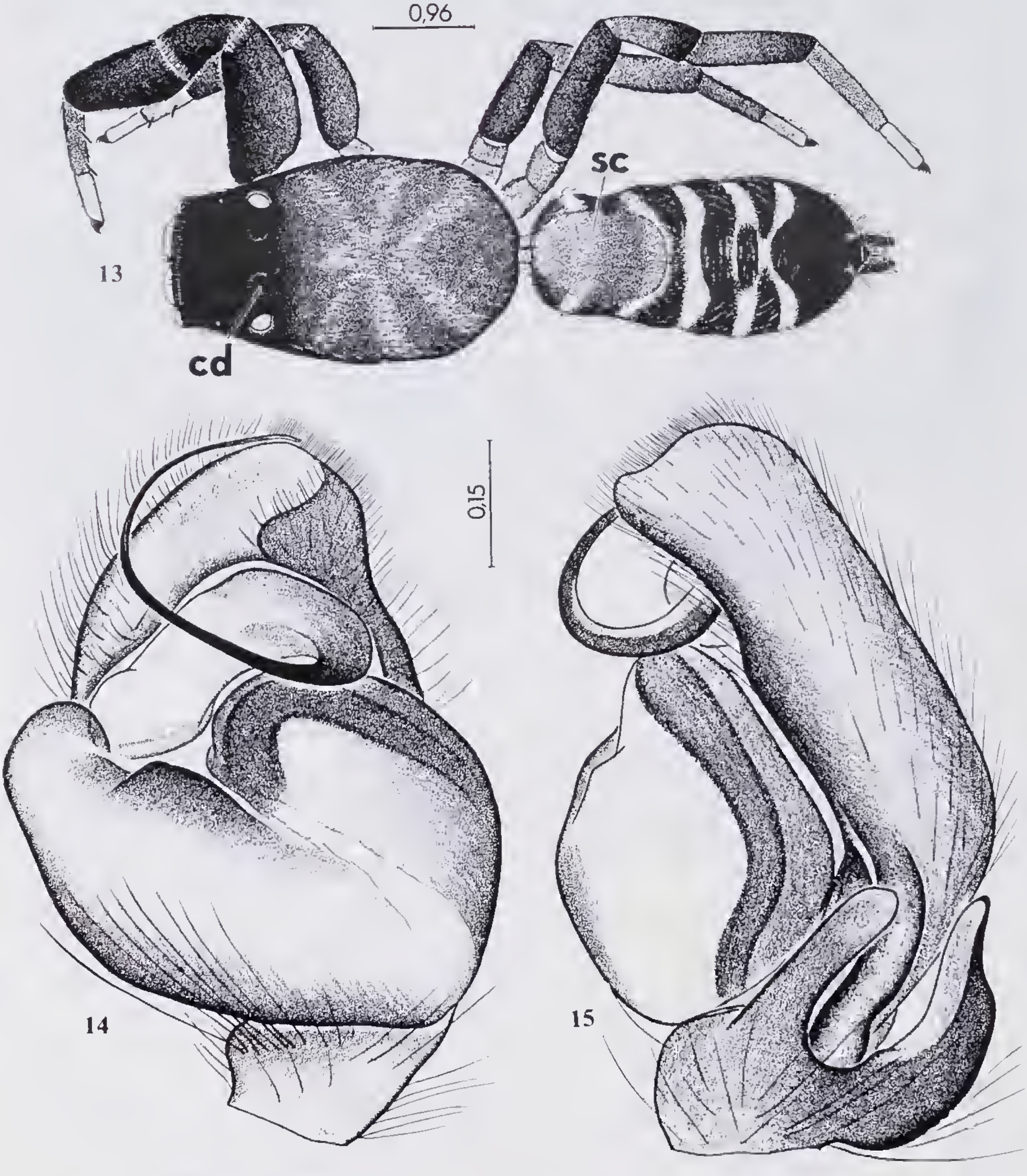
Holoplatys quinquecingulata Simon, 1909: 199.

Material

Western Australia: female lectotype, Day Dawn, SW Austral. Exp., 1905, Stat. 76, 9/10 July 1905, ZMB 18747.



Figures 10-12 ♀ *Zebraplatys quinquecingulata* (Simon, 1909): general appearance (10), epigyne (11) and internal genitalia (12). Lectotype, ZMB 18747.

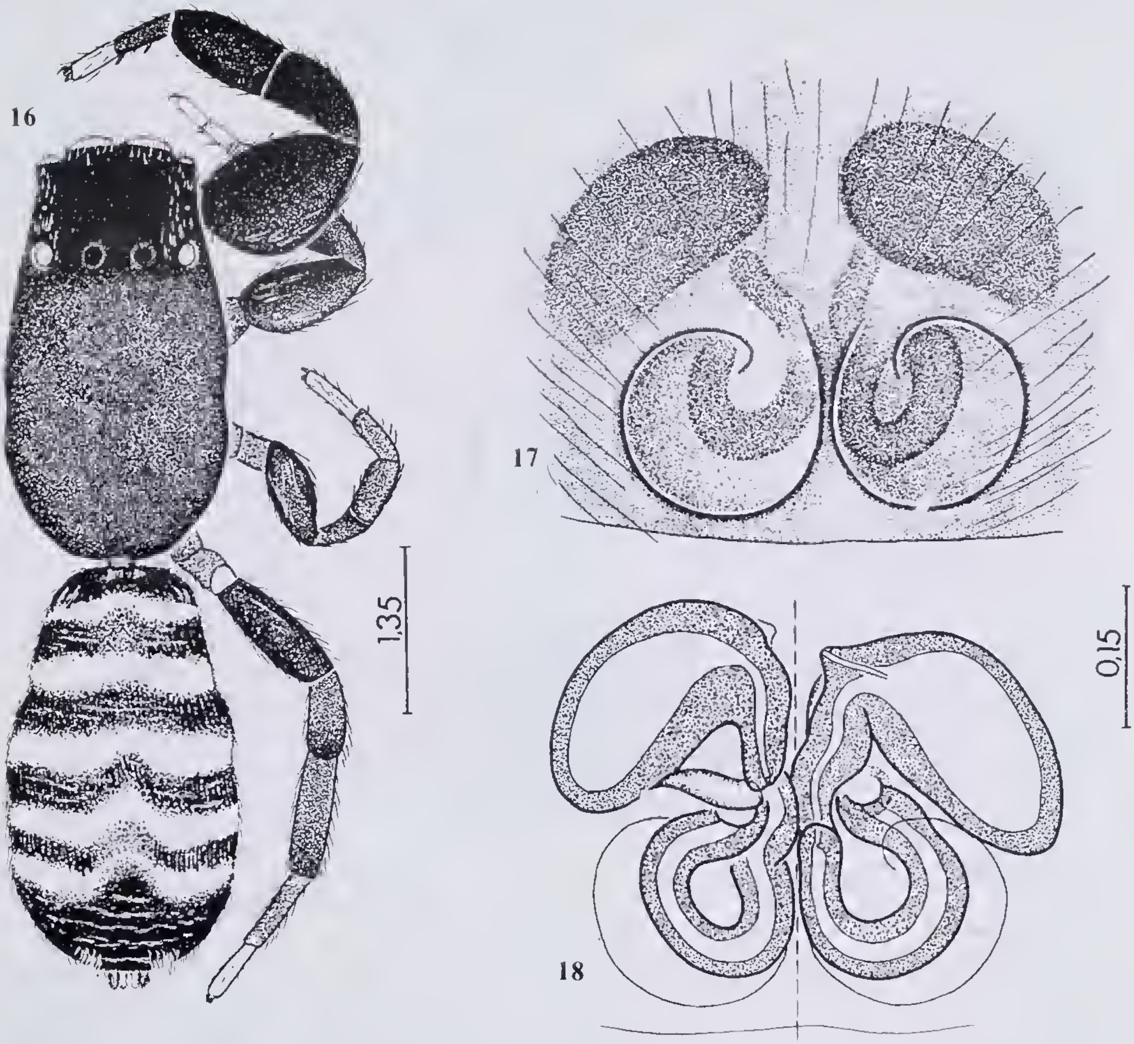


Figures 13-15 ♂ *Zebraplatys harveyi* sp. nov.: general appearance (13) and palpal organ (14-15). Holotype, SAM ARA1988356.

Diagnosis

Epigyne with double posterior pocket, insemination ducts "S"-shaped.

Female (Figure 10). Cephalothorax dark. Clypeus and chelicerae brown, pedipalps lighter, maxillae, labium and sternum dirty-orange. Venter beige centrally, darkening



Figures 16-18 ♀ *Zebraplatys harveyi* sp. nov.: general appearance (16), epigyne (17) and internal genitalia (18). 16 — allotype, AM KS18836. 17-18 — paratype, Yaapeet.

laterally. Legs I orange-brown with yellow tarsi, other legs dirty-yellow, segments darker distally.

Epigyne as illustrated in Figures 11-12.

Leg spination. mI: p1-1, r1-1; mII: p1-1, r1-1.

Dimensions

CL 2.47, CW 1.38, ratio CW: CL 0.56, EFL 0.70, ratio EFL: CL 0.28, AEW 1.02, PEW 1.02, AL 3.82.

The male is unknown.

Zebraplatys harveyi sp. nov.

Figures 13-18

Material

South Australia: male holotype, Mundulla, SW of Bordertown, under bark, 27 January 1984, D. Hirst, SAM ARA1988356. New South Wales: female allotype, Tarana, 23 April 1966, R. Mascord, AM KS18836. Victoria: female paratype, 15 km WNW of Yaapeet, Lake Albacutya, under bark of *Eucalyptus camaldulensis;* female paratype, 1 July 1982, M.S. Harvey, B.E. Roberts, WAM 89/281.

Diagnosis

Male thorax with radial stripes of white seattered hairs and palpal organ of different structure (embolus, tegulum, apophyses) than in two other species. Insemination ducts coiled, internal genitalia close to the epigastric furrow.

Male (Figure 13). Eye field black-brown with scattered white hairs. Thorax lighter with dark margins and radial stripes of white hairs. Abdomen with anterior orange scutum. Spinnerets dirty-brown. Clypeus black with white hairs. Chelicerae brown, maxillae and labium dirty-orange. Sternum orange with dark margin. Venter grey, darkening posteriorly and laterally with two rows of lighter spots. Leg I brown, distally lighter, tarsi yellow-orange. Other legs lighter, darker laterally.

Palpal organ (Figure 14-15). Tegulum wide, embolus long and thin, cymbial flange and both tibial apophyses distinctive.

Leg spination. mI: p1-1, r1-1; mII: p1-1, r0-0.

Dimensions

CL 2.67, CW 1.61, ratio CW: CL 0.60, EFL 0.72, ratio EFL: CL 0.27, AEW 1.05, PEW 1.05, AL 2.50.

Female (Figure 16). Eye field black, thorax brown, darker marginally. Spinnerets greyish-orange. Clypeus black with single white and dark hairs. Chelicerae and pedipalps dirty-brown, the last lighter distally. Maxillae and labium brown with lighter tips, sternum dark-orange, marginally darker. Venter grey centrally, laterally darker. Leg I black-brown only tarsi orange, other legs lighter.

Epigyne as illustrated in Figures 17-18.

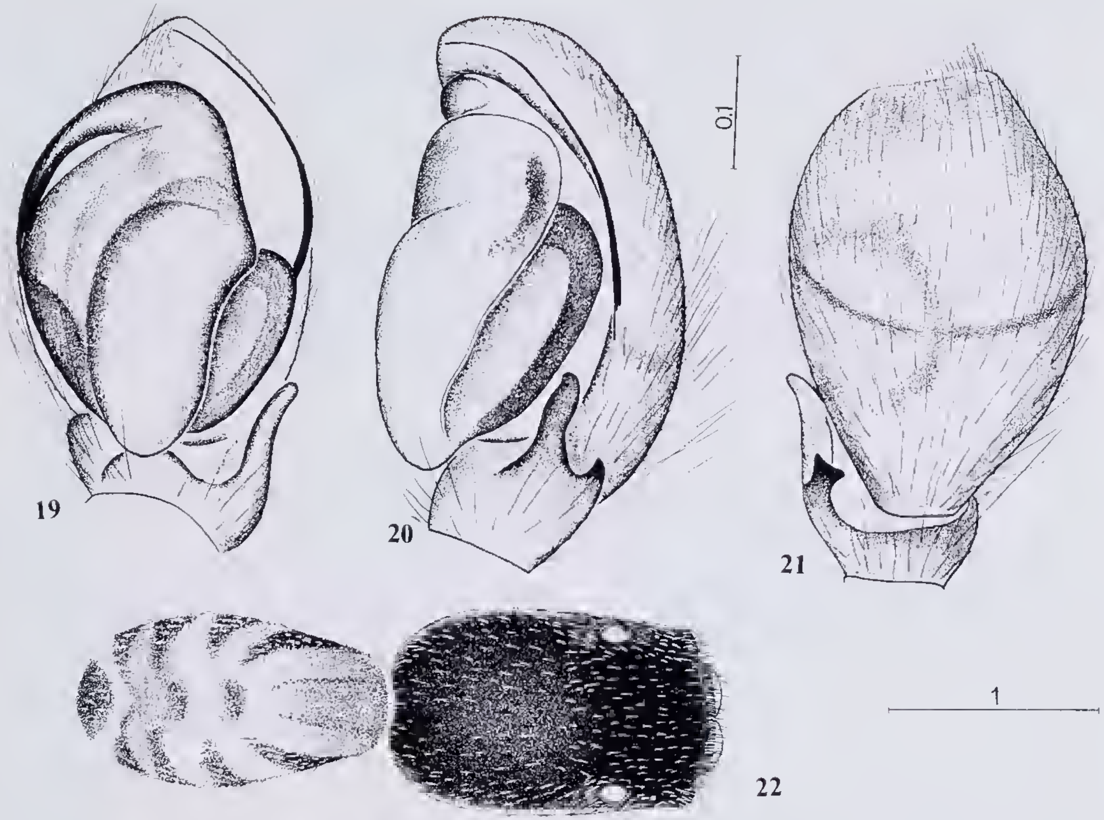
Leg spination. mI: p1-1, r1-1, mII: p1-1.

Dimensions

CL 3.00-3.20 (3.10), CW 1.73-1.85 (1.79), ratio CW: CL 0.58, EFL 0.80, ratio EFL: CL 0.26, AEW 1.18-1.20 (1.19), PEW 1.17-1.21 (1.19), AL 3.22-3.82 (3.52).

Etymology

The specific name is proposed for Dr. Mark S. Harvey (Western Australian Museum, Perth), one of the collectors of the material studied.



Figures 19-22 ♂ *Zebraplatys keyserlingi* sp. nov.: palpal organ (19-21) and general appearance (22). Holotype, WAM 91/601.

Zebraplatys keyserlingi sp. nov.
Figures 19-22

Material

Western Australia: Male holotype, Woodstock Station, site WS2, wet pit traps, 23-30 September, 1988, J. Dell *et al.*, WAM 91/601.

Diagnosis

Unlike other species first tibia with single prolateral spine, embolus longer, cymbial flange missing and tibial apophyses relatively small.

Male (Figure 22). Eye field black, thorax brown with fringe of white hairs along lower margin. White hairs also scattered on the whole surface, more numerous around eyes. Light abdominal stripes greyish-orange. Spinnerets orange. Clypeus black, fringed with white hairs. Chelicerae dark-brown, maxillae, labium and sternum gradually lighter, the last orange-brown. Venter grey. Legs I generally light-brown only prolateral femora black. Other legs orange.

Palpal organ as illustrated in Figures 19-21.

Leg spination. tI: p0-1, r0-0, mI: p1-1, r1-1; mII: p1-1, r0-0.

Dimensions

CL 1.55, CW 1.00, ratio CW: CL 0.64, EFL 0.55, ratio EFL: CL 0.35, AEW 0.82, PEW 0.85, AL 1.55.

The female is unknown.

Acknowledgments

The specimens examined here were kindly sent by Dr. J. Heurtault (Paris), Mr. D. Hirst (Adelaide), Dr. M. Harvey, Miss J. Waldock (Perth) and Dr. M. Moritz (Berlin). M. Harvey and J. Waldock provided some valuable comments on drafts of the manuscript. The research was supported by the fellowship of the Australian Museum, Sydney and by my University grant 234/86/W.

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A new species of *Symphytognatha* Hickman (Araneae: Symphytognathidae) from Western Australia

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Abstract

The first symphytognathid to be recorded from Western Australia, *Symphytognatha picta*, sp. nov., is described. It appears to be most similar to *S. globosa* Hickman from Tasmania.

Introduction

Only three species of the spider family Symphytognathidae have been previously reported from Australia: *Symphytognatha globosa* Hickman, 1931 from Tasmania, *S. blesti* Forster and Platnick, 1977 from New South Wales, and *Anapistula australia* Forster, 1959 from Queensland (see Forster and Platnick 1977; Davies 1985). This paper presents a description of the first symphytognathid from Western Australia.

Materials and Methods

Material is lodged in the Western Australian Museum (WAM) and the American Museum of Natural History, New York (AMNH). The internal female genitalia were examined by dissecting the epigynum and spinnerets from the abdomen and clearing them in warm 10% potassium hydroxide. A male pedipalp was dehydrated, air-dried and mounted on a stub for examination in a Scanning Electron Microscope. The terminology used here for the pedipalpal conductor lobes is somewhat arbitrary, due to incomplete knowledge concerning the homologies of the palpal sclerites (Coddington 1990): the upper portion (as viewed in Fig. 4) is termed the ventral conductor lobe (C1), and the lower portion (which lies behind the embolus nearer to the cymbium) is termed the dorsal conductor lobe (C2).

Systematics

Symphytognatha picta, sp. nov.

(Figures 1-6)

Holotype

♂, 2 km NE. of Lake Yeagarup, Ritter Road, Western Australia, 34°31′S, 115°53′E, under Marri [*Eucalyptus calophylla*] bark, 2 May 1990, M.S. Harvey, J.M. Waldock (WAM 91/1055).

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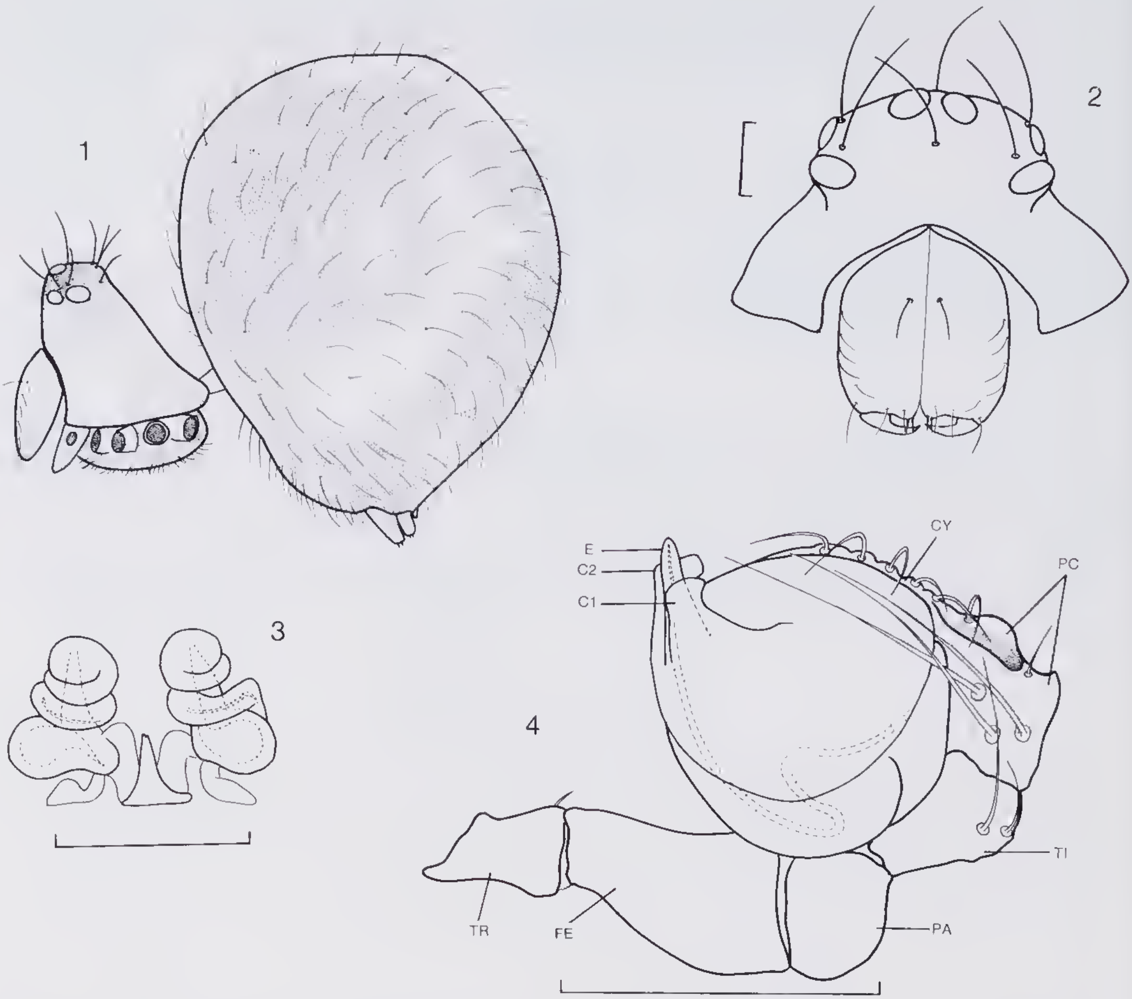


Figures 1-4 *Symphytognatha picta*, sp. nov.: 1, cephalothorax and abdomen, lateral, holotype ♂. 2, carapace and chelicerae, anterior, holotype ♂. 3, spermathecae, dorsal, paratype ♀, WAM 91/1062. 4, left pedipalp, retrolateral, paratype ♂, WAM 91/1056. Scale lines = 0.1 mm. Abbreviations: C1 (ventral conductor lobe), C2 (dorsal conductor lobe), CY (cymbium), E (embolus), FE (femur), PA (patella), PC (paracymbium), TI (tibia), TR (trochanter).

Paratypes

5♂, 2♀, same data as holotype (WAM 91/1056-1062).

Other Material

Western Australia: 1 juvenile, Pemberton, Warren National Park, karri base litter berlesate, 5 July 1980, S. and J. Peck (AMNH); 19♂, 5♀, 13 juveniles, Tall Tingle Tree path, Walpole-Nornalup National Park, 13 June 1987, N.I. Platnick, R.J. Raven (AMNH); 1♂, same data (WAM, 92/65); 1♂, Conspicuous Cliffs, Walpole-Nornalup National Park, 13 June 1987, N.I. Platnick, R.J. Raven (AMNH); 2♂, 13 juveniles, Hilltop Road, Walpole-Nornalup National Park, 12 June 1987, N.I.

Platnick, R.J. Raven (AMNH); 1♂, ZigZag Road, Walpole-Nornalup National Park, berlesate bracken, fungi and litter, 20 June-4 July 1980, S. and J. Peck (AMNH); 1 juvenile, Tingle Tree, Walpole-Nornalup National Park, forest carrion on litter, 18 June-29 July 1980, S. and J. Peck (AMNH); 1♂, 1♀, 2 juveniles, Tingle Tree, Walpole-Nornalup National Park, berlesate log and Casuarina litter, 4 July 1980, S. and J. Peck (AMNH); 2♀, Tingle Tree, Walpole-Nornalup National Park, forest malaise and troughs, 18 June-29 July 1980, S. and J. Peck (AMNH).

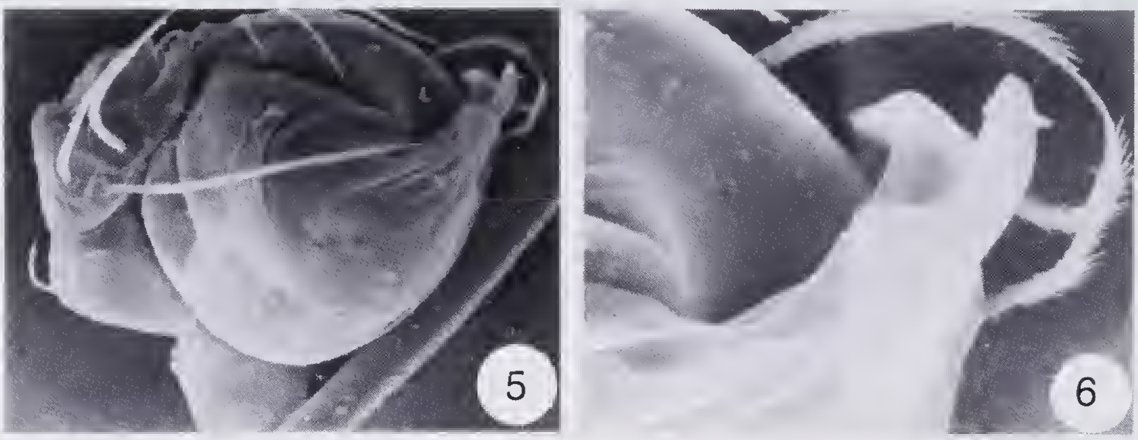
Diagnosis

This species differs from the other Australasian members of *Symphytognatha* as follows: males by the shape of the conductor lobes (Figs 4, 6), and females by the presence of only 2 full coils of the copulatory ducts (Fig. 3).

Description

Colour: carapace dark dusky brown, pars cephalica darkest; sternum dark brown; abdomen mostly purple-grey with broad irregular median pale stripe and irregular lateral pale stripes directed ventrally; chelicerae and legs light brown. Carapace of male (Figs 1-2) with 10 long setae, 1 on clypeus, 1 between PME, 1 pair mesad to ALE, 1 pair mesad to PLE, and 4 on posterior ridge of pars cephalica; carapace of female with 18 long setae, 10 as in male, and 8 along clypeal margin; clypeus slightly oblique. Six eyes, ratio ALE: PME: PLE 1.00: 0.60: 0.95 (♂), 1.00: 0.79: 0.89 (♀). Chelicerae (Fig. 2) fused for most of their length, suture line visible; each chelicera with 6 lateral, 2 mesal and 2 distal setae; distal lobe of fang furrow with 2 large teeth and 1 small tooth. Sternum posteriorly truncate. Male pedipalp (Figs 4-6): trochanter with small subdistal seta, femur and patella without setae, tibia with 2 large and 1 small subdistal seta; subbasal paracymbium present with 3 large setae and deep dorsal notch; outer margin of cymbium with 6 lateral and 3 subdistal plumose setae which extend over bulb; embolus tip blunt, rod-shaped, situated between two conductor lobes; ventral conductor lobe (C1) with rounded distal margin; dorsal conductor lobe (C2) somewhat hooked. Female pedipalp absent except for coxa. Leg formula 4123; patella and tibia with dorsal erect bristle. Superior tarsal claws I and II with 7-8 teeth, superior tarsal claws III and IV without accessory teeth; inferior tarsal claws I-IV long and slender. Female epigyne (Fig. 3) apparently with only 1 external pore; heavily sclerotised triangular apophysis present; copulatory ducts with 2 tight coils around spermatheca. Colulus absent.

Dimensions (mm), holotype ♂, WAM 91/1055 (paratype ♀, WAM 91/1061): total length (excluding chelicerae) 1.06 (0.98). Carapace length 0.32 (0.32) width 0.38 (0.38), height 0.30 (0.32). Eyes: ALE 0.06 (0.06), PME 0.03 (0.04), PLE 0.06 (0.05), PME-PME 0.01 (0.01), PME-PLE 0.09 (0.09), PLE-ALE 0.01 (0.01), eye group width 0.31 (0.32). Sternum length 0.28 (0.30), width 0.21 (0.21). Abdomen length 0.78 (0.68), width 0.79 (0.70), height 0.93 (0.81). Pedipalp: femur 0.06 (-), patella 0.04 (-), tibia 0.05 (-), tarsus 0.12 (-), total 0.27 (-). Leg I: femur 0.37 (0.29), patella 0.15 (0.14), tibia 0.20 (0.16), metatarsus 0.17 (0.16), tarsus 0.19 (0.17), total 1.08 (0.92). Leg II: femur 0.29 (0.27), patella 0.13 (0.15), tibia 0.17 (0.15), metatarsus 0.13 (0.14), tarsus 0.21 (0.18),



Figures 5-6 *Symphytognatha picta*, sp. nov., paratype , WAM 91/1056, right pedipalp, scanning electron micrographs: 5, ventral view. 6, detail of tip of bulb.

total 0.93 (0.89). Leg III: femur 0.26 (0.23), patella 0.11 (0.13), tibia 0.14 (0.12), metatarsus 0.13 (0.11), tarsus 0.17 (0.22), total 0.81 (0.81). Leg IV: femur 0.38 (0.32), patella 0.12 (0.12), tibia 0.23 (0.17), metatarsus 0.17 (0.13), tarsus 0.20 (0.23), total 1.10 (0.97).

Etymology

The specific epithet refers to the abdominal colour pattern (*picta*, Latin, painted).

Remarks

The four known Australasian species of *Symphytognatha* possess a copulatory duct which encircles the spermatheca 2-6 times (Griswold 1987). Three species of this group (*S. globosa*, *S. picta* and *S. blesti*) are united by a distinct abdominal colour pattern which consists of a dark background with dorsal and lateral pale stripes (*S. ulur* from Papua New Guinea lacks the lateral stripes), and possibly by the single median opening of the vulva. *Symphytognatha globosa* and *S. picta* appear to be sister species, as they share the following traits [I was able to directly compare *S. picta* with a female *S. globosa* from Cataract Gorge, Tasmania, 41°27′S, 147°10′E, collected on 18 November 1986, by M.S. Harvey and P.K. Lillywhite (WAM 91/1063)]:

1. The male pedipalp of *S. picta* closely resembles that of *S. globosa*: both possess a rod-shaped embolar tip (Figs 4, 6; Forster and Platnick 1977, fig. 9), which is quite unlike the embolus of other *Symphytognatha* species (Forster and Platnick 1977, figs 28, 38). This is presumably a synapomorphy uniting the two species. However, males of most other *Symphytognatha* species are currently unknown, and are required before definitive statements concerning character polarity can be made.

2. The epigynes of *S. picta* and *S. globosa* (see Hickman 1931, fig. 6) possess a heavily sclerotised triangular apophysis leading anteriorly from the vulva. It is not known whether other Australasian species of the genus possess such an apophysis due to the somewhat simplified epigynal illustrations of Forster and Platnick (1977) and Platnick (1979) (e.g. compare Hickman 1931, fig. 6 with Forster and Platnick 1977, fig. 12). However, it is clear that *S. imbulunga* Griswold, 1987 from South Africa lacks such an apophysis. *S. picta* differs from *S. globosa* (and all other members of the genus) by the presence of only two coils of the copulatory duct around the spermatheca (Fig. 3).

Habitat

The specimens from the type locality were taken from under the bark of a Marri tree in a mixed Marri/Karri [*Eucalyptus calophylla* and *E. diversicolor*, respectively] forest with a sparse shrub layer. It appeared that the forest had been burnt within the past few years, but the Marri bark had not been destroyed. This possibly allowed small spiders such as *S. picta* to survive.

Acknowledgements

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A new species of damselfish (genus *Pomacentrus*) from north-western Australia

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Abstract

A new species of damselfish, family Pomacentridae, is described from Churchill Reef, off the Kimberley coast of north-western Australia. *Pomacentrus limosus* sp. nov. is described from two specimens, 45.7 and 28.9 mm SL, collected by the author during August 1991. It is similar in appearance to *P. amboinensis*, *P. azuremaculatus*, and *P. javanicus*, but differs primarily in its higher counts of tubed lateral-line scales and pectoral rays, and also certain features related to colour pattern. The habitat of *P. limosus* consists of rocky outcrops on relatively flat, silty bottoms.

Introduction

The pomacentrid genus *Pomacentrus* contains 54 currently recognised species that are widely distributed in the tropical Indo-west and central Pacific region (Allen, 1991). The present paper describes a new species, assigned to this genus, collected on a recent expedition by the Western Australian Museum to reefs and islands along the Kimberley coast of north-western Australia. Two specimens were obtained by the author while SCUBA diving at Churchill Reef.

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 is presented in Table 1. Type specimens are deposited at the Western Australian Museum, Perth (WAM).

Systematics

Pomacentrus limosus sp. nov.

Figure 1

Holotype

WAM P. 30317-001, 45.7 mm SL; Churchill Reef, Western Australia (15°31'S, 123°17'E), 8.9-8.5 m depth, rotenone, G. Allen, 24 August 1991.

Paratype

WAM P. 30317-002, 28.9 mm SL, collected with holotype.

Diagnosis

A species of *Pomacentrus* Lacepède characterised by the following combination of features: dorsal rays XIII,15; anal rays II,15-16; pectoral rays 18; tubed lateral-line scales

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Table 1: Morphometric proportions (as percentage of standard length) for type specimens of *Pomacentrus limosus*.

Character	Holotype	Paratype
Standard length (mm)	45.7	28.9
Body depth	47.0	46.7
Body width	21.9	17.6
Head length	31.1	32.9
Snout length	5.9	6.6
Eye diameter	13.1	14.2
Interorbital width	8.1	6.9
Least depth caudal peduncle	13.1	12.5
Length caudal peduncle	13.8	14.5
Snout to origin dorsal fin	36.1	37.4
Snout to origin anal fin	65.0	60.2
Snout to origin pelvic fin	37.6	36.7
Length dorsal-fin base	62.6	63.3
Length anal-fin base	29.5	36.3
Length pectoral fin	27.6	28.0
Length pelvic fin	36.5	36.7
Length pelvic spine	16.8	17.6
Length 1st dorsal spine	6.3	6.2
Length 7th dorsal spine	13.8	15.2
Length 13th dorsal spine	16.8	18.0
Length longest soft dorsal ray	22.8	20.8
Length 1st anal spine	6.8	6.9
Length 2nd anal spine	16.0	18.3
Length longest soft anal ray	21.9	21.1
Length caudal fin	29.5	37.0

18; total gill rakers on first arch 21; colour pale grey without conspicuous markings, except membranous tips of dorsal spines black and juvenile with black ocellus at base of soft dorsal fin. It is similar in appearance and perhaps closely related to *P. azuremaculatus* Allen, but this species differs in having only 14-16 tubed lateral-line scales and horizontal rows of prominent blue spots on the dorsoanterior part of the body.

Description

Dorsal rays XIII, 15; anal rays II, 16 (II, 15); pectoral rays 18, branched caudal rays 13, gill rakers on first branchial arch 8 + 13 (7 + 14); lateral-line scales with tubes 18; vertical scale rows 28; scales above lateral-line to base of dorsal spines 1½; scales below lateral-line to anus 9.

Body moderately deep for the genus, the depth 2.1 in standard length, and compressed, the width 2.2 (2.6) in depth; head length contained 3.2 (3.0) in standard length; snout 5.3 (5.0); eye 2.4 (2.3); interorbital width 3.8 (4.8), least depth of caudal peduncle 2.4 (2.6) length of caudal peduncle 2.3, all in length of head.

Figure 1: *Pomacentrus limosus*, holotype, 45.7 mm SL.

Mouth oblique, lower jaw slightly inferior, the maxilla reaching level of anterior part of pupil; teeth of jaws biserial, those of outer row conical with narrowly rounded tips, upper jaw with about 34 teeth in outer row, the largest about equal to diameter of nostril in height; lower jaw with about 32 teeth in outer row, the largest slightly larger than upper teeth; a secondary row of slender buttress teeth behind those of outer row in the spaces between them; single nasal opening on each side of snout; nostril with a low fleshy rim; preorbital with moderately large, posteriorly directed spine; suborbital with a few small serrae; pre-suborbital relatively narrow, the greatest depth about one-third of eye diameter, the lower margin free; vertical limb of preopercle distinctly serrate; opercle series entire except a single flattened spine present on upper portion near angle. Scales of head and body finely ctenoid; preorbital, suborbital, snout tip, lips, chin, and isthmus scaleless; preopercle with 3 major scale rows and an additional row of small 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 about half length of pelvic spine.

Tubes of lateral-line ending below anterior rays of soft portion of dorsal fin; 1-2 pored scales posterior to tubed scales; a series of 8 pored scales midlaterally on caudal peduncle to caudal base.

Origin of dorsal fin at level of fourth tubed scale of lateral line; spines of dorsal fin gradually increasing in length to last spine, membrane between spines moderately incised; last dorsal spine 1.8 in head; first dorsal spine 2.7 (2.9) in last spine; seventh dorsal spine 1.2 in last dorsal spine; longest soft dorsal ray 1.4 (1.6) in head; length of base of dorsal fin 1.6 in standard length; first anal spine slightly longer than first dorsal spine, its length 2.4 (2.7) in second spine; second anal spine 1.9 (1.8) in head; longest soft anal ray 1.4 (1.6) in head; base of anal fin 2.1 (1.7) in base of dorsal fin; caudal fin emarginate with slightly rounded lobes, its length 1.1 (0.9) in head length; pectoral fin relatively short, reaching to about level of anus, the longest ray 1.1 (1.2) in head length; filamentous tips of pelvic fins reaching beyond origin of anal fin, the longest ray 0.9 in head length.

Colour in life

Overall pale grey, nearly whitish with scattered blue spots on head; narrow black margin distally on spinous dorsal fin; juvenile paratype with pale-rimmed black spot, about pupil size, at base of soft dorsal rays 8-11.

Colour in alcohol

Grey, darker on top of head and dorsoanterior portion of body; a small, inconspicuous dusky "ear" spot near origin of lateral line; membranous tips of dorsal spines black, giving appearance of narrow black margin; juvenile paratype with small black ocellus at base of soft dorsal rays 8-11.

Remarks

P. limosus differs from most other members of the genus in having a relatively high number of pectoral rays and tubed lateral-line scales (both 18 in number) in combination with a plain pale colouration. Among sympatric species of *Pomacentrus, P. amboinensis* Bleeker is most similar. However, it differs in usually having fewer (16-17) pectoral rays and tubed lateral-line scales and a slightly higher (22-24) gill raker count. Moreover, it usually possesses a pale yellowish colouration and has a pronounced dark spot at the base of the upper pectoral-fin rays. Additionally, in the juvenile stage the ocellus is situated in the middle portion of the soft dorsal fin rather than at its base.

Other similar species, not present along the Kimberley coast, include *P. azuremaculatus* Allen from the Java Sea and west coast of Thailand, and *P. javanicus* Allen from the Java Sea. The former species has similar counts and proportions to *P. limosus* except for a lower (14-16) tubed lateral-line scale count. It also differs in having horizontal rows of prominent blue spots on the dorsoanterior part of the body. *Pomacentrus javanicus* has a similar appearance, but generally has lower counts, including 13-14 soft dorsal rays, 16-17 pectoral rays, 16 tubed lateral-line scales and 19-20 gill rakers. Its juvenile stage lacks an ocellus on the soft dorsal fin, instead it possesses a small black spot on the upper caudal peduncle, just behind the last dorsal ray. All of the above mentioned species are illustrated and diagnosed in Allen (1991).

P. limosus was encountered only at Churchill Reef, one of many sites collected between Wyndham and Broom, during the 1991 expedition. This locality is situated approximately 80 km offshore from the mainland and some 10-12 km from Adele Island, lying immediately west. Churchill Reef is an area of heavy siltation, very limited underwater visibility, and massive (about 6-8 m) tidal fluctuations. Nevertheless corals are well represented. About 20-30 individuals of *P. limosus* were observed in 8-10 m depth, around rocks outcrops surrounded by more or less flat silt-sand bottom.

The species is named *limosus* (Latin: muddy) with reference to the silty nature of the habitat in which this fish occurs.

Acknowledgements

Thanks are due to fellow Kimberley expedition members: Paddy Berry, Clay Bryce, Dianne Jones, Loisette Marsh, Gary Morgan, and Fred Wells, all of WAM, Russell Hanley of NTM, and Perth physician Tony Celenza. I also thank Craig Howson, captain of our charter vessel, "North Star IV." The expedition was funded by the Australian Heritage Commission, Australian Geographic Magazine, Mr Harry Butler, and the Western Australian Museum. I also thank Anne Nevin for her careful preparation of the typescript.

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A new species of cardinalfish (apogonidae) from northern Australia

Gerald R. Allen*

Abstract

Pseudamia nigra sp. nov. is described from 29 specimens, 13.5-49.6 mm SL, from coastal localities of Western Australia, Northern Territory and Queensland. It differs from all other species of *Pseudamia* in having smaller scales (43-50 in a longitudinal series), a longer maxilla (extends well past eye), 19-20 pectoral rays (15-17 in other species), and a uniform dark brown to blackish coloration in life. The habitat of *P. nigra* consists of river mouths, tidal creeks, and mangrove shores.

Introduction

The apogonid genus *Pseudamia* Bleeker was reviewed by Randall *et al.* (1985). They recognised five species: *P. amblyuroptera* (Bleeker) from the Indo-Malayan region, *P. gelatinosa* Smith from the Indo-W. Pacific, *P. hayashii* Randall, Lachner, and Smith from the Indo-W. Pacific, *P. tarri* Randall, Lachner, and Smith from the Persian Gulf, and *P. zonata* Randall, Lachner, and Smith from the far western Pacific. The present paper describes a sixth species collected by the author on a recent Western Australian Museum expedition to the Kimberley Coast of north-western Australia. A single specimen, 49.6 mm SL, was obtained in shallow water in the scenic King George River Gorge. It was subsequently discovered that additional specimens taken between 1981-1990 were amongst the collection of the Northern Territory Museum of Arts and Sciences, Darwin.

Methods of counting and measuring follow those of Randall *et al.* (1985). Proportional measurements for selected type specimens are presented in Table 1. The holotype is deposited at the Western Australian Museum, Perth (WAM) and paratypes at the Northern Territory Museum of Arts and Sciences, Darwin (NTM).

Systematics

Pseudamia nigra sp. nov.

Figure 1

Holotype

WAM P.30300-001, 49.6 mm SL, King George River Gorge, about 500 m downstream from King George Falls, East Kimberley District, Western Australia (approximately 14°03'S, 127°19'E), 0.5-2 m depth, rotenone, G.R. Allen, 12 August 1991.

Paratypes

NTM S.10006-028, 3 specimens, 19.3-28.0 mm SL, Burford Island, Cobourg Peninsula, Northern Territory (approximately 11°29'S, 131°57'E), to 0.5 m depth, mangrove shore, rotenone, H. Larson, 13 October 1981; NTM S.10718-058, 22 specimens, 13.5-37.8 mm SL, Pearl Raft Creek, East Arm, Darwin

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Table 1 Morphometric proportions of selected type specimens of *Pseudamia nigra* n. sp. expressed as percentage of the standard length.

Character	Holotype WAM P.30300-001	Paratypes NTM S.12870-001		NTM S.10718-058	NTM S.10006-028
Standard length (mm)	49.6	39.7	37.8	33.2	28.0
Body depth	27.2	28.5	27.7	25.3	26.4
Body width	17.1	13.9	16.1	15.1	14.3
Head length	38.3	41.6	37.0	40.7	37.9
Snout length	8.1	9.1	8.2	9.3	8.9
Eye diameter	6.5	8.1	7.4	8.1	7.1
Interorbital width	8.3	8.8	8.5	7.5	9.3
Maxillary length	19.8	21.9	21.2	21.1	22.1
Caudal peduncle depth	13.1	12.8	14.8	14.8	12.1
Caudal peduncle length	22.2	21.2	20.6	22.0	23.2
Predorsal length	40.5	43.3	42.1	41.0	41.8
Preanal length	65.3	65.2	65.6	62.7	60.0
Prepelvic length	32.9	36.0	39.7	42.2	36.8
Length 1st dorsal spine	7.9	9.3	8.5	10.2	11.1
Length 2nd dorsal spine	8.9	10.3	9.5	12.4	12.5
Length longest soft dorsal ray	17.3	20.2	17.7	19.6	17.5
Length 1st anal spine	2.4	2.5	3.2	3.6	2.1
Length 2nd anal spine	6.0	8.8	*4.8	9.0	7.5
Length longest soft anal ray	21.2	21.4	18.0	20.5	17.1
length caudal fin	33.1	32.0	31.7	*24.1	36.1
Length pectoral fin	34.7	31.2	27.5	33.4	31.8
Length pelvic spine	7.1	9.3	9.3	10.2	9.6
Length pelvic fin	17.5	19.9	18.3	18.7	19.6

*denotes damaged condition

Harbour, Northern Territory (approximately 12°30′S, 130°55′E), 1.5 m depth, rotenone, 31 December, 1982; NTM S.1124-003, 19.1 mm SL, Woods Inlet, Darwin Harbour, Northern Territory (approximately 12°29′S, 130°46′E), 0-2 m depth, rotenone, H. Larson and R. Williams, 16 March 1984; NTM S.12870-001, 2 specimens, 18.3-39.7 mm SL, Heales Creek, Cape York Peninsula, Queensland (approximately 14°22′S, 141°54′E), S. Blaber, 30 October 1990.

Diagnosis

A species of *Pseudamia* Bleeker characterised by relatively small scales (43-50 in longitudinal series), an elongate maxilla that extends well past the eye, 19-20 pectoral rays, and a uniform dark-brown to blackish coloration (except for translucent pectoral fins) in life. The other 5 species in the genus differ in having 23-43 scales in a longitudinal series, maxilla extending to about rear edge of eye, pectoral rays 15-17, and more or less distinctive colour patterns.

Description

Dorsal rays VI-I, 10; anal rays I, 10; pectoral rays 19 (2 paratypes with 20), the uppermost and two lowermost unbranched; principal caudal rays 17, the upper and lower unbranched; upper and lower procurrent caudal rays 5; scales in longitudinal

Figure 1 *Pseudamia nigra*, holotype, 49.6 mm SL.

series 50 (scales missing in most paratypes, but counts of scale pockets indicate range of about 43-50); scales above lateral line to origin of dorsal fin 7; scales below lateral line to origin of anal fin 17; predorsal scales about 20 (embedded anteriorly and therefore difficult to count); circumpeduncular scales 29; gill rakers 5 + 15, the developed rakers 4 + 11 (most paratypes with total raker count of 6-7 + 16-17).

Body relatively slender, the greatest depth 3.7 (3.5-4.0) in standard length; greatest width of body 1.6 (1.7-2.0) in greatest depth; head length 2.6 (2.4-2.7) in standard length; predorsal length 2.5 (2.3-2.4), preanal length 1.5 (1.5-1.7), and prepelvic length 3.0 (2.4-2.7), all in standard length; snout length 4.8 (4.2-4.6), eye diameter 5.9 (5.0-5.3), interorbital width 4.6 (4.1-5.4), maxillary length 1.9 (1.7-1.9), depth of caudal peduncle 2.9 (2.5-3.2), length of caudal peduncle 1.7 (1.6-2.0), length of first dorsal spine 4.9 (3.2-4.5), length of second dorsal spine 4.3 (3.6-4.1), longest soft dorsal ray 2.2 (2.1-2.2), length of second anal spine 1.8 (1.9-2.2), longest soft anal ray 1.8 (1.9-2.2), length of pectoral fin 1.1 (1.2-1.3), length of pelvic fin 2.2 (1.9-2.2), and length of caudal fin 1.2 (1.0-1.3), all in head length. First anal spine very short and inconspicuous, its length 2.5 (2.5-3.5) in length of second anal spine; length of pelvic spine 2.5 (1.8-2.1) in length of pelvic fin.

Mouth oblique, more or less terminal, the lower jaw projecting very slightly; maxilla extending about one full eye diameter beyond rear edge of orbit; posterior margin of maxilla truncate, the corners rounded; teeth of jaws depressible, villiform, in band that narrows in width posteriorly; inner row of teeth caniniform, much larger than anterior teeth, those near symphysis particularly enlarged and aligned almost horizontally; vomer and palatines also with villiform teeth.

Posterior nostril close to orbit in front of centre of eye, ovoid and large, its vertical axis about one-third pupil diameter; anterior nostril small, in a membranous tube which is

Figure 2 Type locality of *Pseudamia nigra* (arrow indicates where holotype collected).

notched anteriorly, lying in front of posterior nostril by a distance about equal to half pupil diameter.

Margin of opercle broadly membranous with a prominent, very pointed, dorsoposterior flap; margin of preopercle crenulate, the rounded corner with 3 poorly defined serrae.

Scales cycloid, thin, deciduous; scales of opercle slightly larger than those of body; remainder of head scaleless with longitudinal and transverse-vertical rows of sensory pitlines; a pair of inconspicuous lateral lines (mainly indicated by notched scales and narrow pale line), one dorsal and one ventral on body.

Colour of holotype when fresh:

Uniform blackish except first dorsal fin brown and pectorals translucent.

Colour in alcohol

Holotype generally brown with darker scale centres; fins are dark brown, except pectorals translucent.

The paratypes are generally much lighter brown in colour than the holotype. They possess very small brown spots that are arranged in horizontal lines, one per scale row. The median fins of most paratypes are dark brown and strongly contrasted with the lighter body colouration. Some paratyes under 30.0 mm standard length have a white margin on both dorsal fins and the anal fin.

Remarks

Members of the genus *Pseudamia* are mainly inhabitants of crevices and caves. They are seldom seen except when flushed out with chemical ichthyocides. The type locality (Figure 2) of *P. nigra* is located at the base of a rock slide in a winding sandstone gorge, about 8 km inland from the river mouth and 500 m from a spectacular 80 m high waterfall, the base of which is the extreme limit of marine conditions. The falls were reduced to a small trickle during the time of our visit, which was during the height of the dry season. The water below the falls and at the nearby type locality was not tested for salinity, but the taste was approximately that of full strength sea water. However, during the summer wet season the site would be exposed to considerable freshwater discharge, particularly at low tide (tidal amplitude is typically in the range of 6-8 m). The holotype was collected next to shore amongst boulders. Paratypes were collected in very shallow (less than 2 m) depths, generally from tidal mangrove creeks.

The habitat requirements of *Pseudamia nigra* appear most similar to those of *P. amblyuroptera* which is usually found in turbid estuarine waters in less than 2 m depth. The other members of the genus generally occur on coral reefs in relatively clear water to a depth of approximately 30-40 m. The genus was previously unknown from the Kimberley coast of north-western Australia. Other species of *Pseudamia* previously recorded (Randall *et al.* 1985) from Western Australia include *P. gelatinosa* (Rowley Shoals and Monte Bello Islands) and *P. hayashii* (Rowley Shoals).

The species is named *nigra* (Latin: black) with reference to the coloration.

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Type material of spiders (Chelicerata: Araneae) collected on the Michaelsen and Hartmeyer Expedition of 1905 and lodged in the Western Australian Museum

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Abstract

Those type specimens of spiders (Araneae) collected in south-western Australia during an expedition of the Berlin and Hamburg Museums led by W. Michaelsen and R. Hartmeyer in 1905 and subsequently lodged in the Western Australian Museum are listed. The current type status of the 42 specimens is discussed.

Introduction

Spiders collected by the Michaelsen and Hartmeyer Expedition to south-western Australia in 1905 were described by Simon (1908, 1909). In this work, some 228 species, including 160 new species (five of these from outside the region) and 121 genera, of which 21 were new, were recorded by Simon. At the time, this represented the most comprehensive regional collection of spiders made from anywhere within Australia. The specimens were distributed between the Musum National d'Histoire Naturelle, Paris (MNHP), the Zoologisches Staatsinstitut und Zoologisches Museum, Hamburg (ZMH), the Institut für Zoologie und Zoologisches Museum, Berlin (ZMB) and the Western Australian Museum, Perth (WAM).

The specimens in the European museums have subsequently been the source of further taxonomic records but those in the Western Australian Museum have not been cited apart from brief references by McKay (1973, 1985) and Main (1982, 1985), probably because most workers have been unaware of their existence.

Simon did not designate primary types and for most species he cited several localities. However, several later workers have assigned particular type status to specimens of some species, but without reference to those specimens in the Western Australian Museum. These specimens, although originally in alcohol, were unfortunately at an early date pinned and/or glued on cards. Original labels were retained, including identification labels in Simon's handwriting. In 1980, one of us (BYM) returned the specimens to alcohol with all labels, including the WAM registration labels.

The collection contains 42 type specimens of 41 species, comprising 39 syntypes (38 species) and three paralectotypes. The specimens consist of 10 adult females (including a paralectotype for each of two species), three adult males, and 29 juveniles (including a paralectotype of one species).

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The order of families follows Platnick (1989, 1990). The families, subfamilies and tribes adopted by Simon (1908, 1909) are given in brackets after the citation. Simon's original spellings and combinations are followed in the species list. The station numbers employed by Michaelsen and Hartmeyer are listed in parentheses for each locality.

Systematics

Nemesiidae

Proshermacha subarmata Simon

Proshermacha subarmata Simon, 1908: 364 (Aviculariidae: Ctenizinae: Nemesieae).

Paralectotype

1 immature, Wooroloo (Stat. 98), WAM 11/4272.

Remarks

This species is now regarded as a junior synonym of *Chenistonia tepperi* Hogg (Main 1982, 1985). Lectotype and paralectotype were designated by Main (1985).

Segestriidae

Ariadna thyrianthina Simon

Ariadna thyrianthina Simon, 1908: 380 (Dysderidae).

Syntype

1 ♀, Norseman (Stat. 90), WAM 11/4268.

Hersiliidae

Tama brachyura Simon

Tama brachyura Simon, 1908: 406 (Hersiliidae).

Syntype

1 immature, Geraldton (Stat. 75), WAM 11/4262.

Remarks

This species was designated as a nomen dubium by Baehr and Baehr (1987).

Theridiidae

Billima attrita Simon

Billima attrita Simon, 1908: 430 (Argiopidae: Argiopinae: Theridiosomateae).

Paralectotype

1 ♀, Subiaco North (Stat. 109), WAM 11/4280.

Remarks

Levi (1967) transferred this species to *Theridion*, and designated a female lectotype. The WAM specimen is therefore a paralectotype.

Enoplognatha bidens Simon

Enoplognatha bidens Simon, 1908: 414 (Theridiidae: Asageneae).

Syntype

1 ♀, Fremantle (Stat. 117), WAM 11/4294.

Theridion mortuale Simon

Theridion mortuale Simon, 1908: 409 (Theridiidae: Theridieae).

Syntype

1 ♂ immature , Collie (Stat. 137), WAM 11/4267.

Linyphiidae

Linyphia cupidinea Simon

Linyphia cupidinea Simon, 1908: 417 (Argiopidae: Linyphiinae: Linyphieae).

Paralectotype

1 ♀, Subiaco North (Stat. 109), WAM 11/4277.

Remarks

A male lectotype was selected by van Helsdingden (1972), which automatically makes the WAM specimen a paralectotype. Van Helsdingen (1972) transferred the species to *Laperousea* and Millidge (1988) synonymised it with *Laperousea blattifera* (Urquhart).

Tetragnathidae

Nanometa gentilis Simon

Nanometa gentilis Simon, 1908: 421 (Argiopidae: Tetragnathinae).

Syntype

1 ♀, Lion Mill (Stat. 100), WAM 11/4287.

Tetragnatha luteocincta Simon

Tetragnatha luteo-cincta Simon, 1908: 420 (Argiopidae: Tetragnathinae).

Syntype

1 immature, Midland (Stat. 102), WAM 11/4292.

Tetragnatha maeandrata Simon

Tetragnatha maeandrata Simon, 1908: 421 (Argiopidae: Tetragnathinae).

Syntype

1 immature, Serpentine (Stat. 131), WAM 11/4292a.

Araneidae

Araneus cyphoxis Simon

Araneus cyphoxis Simon, 1908: 426 (Argiopidae: Argiopinae: Araneae).

Syntype

1 immature, Perth (Stat. 105), WAM 11/4285.

Araneus senicaudatus Simon

Araneus senicaudatus Simon, 1908: 425 (Argiopidae: Argiopinae: Araneae).

Syntype

1 immature, Serpentine (Stat. 131), WAM 11/4265.

Remarks

This specimen is probably *Eriophora pustulosa* (Walckenaer).

Araneus senicaudatus simplex Simon

Araneus senicaudatus simplex Simon, 1908: 426 (Argiopidae: Argiopinae: Araneae).

Syntype

1 immature, Brunswick (Stat. 139), WAM 11/4289.

Lycosidae

Lycosa meracula Simon

Lycosa meracula Simon, 1909: 190 (Lycosidae).

Syntype

1 immature, Denham (Stat. 65), WAM 11/4303.

Remarks

Rack (1961) and McKay (1985) regarded specimens in ZMH and WAM, respectivley, as paratypes. Another specimen is lodged in MNHP. Since Simon never designated holotypes, all specimens are syntypes.

Lycosa phegeia Simon

Lycosa phegeia Simon, 1909: 189 (Lycosidae).

Syntype

1 immature, Cannington (Stat. 123), WAM 11/4301.

Remarks

This species is now referred to as *Trochosa tristicula phegeia* (Simon) (McKay 1979). Rack (1961) listed a "♀ paratypoid" in ZMH; however, this is a syntype. Rack (1961) placed the species in *Triccosta*. There are also syntypes in MNHP and ZMB. Simon (1909) listed only one locality and described a male and female.

Lycosa propitia Simon

Lycosa propitia Simon, 1909: 186 (Lycosidae).

Syntype

1 immature ♂, Cannington (Stat. 123), WAM 11/4302.

Remarks

Rack (1961) cited a "holotype" ♀ in ZMH. However, there are specimens in MNHP, ZMB and WAM, all from Cannington, which are regarded as syntypes.

Lycosa woodwardi Simon

Lycosa woodwardi Simon, 1909: 182 (Lycosidae).

Syntype

1 ♀, Dongarra (Stat. 83), WAM 11/4300.

Desidae

Amaurobius microps Simon

Amaurobius microps Simon, 1908: 366 (Dictynidae; misspelt as Dictyonidae throughout the text, but not in the index).

Syntype

1 immature, Albany (Stat. 165), WAM 11/4274.

Remarks

Transferred to *Badumna* Thorell by Lehtinen (1967).

Aphyctoschaema armigerum Simon

Aphyctoschaema armigerum Simon, 1908: 370 (Dictynidae).

Syntype

1 immature ♂, Watheroo (Stat. 87), WAM 11/4276.

Remarks

This species is now placed in the genus *Forsterina* Lehtinen (Lehtinen 1967).

Aphyctoschaema vultuosum Simon

Aphyctoschaema vultuosum Simon, 1908: 373 (Dictynidae).

Syntype

1 ♀, Mundaring Weir (Stat. 101), WAM 11/4275.

Remarks

This specimen is clearly labelled "Mundaring Weir (Stat. 101)", however, Simon (1908) did not record *A. vultuosum* from this locality. Nevertheless, the specimen is treated as a syntype. *Aphyctoschaema vultuosum* is now placed in the genus *Forsterina* Lehtinen (Lehtinen 1967).

Callevophthalmus lividus Simon

Callevophthalmus lividus Simon, 1908: 378 (Dictynidae).

Syntype

1 ♂, East Fremantle (Stat. 116), WAM 11/4290.

Remarks

Lehtinen (1967) synonymised *C. lividus* with the type species of *Callevophthalmus*, *Lathys albus* Keyserling from New South Wales. If this synonymy is upheld, then the valid name for *C. lividus* is *C. albus*. Rack (1961) listed one ♂ male syntype in ZMH which is in fact a juvenile ♂ (M.R. Gray, pers. comm.).

Desis hartmeyeri Simon

Desis hartmeyeri Simon, 1909: 180 (Agelenidae: Cybaeinae).

Syntype

1 immature, Albany (Stat. 165), WAM 11/4320.

Remarks

Rack (1961) cited a juvenile female in ZMH as "holotype". However, there are syntypes in ZMB and WAM.

Phryganoporus gausapatus occidentalis Simon

Phryganoporus gausapatus occidentalis Simon, 1908: 367 (Dictynidae).

Syntype

1 immature, East Cannington (Stat. 125), WAM 11/4269.

Remarks

This species was transferred to *Badumna* and synonymised with *B. candida* (L. Koch) by Gray (1982).

Phryganoporus tubicola Simon

Phryganoporus tubicola Simon, 1908: 367 (Dictynidae)

Syntypes

1 immature ♂, 1 immature ♀, Denham (Stat. 65), WAM 11/4279, 4279a.

Remarks

This species was synonymised with *Badumna candida* (L. Koch) by Gray (1982).

Stiphidiidae

Epimecinus volucripes Simon

Epimecinus volucripes Simon, 1908: 377 (Dictynidae).

Syntype

1 immature, Bunbury (Stat. 142), WAM 11/4281.

Remarks

This species is the type species of *Baiami* Lehtinen (Lehtinen 1967).

Miturgidae

Miturga catograpta Simon

Miturga catograpta Simon, 1909: 170 (Clubionidae: Cteninae; Miturgeae).

Syntype

1 immature, Lion Mill (Stat. 99), WAM 11/4307.

Miturga occidentalis Simon

Miturga occidentalis Simon, 1909: 169 (Clubionidae: Cteninae: Miturgeae).

Syntype

1 ♀, Tamala (Stat. 70), WAM 11/4308.

Clubionidae

Chiracanthium nervosum Simon

Chiracanthium nervosum Simon, 1909: 161 (Clubionidae: Clubioninae).

Syntype

1 immature, North Fremantle (Stat. 115), WAM 11/4317.

Remarks

The current spelling of the generic name is *Cheiracanthium* C.L. Koch (Platnick 1989).

Clubiona laudabilis Simon

Clubiona laudabilis Simon, 1909: 161 (Clubionidae: Clubioninae).

Syntype

1 immature, Denham (Stat. 65), WAM 11/4318.

Remarks

Rack (1961) cited a ♀ holotype in ZMH; however, the specimen is an immature (B.Y. Main, personal observation) and as additional specimens are lodged in MNHP, ZMB and WAM, all are syntypes.

Zodariidae

Storena tricolor Simon

Storena tricolor Simon, 1908: 405 (Zodariidae).

Syntype

1 immature, Lion Mill (Stat. 99), WAM 11/4286.

Corinnidae

Aristerus phaleratus Simon

Aristerus phaleratus Simon, 1909: 179 (Clubionidae: Corinninae).

Syntype

1 ♂, Yalgoo (Stat. 77), WAM 11/4312.

Remarks

Platnick (1989) tacitly accepted Simon's placement of *Aristerus* in the Corinninae, which has since been elevated to family level. *Aristerus* may be better placed in the Gnaphosidae.

Gnaphosidae

Corimaethes campestratus Simon

Corimaethes campestratus Simon, 1908: 385 (Drassidae: Hemicloeinae).

Syntype

1 immature, Day Dawn (Stat. 76), WAM 11/4273.

Remarks

Rack (1961) listed a holotype in ZMH. However, since there are also specimens in MNHP, ZMB and WAM, all specimens are syntypes.

Drassodes respersus Simon

Drassodes respersus Simon, 1908: 387 (Drassidae: Drassodinae).

Syntype

1 ♀, Northampton (Stat. 71), WAM 11/4282.

Remarks

This species was correctly transferred to *Anzacia* Dalmas by Roewer (1954). Rack (1961) listed the ZMH ♂ as holotype. However, specimens are deposited in MNHP, ZMB and WAM, and all are syntypes.

Hemicloea insidiosa Simon

Hemicloea insidiosa Simon, 1908: 382 (Drassidae: Hemicloeinae).

Syntype

1 immature ♂, East Fremantle, Recreation Ground (Stat. 116), WAM 11/4306.

Hemicloea sublimbata Simon

Hemicloea sublimbata Simon, 1908: 383 (Drassidae: Hemicloeinae).

Syntype

1 ♀, Kalgoorlie (Stat. 93), WAM 11/4263.

Megamyrmaecion penicillatum Simon

Megamyrmaecion penicillatum Simon, 1908: 394 (Drassidae: Drassodinae).

Syntype

1 immature, Torbay (Stat. 162), WAM 11/4278.

Remarks

The current spelling of the generic name is *Megamyrmaekion* Reuss (Platnick 1989).

Lamponidae

Lampona punctigera Simon

Lampona punctigera Simon, 1908: 399 (Drassidae: Drassodinae: Lamponeae).

Syntype

1 immature, Torbay (Stat. 162), WAM 11/4284.

Heteropodidae

Isopoda cerussata Simon

Isopoda cerussata Simon, 1908: 439 (Clubionidae: Sparassinae: Deleneae).

Syntype

1 immature, Northampton (Stat. 71), WAM 11/4259.

Remarks

Rack (1961) cited a paratype ♂ in ZMH. However, more than one specimen was described by Simon (1908), and all are regarded as syntypes. This species has been transferred to the genus *Isopedella* Hirst by Hirst (1990). The current spelling of the generic name is *Isopeda* (Platnick 1989).

Thomisidae

Xysticus periscelis Simon

Xysticus periscelis Simon, 1908: 431 (Thomisidae: Misumeninae).

Syntype

1 ♀, Perth (Stat. 105), WAM 11/4295.

Salticidae

Opisthoncus devexus Simon

Opisthoncus devexus Simon, 1909: 205 (Salticidae: Triteae).

Syntype

1 immature, Brown Station, Dirk Hartog (Stat. 67), WAM 11/4319.

Remarks

Rack (1961) referred to the ZMH male specimen as the holotype, however, since there are also specimens in MNHP, ZMB and WAM, all are syntypes.

Servaea spinibarbis Simon

Servaea spinibarbis Simon, 1909: 204 (Salticidae: Servaeae).

Syntype

1 immature ♀, Cottesloe (Stat. 113), WAM 11/4315.

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Australites from Pinjin Pastoral Station, Western Australia

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Abstract

Australites from Pinjin Pastoral Station are typical of the Eastern Goldfields region if some allowance is made for the quality of the available sample. The specific gravity range of 2.422-2.469 with 55% of the values in the 2.45-2.46 interval indicates that the australites are of the "normal" chemical type of Chapman (1971). The aberrant forms include a rare "tailed" core.

Introduction

The homestead of Pinjin Pastoral Station is 141 km east-north-east of Kalgoorlie, Western Australia, near the south end of the Pinjin line of gold workings and close to the site of the former town of Pinjin at 30°05′S, 122°44′E. A complex system of salt lakes within the station includes elongated parts of Lake Rebecca, the partly choked and much modified remnants of a river system which flowed to the south-east in more humid times. The region is now semi-arid with internal drainage. Mean rainfall at the nearest recording station (Edjudina, adjoining to north) is 209 mm/a. The small mining centres of Mulgabbie and Pinnacles are within the station (Figure 1). Australites occur on the surface of the ground, in rain-wash gutters leading to the lakes, on alluvial fans, and around the margins of claypans and lakes.

Australite sample and laboratory procedure

The following six small parcels of australites collected from various parts of Pinjin Station were available for examination: — Tillotson private collections — 19 specimens from small dry lakes south-west of Old Pinjin (a former homestead), and 98 specimens from 8 km west-north-west of Old Pinjin; Western Australian Museum — two collections totalling 50 specimens from Mulgabbie; South Australian Museum — 27 from dry lake in the vicinity of Pinnacles and 33 from "Tinjin" ex S.F.C. Cook collection. The last item was accepted as being from the Pinjin Mining Centre. The Cook collection was very poorly documented. There has never been a "Tinjin" in Western Australia (pers. comm. from Department of Land Administration), but Pinjin was an active mining centre when Cook was assembling his collection by purchases from prospectors and mining men. Cook's collection contained australites from mining centres neighbouring Pinjin to north-west (Edjudina) and to south-west (Kurnalpi).

The marked imbalance in distribution of the above parcels (Figure 1) was partially corrected by collecting from several points in the central and south-eastern parts of the station. Australites were sparsely present and small. Most were found on the margins of claypans or salt lakes. Only five of 78 australites collected weighed more than two grams

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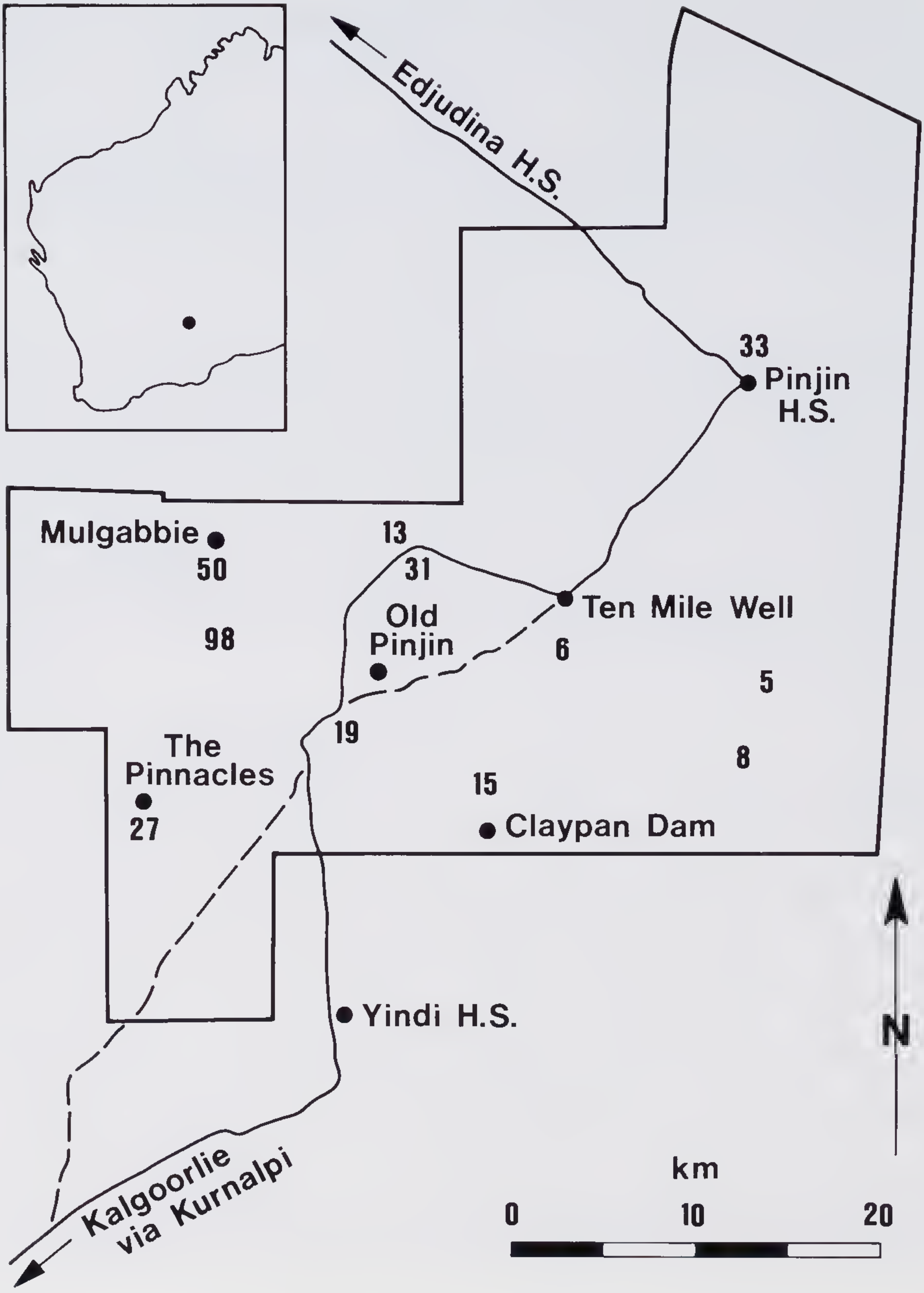

Figure 1. Map of Pinjin Pastoral Station showing numbers and find sites of australites examined. Inset: Western Australia showing location of Pinjin H.S.

each and the recovery rate was less than two australites per person per hour. The absence of large australites from the eastern section may explain why the area was not represented in earlier collections. The additional specimens bring the total number available to 305, a sample of minimally acceptable size for this work.

Australites were classified morphologically, the results tabulated, and extracts made (Table 1, column 1) according to the system and methods of Cleverly (1986). This procedure was used to enable the comparison of the Pinjin australites with those from other areas previously quantified by the same system and methods. The specific gravities of 80 australites drawn from all parcels were determined.

Discussion and conclusion

The Pinjin australite sample was gathered by various people at various times, and it is likely that the greater part of the station has never been searched. Moreover, the parcels in the sample vary greatly in quality. There is a natural variation in australite size from place to place as shown, for example, by the distinct sectors in which very large australites occur (Cleverly and Scrymgour 1978). However, mean size may also be influenced by the degree of care in collecting. Thus, in the Pinjin sample, there are parcels resulting from the experienced and thorough collecting of the Tillotsons with average specimen weight 1.0 g, and on the other hand, the casual and perhaps accidental finds of prospectors contributing to the Cook collection, average weight 3.4 g. In conformity with weight difference, the ratio of the larger core-type specimens to the smaller lens-forms in the Tillotson contribution is 0.18 (i.e. fewer cores than lens-forms), while the ratio for the Cook collection is 2.40 (the reversed situation). That these differences are related to thoroughness of sampling rather than to differences in the material available is suggested by comparable figures for australites from other areas in the same collections. For example, figures for the Leonora district are:

Collection	Mean weight	Cores/lens-forms
Tillotson	0.8 g	0.06
Cook	8.2 g	2.53

Features of the Pinjin sample and average Eastern Goldfields australites are compared in Table 1. Small percentage differences in major constituents are in the directions expected from the nature of the sample. The higher than average percentage of classifiable specimens (Table 1, item 3, 56.8%) is understandable as the result of casual or fortuitous discovery of the larger specimens present in some parcels. This is true also for the higher than average percentage of round plus broad oval forms (item 8, 81.0%), which are especially abundant amongst larger specimens (Cleverly 1991b). It follows also for the higher percentage of the larger cores (item 17, 41.7%), lower percentage of the smaller lens-forms (item 15, 52.4%) and consequent larger cores/lens-forms ratio (item 18, 0.80).

Table 1. Comparison between morphological features and mean weights of australites from 1. Pinjin Pastoral Station (this paper) and 2. average of seven australite samples from the Eastern Goldfields (Cleverly 1986, 1988, 1990, 1991a).

		1	2
1	Complete forms or essentially so %	44.3	37.3
2	Incomplete but classifiable %	12.5	12.9
3	Total classifiable %	56.8	50.2
4	Unclassifiable, mostly fragments %	42.6	48.6
5	Flakes and flaked cores %	0.6	1.2
6	Round forms %	73.9	68.2
7	Broad oval forms %	7.1	8.4
8	Total round and broad oval forms %	81.0	76.6
9	Narrow oval forms %	6.5	7.7
10	Boat forms %	5.4	5.1
11	Dumbbell forms %	6.5	7.3
12	Teardrop forms %	0.6	3.3
13	Flanged, disc and plate, bowl and canoe forms %	3.0	2.3
14	Indicators I %	1.2	1.8
15	Lens-forms %	52.4	61.6
16	Indicators II %	1.8	1.1
17	Cores, including conical cores %	41.7	33.2
18	Cores/lens-forms	0.80	0.54
19	Number of whole australites	135	
20	Mean weight of whole australites (g)	2.82	2.74
21	Total number of specimens	305	
22	Mean weight of all specimens (g)	1.92	1.86

The mean weights (items 20 and 22) of the Pinjin sample are only fractionally higher than average but this is partly accountable to painstaking collecting in the eastern portion of the station, which would not otherwise have been represented. The 78 specimens collected there have mean weight only 0.82 g.

The percentages of some minor constituents such as teardrop forms (item 12, 0.6%) are distinctly different from average, but such differences must be expected when the sample is of minimally acceptable size. Only 168 specimens are available for distribution in the group of items Nos. 6-12 (Table 1). Previous experience of samples having 103-304 specimens in that group is that the percentage of teardrop forms varied widely from 1.0 to 5.2% (Cleverly 1991a). It would require the recognition of only a single additional teardrop from amongst the 130 un-named, weathered or fragmented, Pinjin specimens to bring their percentage within that range.

The 80 measured specific gravities are in the range 2.422-2.469. The frequency distribution of the specific gravities is unimodal with 55% of them in the 2.45-2.46 interval. These features are typical of the frequency diagram for the "normal" australite chemical type of Chapman (1971).

Table 2. Comparison between australite from Mulgabbie and other "tailed" or "beaked" australite cores.

Collection Find site	WAM 12 170 Mulgabbie, W.A.	1. WAM 1645 Kookynie, W.A.	SAM 1389 Finke, N.T.	2. K. Jenkins coll. Eastern Goldfields
Core				
Shape type	Round	Round	Round	Round
Dimensions mm	(23.5-22.9) x 20.3	(30.4-30.1) x 26.6	(24.5-24.0) x 19.7	(31-29.5) x 32
Mass g	12.85	29.26	13.36	33.07
S.G.	2.45	2.46	2.43	2.43
Primary body				
Diameter mm	25.6	33.5	28.0	c.40
Mass g	21.5	48.9	27.9	c.80
Losses from primary body				
Mass %	40	40	52	c.55
Thickness %	21	20	30	c.20

1: Data from Cleverly (1974); others, this work.
2: Figures for primary body from visual estimates of curvature and complicated by flake losses.

The five aberrant forms in the sample constitute 2.9% of classifiable specimens, which is close to the mean of 3.0% for seven Eastern Goldfields samples previously examined. The aberrant specimens include a weathered, "tailed" or "beaked", round core from Mulgabbie (WAM 12 170). It is compared in Table 2 with a better preserved specimen described by Cleverly (1974) and two other examples. The origin of the form is uncertain. One possibility is that after the parting of a slim-waisted dumbbell primary mass, the two resulting apioids tended to adopt spherical shape under the influence of surface tension, being no longer constrained within a rotating system. Such a tendency would be expected especially in medium sized and larger bodies with longer liquid life. A mass failing to attain spherical shape would orient in ablation flight like other apioids with the unabsorbed "tail" as an extension of the posterior surface, and the resulting secondary shape would be round or nearly so. The four examples of the "tailed" form known to the writer had such an orientation and are round forms. "Tailed" forms would thus be apioids which has progressed further than most others towards the adoption of a spherical shape.

The only two australite flakes in the sample were found on adjacent clypans 12 km east-south-east of Ten Mile Well (Figure 1), where flakes and flaked cores of chalcedony and various siliceous rocks are also sparsely present. The australite flakes are therefore presumed to be artifacts. The area was evidently not particularly favoured by Aborigines. It is improbable that destructive use of australites could have contributed significantly to the scarcity and small size of australites in the general area. No evidence was seen of the removal of australites from the area.

The Pinjin australites do not differ significantly from others in the Eastern Goldfields except insofar as their features are influenced by the quality of the available sample.

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I thank A.W.R. Bevan, A. Pring and R.G. Tillotson for the loan of australites, E.I. Cleverly for assistance in australite search and for typing the manuscript, and J.M. Wearne for drafting Figure 1. Messrs Bruce Agars and Philip Agars allowed ready access to the station and offered numerous courtesies during the course of three visits.

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Three new, monolectic species of *Euryglossa* (*Euhesma*) from Western Australia (Hymenoptera: Colletidae)

Terry F. Houston*

Abstract

Three new species of *Euryglossa* (*Euhesma*) (*E. aureophila*, *E. morrisoni* and *E. semaphore*) are described and figured. All are endemic to the Swan Coastal Plain of Western Australia. *Euryglossa aureophila* and *E. morrisoni* are monolectic on closely related species of *Verticordia* and *E. semaphore* appears to be monolectic on *Pileanthus filifolius* (all Myrtaceae). Males of *E. semaphore* are remarkable for their highly modified, spatulate antennae.

Introduction

The object of this paper is to make available names for three species of bees that have been the subject of investigation in Western Australia.

Interest in these species has centred around their strict plant preferences. Many species of bees are known to confine their foraging for pollen and often nectar to closely related species or genera of plants (oligolecty). However, cases of bees confining their foraging exclusively to one plant species (monolecty) are comparatively rare. Hence, it has been of interest to discover three species of euyglossine bees near Perth, Western Australia, which do just that.

Two of the species described here are monolectic on species of *Verticordia* with unusual anthers and appear to be the plants' prime pollinators. The pollination biology of the two *Verticordia* species (*V. aurea* George and *V. nitens* (Lindley)) has recently been investigated by myself and Dr Byron Lamont and names for their pollinating bees are required to facilitate publication of our findings.

The third species, discovered during our *Verticordia* studies, appears to be monolectic on *Pileanthus filifolius* Meisn. Description of this bee species is warranted because of the extraordinary form of the antennae of males and the likelihood of investigations into the species' ecology and behaviour.

Morphological terminology largely follows that of Michener (1965) and terminology of surface sculpturing largely follows Harris (1979).

Abbreviations of collections are ANIC, Australian National Insect Collection, CSIRO, Canberra; UQIC, University of Queensland Insect Collection, Brisbane; WAM, Western Australian Museum, Perth.

Abbreviations for certain measurements are as follows: *AOD* antennocular distance; *ASD* antennal socket diameter; *BMW* basal width of mandible; *CAD* clypeantennal distance; *CL* clypeal length; *CW* clypeal width; *FL* flagellum length; *HL* head length; *HW* head width; *IAD* interantennal distance; *LFW* lower width of face; *LPL* labial palp

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length; *ML* mandible length; *MOD* diameter of mid ocellus; *MPL* maxillary palp length; *MSL* malar space length; *OOD* ocellocular distance; *SL* scape length; *SW* scape width; *UCW* upper width of clypeus (distance between lower ends of subantennal sutures); *UFW* upper face width (maximum width of face above antennae); *WOC* width of ocellar cluster.

Systematics

Colletidae: Euryglossinae

Genus *Euryglossa* Smith, 1853

Subgenus *Euhesma* Michener, 1965

Euhesma is the largest and most diverse subgenus within *Euryglossa* and has yet to be revised. Revisionary studies of the group have been commenced by Dr Elizabeth Exley and she has confirmed the undescribed status of my species. Given that completion of her studies is some considerable time away, she has graciously consented to me describing them ahead of her revision.

Euryglossa (Euhesma) morrisoni, sp. nov.

Figures 1-3, 8, 9, 11, 12, 15, 16, 18-20

Holotype

In WAM (91/544), ♂, Melaleuca Park, 11 km NE of Wanneroo, Western Australia, 20 December 1990, T.F. Houston, on flowers of *Verticordia nitens*.

Paratypes

Western Australia: 6♂, 7♀, WAM 91/545-57, data as for holotype; 3♂, 1♀, WAM 91/540-3, ditto but 16 Dec.; 1♂, WAM 91/539, ditto but 22 December 1989; 1♂, 11♀, WAM 91/604-614, 12 km WNW Harvey, 4 Jan. 1991, T.F. Houston, on flowers of *Verticordia nitens*; (8♂, 9♀, WAM 91/522-38, 20 Dec. 1989; 1♂, 27♀, WAM 91/539, 91/577-603, 31 Dec. 1989) Moore River National Park, 31.10 S, 115.40 E, T.F. Houston, on flowers of *Verticordia nitens*.

Diagnosis

A morphologically unspecialised *Euhesma* lacking pale maculations. Distinguishable from other *Euhesma* within its geographic range by combining a shining and distinctly punctate head and thorax, yellow-orange metasoma and appendages and slender, widely divergent hind tarsal claws in female.

Very close to *E. aureophila*, distinguished as follows: ventral margin of clypeus, labrum and mandibles yellow-brown; metasoma and legs almost wholly yellow-orange; wing veins uniformly mid-brown (male) or dark brown (female); legs relatively longer.

Description

Male (holotype)

Head width 1.3 mm; body length *ca.* 4.3 mm.

Relative dimensions: HW 100; HL 92; UFW 65; LFW 54; MOD 9; WOC 37; OOD 15; IAD 16; ASD 9; AOD 13; CAD 7.5; UCW 23; MCW *ca.* 51; MCL 33; MSL 0; BMW 13; ML 40; MPL 40; LPL 26; SL 29; SW 8; FL 71.

Morphology: Head fairly rounded in anterior view (Figure 1); vertex slightly elevated above level of ocelli medially only; facial foveae not evident; inner orbits converging only slightly ventrally; face gently convex in profile and transversely; genae about 0.5 X as wide as compound eyes viewed laterally; antennae inserted above middle of face, sockets separated by 1.8 X their own diameter; antennae simple; proximal articles of flagellum about half as long as wide, tenth nearly as long as wide; mandibles distinctly bidentate, posterior tooth exceeding anterior tooth (Figure 8); labium, maxilla and palpi unspecialized, palpus segments subequal; fore tarsi slender, simple, excluding claws 0.67 X as long as HW; hind tibiae 0.8 X and hind tarsi 1.2 X as long as HW; tarsal claws bifid, prongs subequal, divergent only distally (Figure 15).

Colouration: Head and mesosoma largely black; the following are dull orange-yellow —antennae (except pedicels and flagella dark brown dorsally), ventral margin of clypeus, labrum, mandibles (except dark red apices), legs (except blackish fore and mid coxae) and metasoma (except for dark brown suffusion on tergum 1 and fainter patches on others and large, black-brown, elliptical foveae); pronotal tubercles and medial edges of otherwise hyaline tegulae cream; wings clear but iridescent in incident light, venation mid-brown generally.

Sculpture: Head and thorax weakly shining, coriarious, with open to sparse, medium setigerous punctures (except propodeal enclosure which is smooth, shining to glossy); metasomal terga weakly shining, coriarious with sparse, minute setigerous punctures.

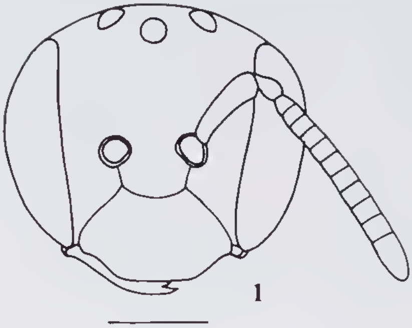
Pubescence: White generally; head and mesosoma with sparse, erect, white, plumose setae, on scutum about 1.5 X as long as an ocellar diameter, densest on lower face but not obscuring integument; metasomal terga almost bare, with sparse, short, simple setae admixed on more apical terga with a few longer slightly plumose setae; metasomal sterna with sparse, long simple setae, forming erect, loose, apical fringes on 4 and 5.

Terminalia: See figures 18-20.

Female: (paratype WAM 91/553)
Head width 1.7 mm; body length *ca.* 6.2 mm.

Relative dimensions: HW 100; HL 92; UFW 62; LFW 56; MOD 9; WOC 34; OOD 14; IAD 16; ASD 9; AOD 14; CAD 8; UCW 22; MCW *ca.* 50; MCL 35; MSL 0; BMW 17; ML 40; MPL 34; LPL 22; SL 27; SW 7; FL *ca.* 50.

Morphology: Much as in male except as follows — flagella relatively shorter (Figure 2); labrum flat, rather triangular with a median process (Figure 3), 0.78 X as long as wide, basal elevation almost obsolete; mandibles fairly straight, bidentate, posterior tooth rounded-obtuse (Figure 9); genae about 0.5 X as wide as compound eyes viewed laterally; basitarsi straight, slender; hind tarsi 0.92 X as long as HW; fore tibial calcars serrated along outer margins, simple apically (Figure 12); basitibial plates scarcely defined but apices marked by tubercle at 1/3 length of tibia; hind tibial spurs simple, finely serrate; tarsal claws bifid with short inner ramus diverging strongly from long, slender, outer ramus (Figure 16); pygidial plate flat, spatulate (Figure 11), 1.4 X as wide as median ocellus.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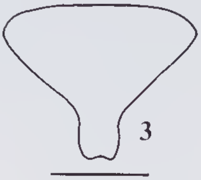
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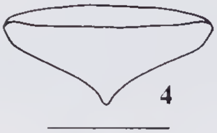
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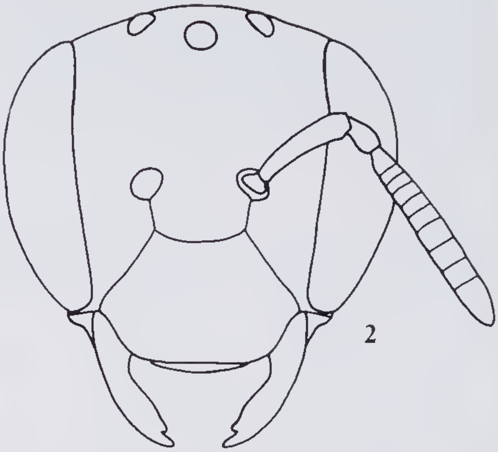
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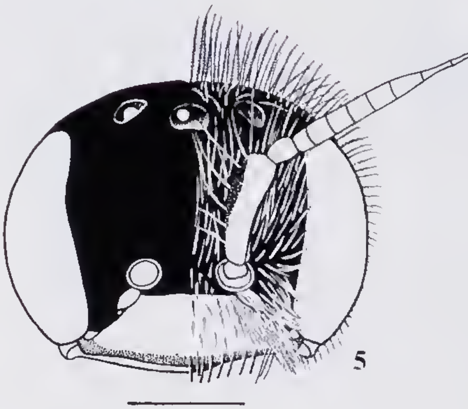
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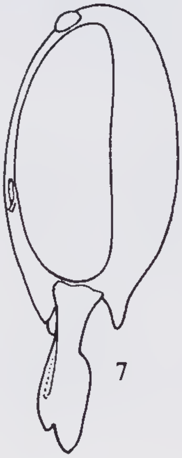
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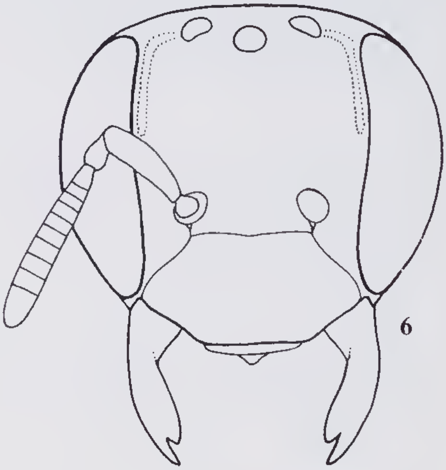
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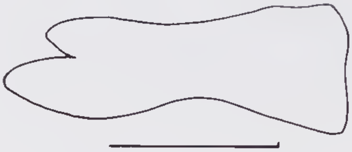
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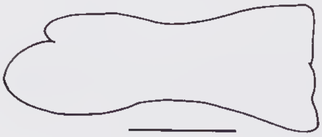
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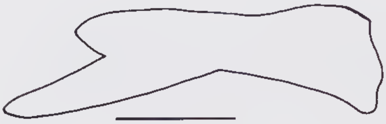
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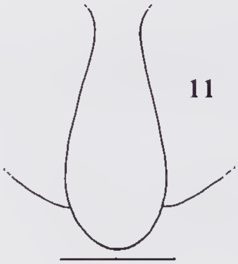
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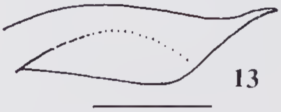
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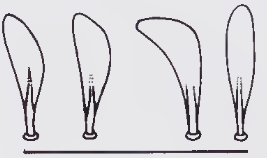
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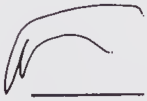
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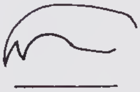
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Colouration: As in male but metasoma with progressively less dark brown suffusion apicomedially on terga 1-4; pygidial plate dark red.

Sculpture: As in male.

Pubescence: Much as in male; labrum densely setose, setae long, tapering, mostly simple; fore tarsi with short, simple brush-hairs ventrally (straight on basitarsi, curved on distitarsi) and longer setae laterally; hind tibiae with numerous short, stiff, curved, distally plumose bristles on outer surfaces and equally numerous long, fine plumose setae on dorsal and ventral margins; setae on metasomal terga 5 and 6 sparse, not obscuring integument.

Variation

Head widths of males range from 1.2-1.5 mm (n 21) and of females from 1.5-1.8 mm (n 56).

Etymology

The specific epithet is derived from the common name of the forage plant (Morrison Feather Flower).

Euryglossa (Euhesma) aureophila, sp. nov.

Holotype

In WAM (91/500), ♂, 10.5 km S Eneabba (29.49 S, 115.16 E), Western Australia, 14-15 November 1990, T.F. Houston, on flowers of *Verticordia aurea*.

Paratypes

8 ♂, 10 ♀, WAM 91/501-518, data as for holotype (except for 1♀, on flowers of *Pileanthus filifolius*), in ANIC, UQIC, WAM.

Diagnosis

Very close to *E. morrisoni*, distinguished as follows: clypeus, mandibles and labrum wholly black, metasoma chiefly brown dorsally, wing veins (except on costal margin) pale brown in female and colourless in male; legs relatively shorter.

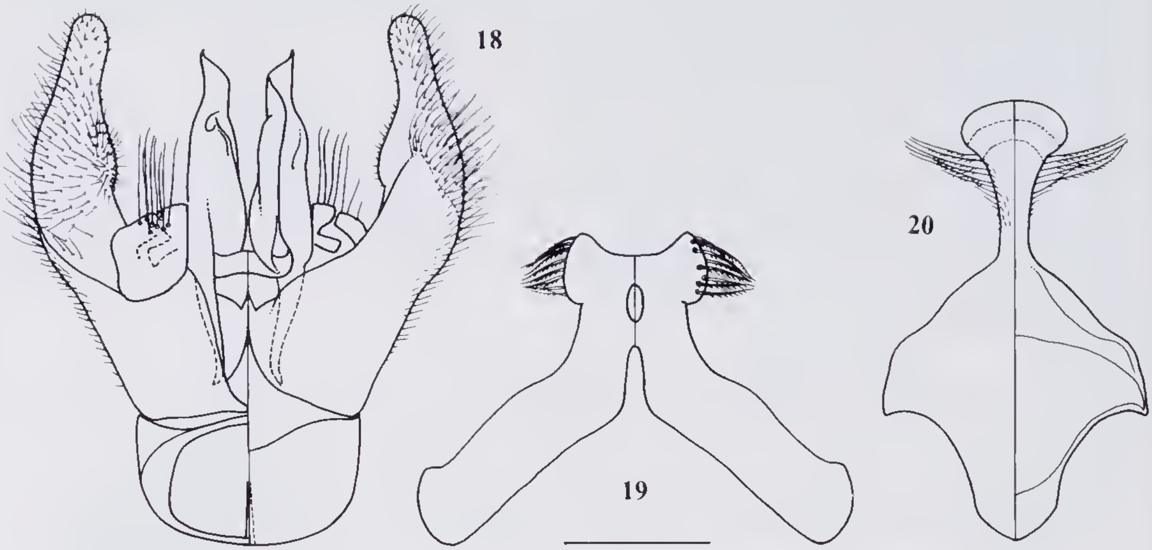
Description

Very similar to *E. morrisoni* except as noted in the diagnosis and with the following additional differences.

Male (holotype)

Head width 1.35 mm; body length *ca.* 4.5 mm.

◀ **Figures 1-17** *Euryglossa (Euhesma)* spp.: (1, 2) heads of male and female of *E. morrisoni* (to same scale); (3) labrum of *E. morrisoni* female, anterior view; (4) same of *E. semaphore* female; (5, 6) heads of male and female of *E. semaphore* (to same scale); (7) profile of head of *E. semaphore* female; (8-10) mandibles of male and female of *E. morrisoni* and male of *E. semaphore*, respectively (outer views); (11) pygidial plate of *E. morrisoni* female; (12-13) fore tibial calcars of females of *E. morrisoni* and *E. semaphore*; (14) highly modified setae from fore basitarsus of *E. semaphore* female; (15-17) hind tarsal claws of male and female of *E. morrisoni* and female of *E. semaphore*. Pubescence not indicated except in Figure 5. Scale lines: (1, 5) 0.5 mm; (3, 4, 8-11) 0.25 mm; others 0.1 mm.



Figures 18-20 *Euryglossa (Euhesma) morrisoni* male: genital capsule, 7th and 8th metasomal sterna (dorsal views on right, ventral views on left). Scale line 0.25 mm.

Relative dimensions: HW 100; HL 84; UFW 63; LFW 56; MOD 9.5; WOC 29; OOD 14; IAD 18; ASD 9; AOD 12; CAD 4; UCW 26; MCW *ca.* 54; MCL 30; MSL 0; BMW 16; ML 40; MPL 34; LPL 23; SL 24; SW 8; FL 60.

Morphology: Head relatively shorter; genae 0.3 X as wide as compound eyes viewed laterally; facial foveae faintly indicated as shallow grooves along inner orbits; antennal sockets separated by twice their own diameter; antennae relatively shorter; legs relatively shorter — fore tarsi (excluding claws) 0.54 X, hind tarsi 0.96 X, and hind tibiae 0.72 X as long as HW.

Colouration: The following are black — head and mesosoma, scapes and pedicels, labrum, mandibles, coxae, trochanters and bases of femora; eyes dark brown; metasomal terga chiefly mid-brown with narrow sinuous subapical cream bands widening laterally; foveae of tergum 2 large, black, rather elliptical; tergal margins hyaline, colourless; the following are creamy yellow-brown — terga 6 and 7, metasomal sterna (with lighter subapical bands), flagella (suffused with dark brown dorsally), and legs more distally; tegulae hyaline, colourless with creamy brown spots medially; wings colourless but milky in incident light; costal venation and pterostigma light brown (subcosta dark brown), venation progressively more colourless posteriorly.

Sculpture: Head and mesosoma shining, obscurely coriarious or smooth with (except propodeal enclosure) open to sparse, distinct medium-sized setigerous punctures; metasomal terga dulled (except peripherally) by strong fine pitted-imbricate sculpturing (each 'cell' with a concavity).

Female (paratype WAM 91/512)

Head width 1.57 mm; body length *ca.* 5.3 mm.

Relative dimensions: HW 100; HL 81; UFW 64; LFW 57; MOD 7; WOC 35; OOD 14; IAD 18; ASD 7.5; AOD 14; CAD 4; UCW 27; MCW *ca.* 50; MCL 32; MSL 0; BMW 16; ML 39; MPL 30; LPL 21; SL 23; SW 6.5; FL 49.

Morphology: Compound eyes scarcely converging ventrally; genae about 0.4 X as wide as compound eyes viewed laterally; hind tarsi (excluding claws) 0.83 X HW; basitibial plates not defined.

Colouration: As in male except as follows — wing veins light brown generally; femora black-brown except for yellowish apices; metasomal terga 1-4 largely dark brown, yellow-brown posterolaterally, with only traces of creamy yellow subapical bands; terga 5 and 6 yellow-brown with pygidial plate dark red-brown; metasomal sterna wholly yellow-brown.

Sculpture: Much as in male.

Variation

Head widths of males range from 1.25-1.37 mm (n 9), of females from 1.45-1.60 mm (n 10). Extent of creamy yellow-brown colouration on metasomal terga varies considerably: in some males it extends to tergum 6 or even tergum 5 (in these lighter males, a pair of dark spots is evident in scallops of cream subapical band of each tergum); in one female, metasoma is largely yellow-brown dorsally, terga 1-4 having progressively less dark-brown suffusion; in some females, tergum 5 is also suffused with dark brown.

Etymology

The specific epithet is Latin for lover of gold and alludes to the species' preference for the rich yellow flowers of *Verticordia aurea.*

Euryglossa (Euhesma) semaphore, sp. nov.

Figures 4-7, 10, 13, 14, 17

Holotype

In WAM (91/487), ♂, 10.5 km S Eneabba (29.49 S, 115.16 E), Western Australia, 14-15 November 1990, T.F. Houston 763-3, on flowers of *Pileanthus filifolius.*

Paratypes

5 ♂, 7 ♀, WAM 91/488-499, same data as for holotype, in ANIC, UQIC, WAM.

Diagnosis

Male immediately recognizable by its unique antennal form: articles 9-12 of flagellum constricted to about one quarter diameter of more proximal articles; article 13 greatly expanded, flattened, disc-like; antennae set very low on face, only two socket diameters from ventral margin of clypeus; mandibles with apical teeth divergent, posterior tooth very long.

Female wholly black and dark brown; immediately recognizable by having postgenal protrusions (usually visible from front when mandibles folded) and spatulate setae on fore tibiae and tarsi; antennal sockets situated below middle of face and separated by 2.5 socket diameters.

Description

Male (holotype)

Head width 1.55 mm; body length *ca.* 5 mm.

Relative dimensions: HW 100; HL 80; UFW 66; LFW 57; MOD 11; WOC 41; OOD 13; IAD 15; ASD 10; AOD 12; CAD 1; UCW 26; MCW *ca.* 55; MCL 20; MSL 0.5; BMW 16; ML 50; MPL 33; LPL 25; SL 32; SW 9; FL 93.

Morphology: Head distinctly broader than long (Figure 5); face broadest above antennal insertions; compound eyes converging little ventrally; vertex produced above and behind ocelli; antennae inserted well below middle of face, sockets virtually in contact with clypeus; clypeus over 2.5 X wider than long; malar spaces virtually absent; facial foveae represented by ill-defined depression lateral to each lateral ocellus contiguous with shallow groove extending down eye margin to widest part of face; antennae relatively long; flagella highly modified — articles 7-10 markedly constricted, stalk-like, lacking setae, article 11 expanded, flattened in vertical plane, disc-like; mandibles long, bidentate, teeth divergent, posterior tooth very much longer than anterior tooth (Figure 10); labium and maxillae unspecialised, palpi ordinary but distal segment of each twice as long as penultimate segment; legs unmodified, fore tarsi (excluding claws) 0.42 X, hind tarsi 0.8 X and hind tibiae 0.64 X as long as HW; claws bifid with prongs subequal, divergent only at tips (Figure 17).

Colouration: Head and mesosoma chiefly black with the following white — clypeus, two small spots on lower paraocular areas, mandibles (except dark red apices), labrum, lower genae, antennae (except dorsal edges of scape, pedicel and articles 1-6 of flagellum black-brown, articles 7-10 light brown and article 11 black posteriorly, suffused with cream anteriorly), pronotal tubercles and spots on tegulae; compound eyes pale grey in life, pink-brown in dried condition; metasoma chiefly dark brown dorsally, white ventrally, terga 1-6 each with a narrow subapical cream band; wings colourless but appearing milky in incident light, pterostigma pale brown; venation light to dark brown on costa grading to colourless more posteriorly, wing bases white with dark brown sclerites; legs predominantly white, becoming brown distally on tarsi and with a black-brown patch posteriorly on each femur and tibia.

Sculpture: Face, vertex, scutum and scutellum weakly shining to dull, mostly coriarious with weakly defined, medium-sized setigerous punctures, punctures separated by 1-2 diameters; propodeal enclosure dull, coriarious; metasomal terga feebly shining, much more finely coriarious with minute indistinct setigerous punctures.

Pubescence: White generally; head, mesosoma and legs with a sparse cover of long, erect, slightly plumose setae (about 1.5-2.0 X as long as ocellar diameter), densest on lower paraocular areas and lateral margins of clypeus, otherwise not obscuring integument; clypeus sparsely setose medially with transverse row of stiff, blunt, hyaline bristles arising close to and protruding over ventral margin; metasomal terga with very short, simple setae admixed on terga 4-7 with very long plumose setae; metasomal sterna 4 and 5 with weak apical fringes of plumose setae.

Female (paratype WAM 91/499)

Head width 1.65 mm; body length *ca.* 5.8 mm.

Relative dimensions: HW 100; HL 89; UFW 63; LFW 56; MOD 8.5; WOC 36; OOD 11; IAD 22; ASD 9; AOD 9; CAD 4; UCW 29; MCW *ca.* 53; MCL 30; MSL 2; BMW 15; ML 45; MPL 31; LPL 26; SL 26; SW 8; FL 47.

Morphology: Head, viewed anteriorly, slightly quadrate, inner orbits almost parallel, vertex elevated above level of ocelli (Figure 6); facial foveae as in male but better defined, grooves as long as antennal scapes; face gently convex in profile; clypeus and supraclypeal area rather flat; genae, viewed laterally, about half as wide as compound eyes; lower post-genae produced into rounded, ventrally directed spines each side of proboscidial fossa (Figure 7); antennae relatively small, inserted below middle of face, sockets separated by *ca.* 2.5 X their diameter; flagella rather ordinary, all but terminal articles broader than long; mandibles bidentate, both teeth broad (Figure 7); labrum sub-triangular (Figure 4), 0.46 X as long as wide, concave in profile beneath transverse basal elevation, apron bearing numerous, stiff, sinuate, obtuse-tipped setae; labium and maxillae short and stout, palpi of ordinary form, terminal segment of each longest; fore tarsi slender; fore tibial calcars simple, lacking teeth and serrations (Figure 13); basitibial plates not defined except by a carina posteriorly (a tubercle marks apex of plate on one side only; paratypes lack such tubercles); hind tibial spurs simple, ciliate; pygidial plate flat, spatulate (much as in Figure 11), about 1.6 X as wide as median ocellus.

Colouration: Head and mesosoma black, lacking pale maculations; metasoma brown, hind margins of terga colourless, only terga 3 and 4 with faint cream subapical bands; antennae, mouth-parts and legs black and brown, fore and mid tibiae slightly cream proximally; wings as in male although fore wing venation generally light brown.

Sculpture: Face with strong medium-sized puncturing, shining between punctures; punctures closest on mid frons (separated by one diameter or less), absent around median ocellus, sparse on interantennal area and clypeus (where each pit lies in a depression, creating an uneven surface); vertex, especially medially, dull with denser pitting, interspaces coriarious; scutum, scutellum and metanotum dull with close small puncturing, interspaces coriarious; mesopleura similar but puncturing becoming sparser and coarser more ventrally; otherwise as in male.

Pubescence: Much as in male but sparser on lower face and shorter on scutum (setae mostly about 1.5 X as long as ocellar diameter); clypeus with mostly fine, simple setae but a transverse row of flattened, hyaline bristles arises near and protrudes over ventral margin; inner surfaces of fore tibiae and ventral surfaces of fore tarsi covered with short, highly compressed, expanded, spatulate setae (Figure 14); hind tibiae with short, stiff, curved, simple bristles on outer surfaces and equally numerous long, fine, mostly simple setae on dorsal and ventral margins; setae of metasomal terga 5 and 6 sparse, not obscuring integument.

Variation

Head widths of males range from 1.55-1.70 mm, of females from 1.55-1.65 mm. All paratype males have white spots on supraclypeus. Female paratypes vary in number and extent of cream subapical bands on metasomal terga, two having none and one having full bands on terga 1-5.

Remarks

The extraordinary characters of this species could warrant its placement in a new subgenus but I prefer to place it in *Euhesma* pending a review of this very diverse group.

Given the pronounced sexual dimorphism, it is unlikely that the sexes would have been associated had they not been collected together at flowers.

Observations over two days at the collection locality suggested that foraging is confined to flowers of *Pileanthus filifolius* (Myrtaceae). Petals of this species are brilliant pinkish or purplish red. Many kinds of flowers including those of other Myrtaceae were available to the bees but were not seen to be visited. *P. filifolius* is confined to white sandy soils on the coastal plain from Gin Gin to Geraldton and flowers from November to January.

Etymology

The specific epithet, which alludes to the flag-like apices of the male antennae, should be treated as a noun in apposition.

Acknowledgements

I am grateful to the following for their assistance: Dr Elizabeth Exley, University of Queensland (for confirmation of the undescribed status of the bees and for graciously agreeing to me describing them ahead of her revision of *Euhesma*); Mr Kevin Kenneally, Western Australian Herbarium (for information on forage plant distributions).

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A new species of *Otomops (Chiroptera;Molossidae)* from Alor I., Nusa Tenggara, Indonesia

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Abstract

A single specimen of *Otomops* recently collected from Alor I., Eastern Indonesia, is herein described as a new species.

Introduction

The genus *Otomops* contains five species: *O. martiensseni* (Matschie, 1897) (Djibouti to Angola and south Africa, Madagascar); *O. wroughtoni* Thomas, 1913 (S. India); *O. formosus* Chasen, 1939 (Java); *O. papuensis* Lawrence, 1948 (SE Papua New Guinea); and *O. secundus* Hayman, 1952 (NE Papua New Guinea).

Otomops was diagnosed by Thomas (1913) to be a molossid with: M^3 complete; premaxillae united; basioccipital pits well defined; and a prominent vertical projection of the zygoma. However, Lawrence (1948) and Hayman (1952) pointed out inadequacies in that diagnoses, particularly related to the united premaxillae. More recently; Freeman (1981) characterised *Otomops* (and *Tadarida macrotis*) as bats with: very thin dentaries; low coronoid processes; presence of a large premolar well spaced between canine and PM^4; M^3 with full-sized posterior commissure (N-shaped); dentary condyle little elevated above toothrow; slight development of sagittal and lambdoidal crests; deep basisphenoid pits; large ears joined anteriorly over nose and lips (that are wrinkled either finely or as deep troughs).

Few specimens of the three known South East Asian species have been collected since their original description (Hill 1983, Koopman 1989, Flannery 1990, Boeadi 1990); and these descriptions were based on few (1-4) individuals. Consequently little is known of their general biology in this region apart from the observation in Chasen (1939) and Boeadi (1990) that the holotype male and three other male *O. formosus* were taken from tree holes. Chasen's (1939) specimens were probably from an old nesting hole of a barbet, or woodpecker, in a decayed branch of a rubber tree. Brass (1964) also reports that a specimen of *O. secundus* was shot from a height as it flew rapidly and directly out of a forest at dusk. All molossids are apparently fast-fliers (Fenton 1972).

Elsewhere, Mutere (1973) noted a large colony of *O. martiensseni* in a roost in Kenya, and Brosset (1966) reported a colony of 40 individual *O. wroughtoni* in India and noted that they appeared to be forest bats and have extremely powerful flight.

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From an examination of their musculature and skull, Freeman (1981) concluded that *Otomops* were capable of a very wide gape and probably eat soft bodied prey such as moths. Vaughan (1966) hypothesised that the large ears of *Otomops*, relative to other molossids, may be used as additional aerofoils to keep the head aloft in flight.

In April 1991, a specimen of *Otomops* was collected from the island of Alor, near Timor, by a team from the Western Australian Museum and Balitbang Zoologi. This island is roughly equally distant from the locality of *O. formosus* in W. Java, and the localities of *O. papuensis* and *O. secundus* in Papua New Guinea (see Figure 1).

This paper provides a morphological description of this interesting *Otomops* specimen and considers its taxonomic status.

Taxonomy

Otomops johnstonei sp. nov.

(Table 1; Figures 2 and 3)

Holotype

Western Australian Museum No. M37986, adult male, weight 19.5 gm, skull and dentaries separate, carcase fixed in 10 percent formalin and preserved in 70 percent ethanol; liver and blood stored in ultrafreeze at Western Australian Museum. Purchased alive from villagers on 26 April 1991.

Type Locality

Desa Apui, Alor Island, Nusa Tenggara, Indonesia (08° 15′S, 124° 43′E); altitude *c.* 700m; collected from hollow in tree.

Figure 1: Distribution of *Otomops johnstonei* sp. nov. (■); *O. formosus* (▼); *O. papuensis* (●) and *O. secundus* (★).

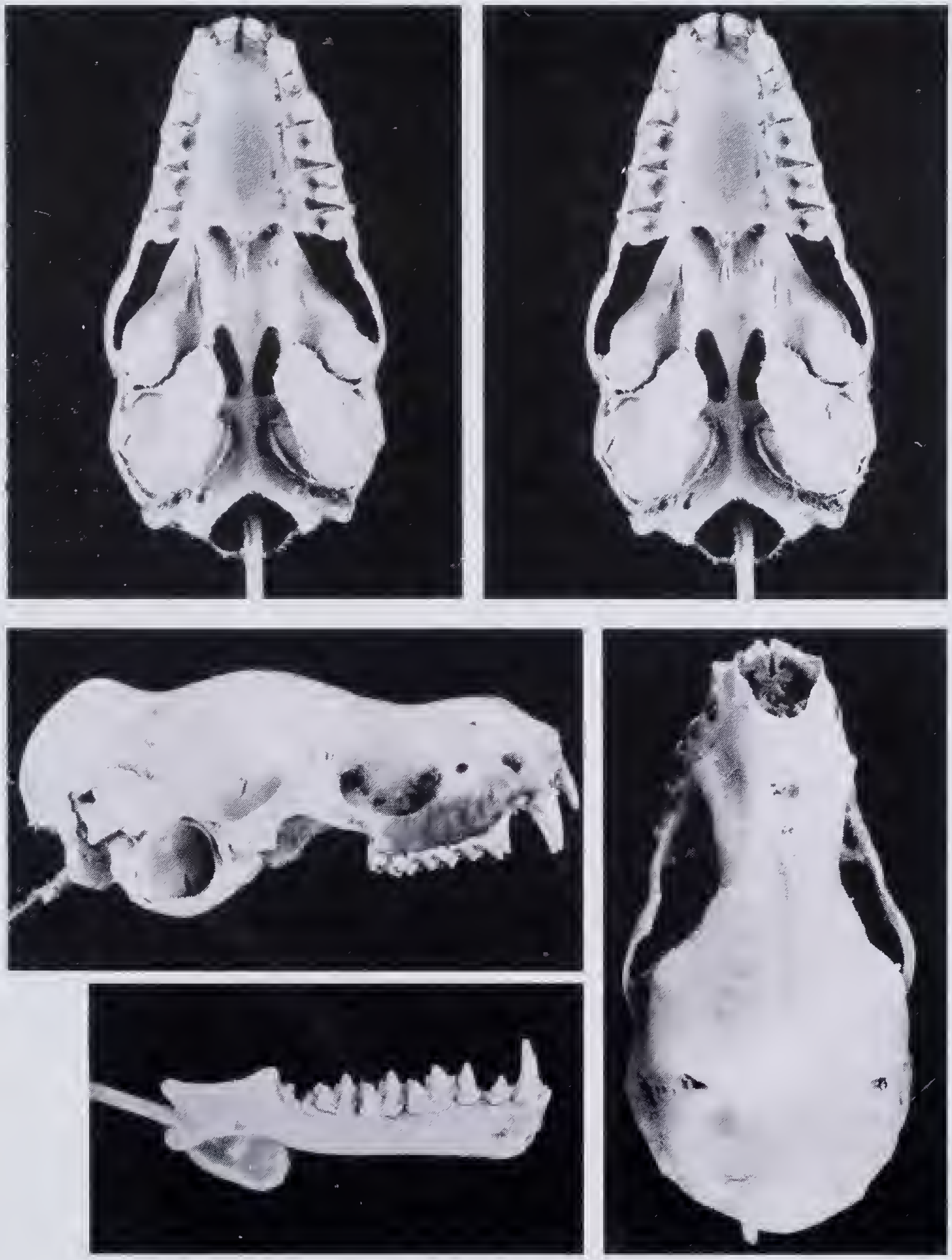

Figure 2: Skull, dentary and dentition of holotype of *Otomops johnstonei* sp. nov. in dorsal, ventral (as stereopair) and lateral view.

Diagnosis (measurements in mm)

Otomops johnstonei was compared directly to two specimens of *Otomops formosus* of similar age in the Museum Zoologicum Bogoriense (MZB 10643 and MZB 14796) It was also compared to photographs of the skull of the *O. formosus* holotype and measurements of this holotype and its paratype – provided by Dr C. Smeenk. It differs from *O. formosus* in having: the pelage at the top of its head the same dark colour as the lower back, rather than a lighter colour (see Chasen 1939); tail to vent length longer relative to head to vent length 0.550 *v.* 0.453-0.456; zygomatic width narrower relative to greatest skull length 0.509 *v.* 0.536-0.556; rostrum relatively narrow, e.g., C^1- C^1 breadth and ML^3-M^3 breadth narrower relative to palatal length 0.561 *v.* 0.600-0.650 and 1.024 *v.* 1.082-1.163, respectively; basial pits much larger, more elongate, much deeper with anterior roof of pit deeply excavated beneath basisphenoid shelf and not gently sloping downward to meet the edge of this shelf; anterior nasal openings much more flared laterally and narrowing more sharply dorsally; dentary angular process more flared laterally, longer; posterior upper premolar with anterolingual edge facing much more posteriorly; first lower premolar much smaller relative to second lower premolar, rounder in occlusal view.

It differs from the description of *O. papuensis* in Lawrence (1948) and Hill (1983) and photograph in Flannery (1990) in having an obvious pale mantle at the back of the neck and under the throat rather than merely a distinct but narrow pale band of hair; presence of a white patch of hair on both the inner (median) and outer base of ears; presence of a line of white hairs demarking margin of dark edge of dorsal pelage on plagiopatagium; all external measurements much larger: e.g., radius length 60.0 *v.* 49.2-50.2; ear length 31.1 *v.* 20.0-22.2; greatest skull length longer 23.0 *v.* 19.6-19.7; zygomatic width narrower relative to greatest skull length 0.509 *v.* 0.533; interorbital width narrower relative to greatest skull length 0.200 *v.* 0.220; much longer toothrow, e.g., C^1-M^3 length 8.6 *v.* 7.0-7.2.

It differs from the description of *O. secundus* in Hayman (1952) and Hill (1983) in having a patch of white hair on the base of the outer margin of the ear (also found in *O. wroughtoni* (Thomas 1913) and *O. martiensseni*); overall body measurements appear a little larger, e.g., radius length 60.0 *v.* 56.8-58.0; ears considerably longer 31.1 *v.* 23-25; tibia larger 17.3 *v.* 12.0-14.9; skull longer 23.0 *v.* 21.0-21.5; and toothrow much longer, e.g., C^1-M^3 8.6 *v.* 7.5-7.8; zygomatic width smaller relative to greatest skull length 0.509 *v.* 0.526; braincase narrower relative to greatest skull length 0.452 *v.* 0.479-0.533.

Description

Skull, dentary, dentition (Table 1, Figure 2)

The holotype of *O. johnstonei* is compared directly with two specimens of *O. formosus* from Cibodas, Java, from an altitude of 1450m (see also Boeadi 1990).

The skull of *O. johnstonei* is of similar length to that of *O. formosus* but is much narrower; it shares all the diagnostic characters of *Otomops*. It has deep and large basisphenoid pits; alisphenoid bulla projects anteriorly to contact pterygoid process; basioccipital deeply excavated laterally for cochlea; cochlea with marked mesial keel;

palate similar to *O. formosus;* premaxilla separate; mesopterygoid wide, almost concealing sphenorbital fissure when viewed from vertical ventral aspect, with blunt median posterior projection; weak lambdoidal ridge (much more so than *O. formosus*) that does not reach the tall, smooth nuchal crest; sagittal crest, from anterobasal point of nuchal crest to point of greatest interorbital constriction faint (more pronounced in *O. formosus*); supraorbital crests very slight, extend only *c.* 1.5mm anterior of sagittal crest and do not surround small but noticeable depression as in *O. formosus*; rostrum slender; lachrymal foramen covered dorsally with small protuberance; zygoma robust, with dorsal squarish projection from mid point; paraoccipital process upright, projects little posteriorly, terminates close to proximal part of occipital condyle; lateral part of mastoid sharply inclined posteroventrally, tympanic bulla considerably inflated ventrally; zygoma narrow, without external lateral flanges immediately posterior of M^3; dentary thin, very small ascending ramus; condyle almost in line with crowns of molar row; angular process long, distal tip well lateral of condyle, much more so than in *O. formosus*; dentition similar to O. formosus in overall proportions; M^3 with N-shaped commissures; incisors tall (1.52), sharply pointed with slight posteroexternal and posterointernal longitudinal grooves; C^1 tall (2.73), occlusal view with marked longitudinal antero- and postero-internal lingual ridges, the corresponding buccal ridges less sharply defined, surrounded by cingulum that is well developed lingually; first premolar small compared to *O. formosus* and more rounded, in contact with canine but not with posterior premolar; premolars with prominent protocones and hypocones, and lingual cingula; lower incisors in straight line; inner incisor with inner cusp approximately twice area of outer cusp; outer incisor sharply inclined against inner incisor row with inner cusp much larger and sharply sloping mesially towards first incisor row; lower canine anterior face smoothly curved but with a marked groove on either side of a sharp posterolingual ridge, surrounded by cingulum that is more developed internally and posteriorly; anterointernal edge of this cingulum with cusplet; first premolar occlusal area subequal to that of second premolar but with its crown height only about two-thirds that of posterior premolar.

Externals (Table 1, Figure 3)

Ears long (31.1), rounded, connected by band of furred skin over nose to form shallow pocket at midpoint of this connection; about 6.2 above rhinarium; antitragus prominent, *c.* 11.2 long, tragus minute, extra lobe on inner side of conch present but small, rounded inner margin of ear with 11-14 small horny excrescences and a number of smaller protuberances (*c.* 7) to apex of ear; upper lip exceeds lower lip by *c.* 7.0, lacks close wrinkling found in other molossid genera; lips drawn into several ill defined folds; a row of thickened short hairs *c.* 1.5 long from upper part of lip anterior to lower lip; tail moderately long (43.7); penis 5.5 long, finely furred but with a small tuft of hairs at its distal tip; glans penis 2.7 long, cigar shaped strongly ridged longitudinally on all surfaces; urethral opening ventral, *c.* 0.8 from its distal end, covered anterodorsally with moderately sharp fleshy part flanked on both sides at its distal end with low lateral fold.

Table 1: Skull, mandible, dentary and external measurements of the holotype of *Otomops johnstonei*. Measurement from other associated *Otomops* spp are provided from the literature.

Characters: Skull, dentary and dentition	*O. johnstonei* (holotype)	*O. secundus** (including holotype)	*O. papuensis*** (including holotype)	*O. formosus* (holotype) ***	 (paratype) ***	 MZB 10643	 MZB 14796
Sex	1♂	2♂, 4♀	1♂, 2♀	1♂	1♀	1♂	1♂
Greatest skull length	23.0	21.0-21.5 (21.3)	19.6-19.7	23.0(24)	23.3	23.7	23.0
Condylocanine length	21.1	19.3-19.9	17.9-20.2	20.6(21)	20.5	21.1	21.2
Basicranial length	19.4	–	16.2	19.3	19.5	19.9	9.4
Least interorbital breadth	4.6	(4.4)	4.3- 4.4	4.8	4.7	4.5	4.6
Zygomatic width	11.7	11.0-11.2 (11.2)	10.4-10.5	12.4(12.8)	12.5	12.7	12.8
Mastoid width	11.6	(11.2)	10.4-10.6	12.4	12.5	12.3	12.4
Bulla to top of braincase	10.8	9.9-10.1	9.7- 9.9	10.7	-	-	-
Mesopterygoid fossa breadth	3.3	(3.4)	3.0	3.5	3.7	3.4	3.5
Height jugal projection of zygoma	2.1		2.1	-	2.7	2.9	2.8
Palatal length	8.2	(7.5)	7.3	8.0	8.5	8.2	8.5
Distance between cochleae	1.3			2.2	2.1	1.5	1.6
Bulla length	6.6			6.0	5.7	-	6.5
Braincase breadth	10.4	10.9-11.2 (10.2)	9.4- 9.5	10.8(10.9)	10.4	10.6	10.7
Basisphenoid pit length	3.2		-		-	2.4	2.3
Dentary length, from condyle	15.0	13.1-14.0	12.2	16.1	15.4	15.7	15.4
C^1-C^1 breadth (alveoli)	4.6	4.2- 4.5	4.2	5.2	-	5.0	5.1
M^3-M^3 breadth (alveoli)	8.4	8.0	7.9	9.3	9.3	9.3	9.2
M^1-M^3 length (cusp)	5.0			6.0	6.9	5.3	5.2
I^3-M^3 length (cusp)	9.4	8.6- 8.7	8.2- 8.5	10.0	9.6	9.6	9.5
L^1-M^3 length (cusp)	8.6	7.5- 7.8 (7.5)	7.0- 7.2	8.4(8.5)	8.5	8.7	8.6
C^1-M^3 length (cusp)	8.9	8.0- 8.2	7.5- 7.7	9.1	-	9.3	9.3
M^3 length	1.3	(1.2)	1.2	1.4	1.4	1.3	1.4
M^3 width	2.1	(1.6)	1.8	2.3	2.3	2.0	2.2

Table 1: cont.

Characters: Externals	*O. johnstonei* (holotype)	*O. secundus** (including holotype)	*O. papuensis*** (including holotype)	*O. formosus* (holotype) ***	(paratype) ***	MZB 10643	MZB 14796
Sex	1♂	2♂, 4♀	1♂, 2♀	1♂	1♀	1♂	1♂
Wt (gm)	19.5					26	27
Radius length	60.0	57 -58 (56.8)	49.2-50.2	58.3(59.7)	57.4	60.5	56.5
Head to vent length	79.4	68 -71 (72)	(86)		86+	79+	
Tail to vent length	43.7	33 -38 (35)	30	(43)		39+	36+
Ear length	31.1	23.0-24.3 (25)	20.0-22.2	(30)		28.6	28.4
Pes length (without claw)	11.9	10 (9)	10.0-10.6	}		10.0	10.9
Tibia length	17.3	12.0-14.9 (14)	–	} c. (29)		16.5	16.6
Calcar length	18.1					14.6	-
MCII (metacarpal, digit II)	59.1					60.8	56.9
MCIII	60.3	- (57.4)	50.8			62.6	58.5
MCIII/phalanx 1 length (PI)	23.7	- (20.3)	18.8			23.6	22.1
MCIII/PII	23.2	- (20.1)	16.9			22.4	21.8
MCIII/PIII	5.4					5.5	6.8
MCIV	55.7	- (53.0)	47.2			57.8	54.6
MCIV/PI	14.6	- (12.9)	11.7			15.1	14.7
MCIV/PII	11.4	- (8.6)	8.5			11.8	10.5
MCV	29.8	- (27.8)	25.3			30.9	29.9
MCV/PI	20.4	- (17.9)	15.8			18.1	17.9
MCV/PII	8.6	- (7.8)	7.6			7.6	8.7

* from Hayman (1952) and Freeman (1981), measurements in brackets are average of 1♂ and 1♀ — from Freeman (1981)

** from Lawrence (1982) and Hill (1983)

*** recorded by Dr C. Smeenk (followed in brackets by measurements from Chasen 1939)

\+ from Boeadi (1990)

Figure 3: Photograph of *Otomops johnstonei* sp. nov. while alive (photo R.E. Johnstone and R.A. How).

Pelage

Described from carefully dried alcohol specimen; the colours produced were those of the live specimen which is confirmed by coloured photographs taken of the live animal. Colours described following Ridgway (1912) are capitalised.

Head covered with moderately long hair (5.5), Clove Brown (dark brown) overall but with basal one-third White; wide integument that connects ears, furred with Clove Brown to its anterior margin; anteriormost contact of this integument with ear marked with small patch of White hairs; posterior external edge of ear also marked by small patch of White hair; Clove Brown of head extends to base of neck where it is sharply demarked from a narrow band of long (10.5) Tilleul Buff to Vinaceous Buff (light-greyish buff) hairs. This mantle extends to mid back region as triangle of shorter (*c.* 5.0) hairs with a Smoke Gray (light grey) Wood Brown (grey brown) mottled effect. Lower back and flanks to distal half of tibia Clove Brown. This colour forms a sharp line with plagiopatagium from which it is sharply demarked by a thin line of Smoke Gray. A clear wide stripe of Clove Brown hairs on dorsal propatagium sharply demarked on anterior edge and weakly on posterior edge by thin line of Smoke Gray hairs; thin line of Wood Brown hairs on dactylopatagium along radius outer dorsal edge. Upper lip of face with distal end fringed with short drab coloured hairs. Ventral surface overall a Wood Brown but tipped with Smoke Gray in region of neck and chest, basal one-quarter of these hairs White.

Etymology

Named after our colleague Mr Ronald Eric Johnstone, Western Australian Museum. In recognition of his tremendous assistance and good companionship in the field on seven expeditions to Nusa Tenggara between May 1988 and May 1991.

Remarks

We were fortunate to be able to directly examine two specimens of *O. formosus* from Java. These agree closely with the type description of that species and with measurements and photographs of the *O. formosus* holotype provided by Dr Smeenk.

Previously, when Hayman (1952) described *O. secundus* from Papua New Guinea he noted that "further collection in New Guinea and other parts of the Indo-Australian Archipelago may eventually bring to light intermediate forms and so reduce to subspecific rank some of the named species". The Alor specimen, which is geographically located roughly equidistant between the Papuan and Javan *Otomops* species, tend to reinforce the specific status of the two New Guinea species, both of which appear distinct from the Alor specimen on the basis of their quite adequate descriptions and the skull illustration in Flannery (1990) of *O. papuensis*.

Java has at some time in the Pleistocene almost certainly been joined through Nusa Tenggara to Alor by dry land connections or, at most, very narrow water gaps in the Inner Banda Arc have separated these islands (Kitchener *et al.* 1990). Thus potential recently existed for ready exchange of genes between populations of bats throughout these islands. Despite this potential, our recent taxonomic studies indicate that a number of species or subspecies are endemic to Nusa Tenggara (Kitchener *et al.* 1991, a, b, c, d, e; Kitchener and Maharadatunkamsi 1991, and unpublished data). When these recent discoveries are added to the known endemic rodent and bat fauna in Nusa Tenggara (see Kitchener *et al.* 1990), it is obvious that a number of mammal speciation events have occurred *in situ* in this region. It is not surprising, then, to find that the form of *Otomops* on Alor I. is distinct from that on W. Java.

Acknowledgments

We are particularly grateful for the meticulous care with which Dr Chris Smeenk, Natuurhistorisch Museum, Leiden, compared our description of *O. johnstonei* with the holotype of *O. formosus*; and to the provision to us by Dr Smeenk of photographs of this holotype.

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Mrs N. Cooper, Western Australian Museum prepared the plates.

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Sexual dimorphism in the osteology and myology of monacanthid fishes

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Abstract

Sexual dimorphism in the body form of some monacanthid taxa is very pronounced. The female is usually deeper bodied with a more concave snout profile than the more streamlined male. In addition, the second dorsal and anal fins of the female are generally less elevated anteriorly than those of the male. These differences are reflected in variations of the underlying bones and muscles, particularly those adjacent to the bases of the second dorsal and anal fins. These differences are described and the reasons for them discussed.

Introduction

Differences in morphology between males and females of many species in the family Monacanthidae, commonly known as leatherjackets and filefishes, have caused considerable confusion in the past. Some of these differences now are better known, especially those involving body colour and scale structures (e.g., Randall 1964; Hutchins 1977, 1986; Tyler 1980). However, one which has received less attention in the literature entails the overall shape of the fish. Males of numerous species are usually more elongate than females, and possess convex dorsal profiles to the head, as against a more concave profile in females (Figure 1). These differences are further accentuated by the shape of the second dorsal and anal fins. The anterior portion of each fin often is prominently elevated in males, producing an elongate, swept-back lobe, whereas in females, these fins usually are much lower, the anterior fin rays sometimes being only a little longer than the middle rays (Figure 1). This has led some workers to recognise males and females of the same taxa as separate species (e.g., Fraser-Brunner 1941; Masuda et al. 1975; Hutchins 1977; Kotthaus 1979). This situation recently was explored in detail as part of a larger study on the morphology and phylogeny of the family (Hutchins 1988); however, much of that investigation still remains unpublished. The purpose of the present paper, therefore, is to report on this sexual dimorphism, and show how it is related to hitherto unreported differences in osteology and musculature that appear to be unique to the family.

Methods

Specimens of 96 of the 97 species considered valid (Hutchins 1988) were examined using radiography, whole skeletons, and cleared and stained material. For the last-mentioned examination, specimens were prepared following the trypsin digestion method of Taylor (1967). (The largest specimen cleared and stained was 105 mm SL). Where possible, the material examined for each species included adults of both sexes and unsexed juveniles.

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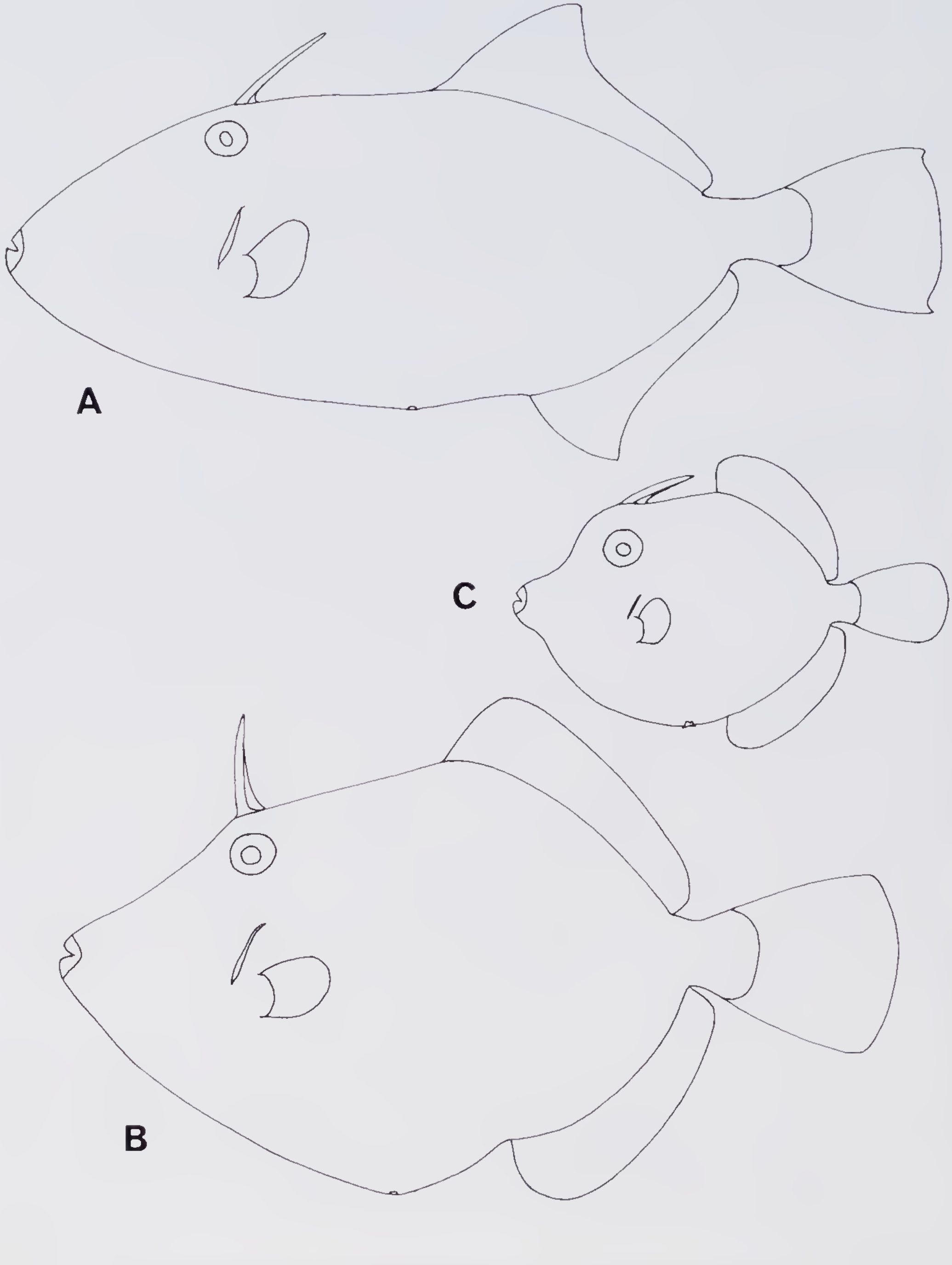

Figure 1 *Eubalichthys mosaicus* showing external differences in body form between A, male, 410 mm SL; B, female, 287 mm SL; and C, juvenile, 43 mm SL.

Results

A total of 57 species showed some form of sexual dimorphism in body and fin shapes, of which 21 species displayed significant variations. Twelve of the latter belong to the genera *Eubalichthys* (four species) and *Paramonacanthus* (eight species). The following synthesis is based on the examination of these taxa.

Internal scrutiny revealed obvious sexually related differences in the shape of the neural and haemal spines of the anterior vertebrae, the positioning of the basal pterygiophores of the second dorsal and anal fins, the size of the rounded spaces located distally between these basal pterygiophores (referred to hereafter as the interpterygiophore spaces), the shape of both the basal pterygiophore of the first dorsal fin and the ethmoid, the structure of the muscles controlling the anterior fin rays of the second dorsal and anal fins, the size of these fin rays and their basal flanges, and the shape of the pelvis. These differences are presented in more detail below.

The four predorsal neural spines of the male are often deformed when compared with those of the female (Figures 2A,B). The spines are more compressed and bent over in the male, the distal ends being deflected posteriorly (the predorsal neural spines of the female also may be curved posteriorly, but generally are shaped more like those of the juvenile [Figures 2B,C]). In some cases, the posterior two predorsal spines of the male are prominently distorted as if crushed (Figure 2A). Furthermore, the subsequent vertebrae may possess dorsal and haemal spines that are more slender in the male than in the female (Figures 2A,B), and, in some species, directed more obliquely rearwards. These differences all appear to be related to the position of the basal pterygiophores of the second dorsal and anal fins (referred to below as the dorsal and anal pterygiophores respectively). In the female and juvenile, the inner extremities of the anterior pterygiophores are always well separated from the centra of the vertebrae (Figures 2B,C). In the maturing male, however, the pterygiophores apparently migrate inwards as the fish grows, pushing over and partly enveloping the neural and haemal spines, and eventually reaching almost to the centra of the vertebrae (Figure 2A). Also, the vertebral spines of the male generally are less robust than those of the female, and thus are more easily deformed as a result of this inwards movement (the movement of the large anteriormost dorsal pterygiophore probably exerts sufficient force on the adjacent vertebrae in some species to almost crush their neural spines). These changes affect only the anterior 10 or so vertebrae of the male, most of which are positioned beneath the elevated portions of the second dorsal and anal fins. The more posterior vertebrae are similar in shape to those of the female.

The interpterygiophore spaces — usually circular to oval in shape — are greatly enlarged anteriorly in the male, but much smaller in size posteriorly (Figure 2A). In the female and juvenile (Figures 2B,C), the spaces are more uniform in size. It appears that as the male matures, bone surrounding the interpterygiophore space is reabsorbed, causing the space to become larger. Even the distal tips of the adjacent neural spines are affected by this absorption (Figure 2A). These enlarged interpterygiophore spaces occur only beneath the elevated portions of the second

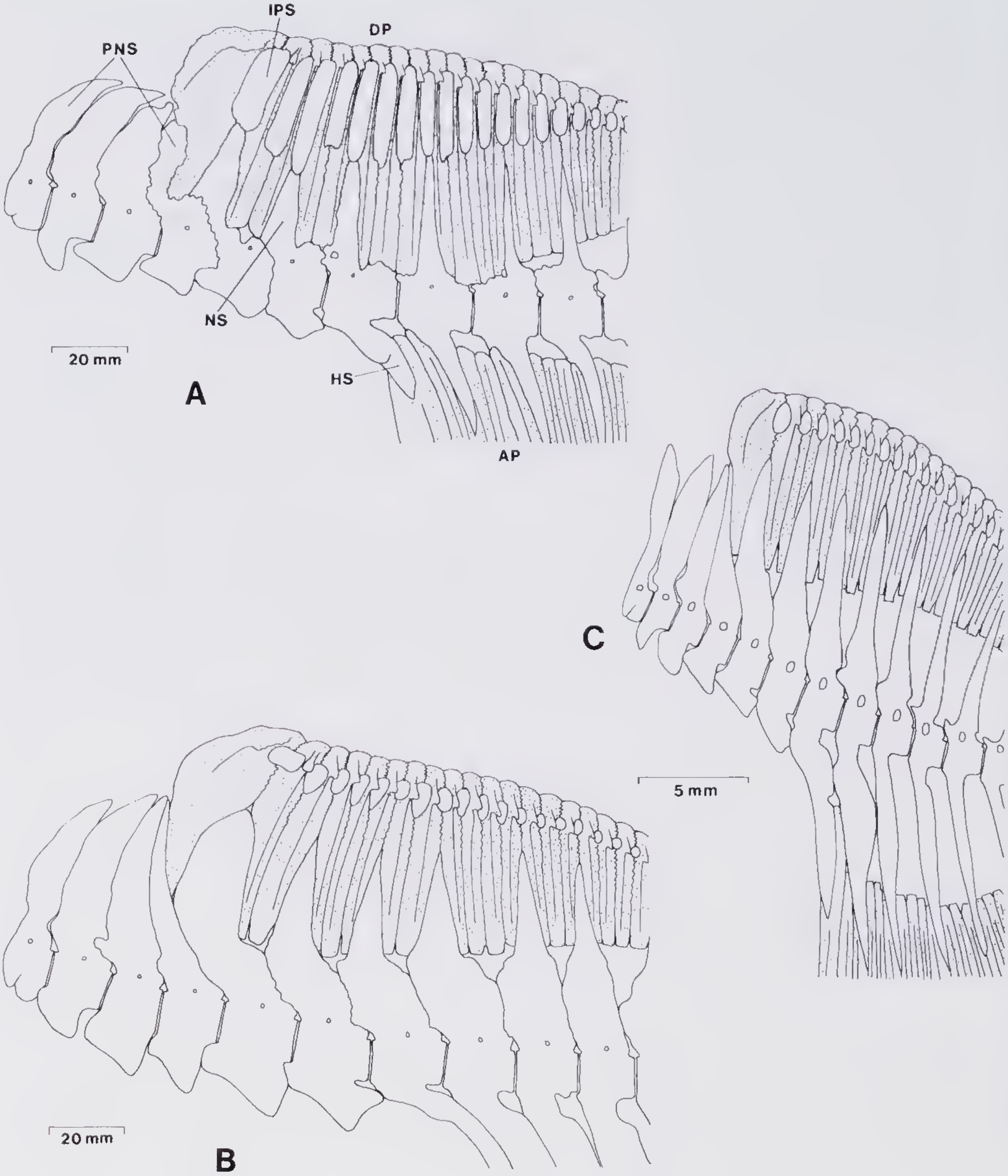

Figure 2 *Eubalichthys mosaicus*, lateral view of anterior portion of axial skeleton showing differences in vertebrae and pterygiophores of A, male, 410 mm SL; B, female, 420 mm SL; and C, juvenile, 53 mm SL (anteriormost vertebra and epipleural ribs not shown, anterior end faces left, and pterygiophores stippled; abbreviations — AP, anal pterygiophores; DP, dorsal pterygiophores; HS, haemal spine; IPS, interpterygiophore space; NS, neural spine; PNS, predorsal neural spines).

dorsal and anal fins of the male. The largest interpterygiophore space is usually associated with the longest fin ray.

Changes to the head shape mostly involve the dorsal profile (lateral view) of the snout and forehead. In the female and juvenile, the dorsal profile of the head is usually straight to concave, whereas in the male it is more convex. This is due to differences in the shape of both the basal pterygiophore of the first dorsal fin, which is located on the dorsal surface of the cranium, and the ethmoid. The pterygiophore of the male generally is longer and lower in height than in the female, the condition in the latter being similar to that of the juvenile; the dorsal profile of the ethmoid in the male is more convex than in the female. In addition, the males of some species of *Paramonacanthus* usually develop a prominent dorsal ridge on the ethmoid which further accentuates the convexity of the snout.

Males of some taxa that are small enough to clear and stain (*Paramonacanthus*) possess certain lateral muscle bands which do not clear in trypsin. The muscles controlling the movement (erectores dorsales and anales, and depressores dorsales and anales, see Winterbottom 1974) of the elevated fin rays of the second dorsal and anal fins remain a translucent brownish colour to almost opaque (Figure 3A), whereas the remaining muscles of the male, as well as all muscle tissue in the female and juvenile, become totally transparent (Figure 3B). Furthermore, when freshly killed male specimens are heated in boiling water (i.e. cooked), these non-clearing muscle bands turn a noticeably more greyish colour than the surrounding flesh which typically is white.

The elevated portions of the second dorsal and anal fins of the male consist of noticeably thickened rays (Figure 3A). The bases of these fin rays possess enlarged, mushroom-shaped ventral flanges, one to each ray. However, the more posterior rays, as well as all fin rays of the female and juvenile, are narrower and possess only small ventral flanges (Figures 3A,B). Furthermore, the distal ends of the dorsal and anal pterygiophores that support these enlarged flanges also are noticeably thickened, a condition not found in the more posterior pterygiophores of the male, nor in any of the pterygiophores of the female and juvenile.

The monacanthid pelvis lies just under the skin along the ventral profile of the abdomen. Sexual dimorphism is sometimes evident in the size of the dorsal lobe near the rear end of the pelvis (small in the female and the juvenile, relatively large in the male) and the shape of the pelvic shaft. In several species of *Eubalichthys*, for example, the shaft is noticeably curved in the deep-bodied female and juvenile, but is much straighter in the more slender male (Figure 4).

In some male individuals of *Paramonacanthus*, sexual dimorphism is not always as obvious as indicated above. These males may be only slightly deeper than the typical female form, with a rather straight snout, and the fin rays only a little more elevated. The sizes of the interpterygiophore spaces also are only slightly larger in these examples, and the inner extremities of the basal pterygiophores do not reach the neural and haemal arches. Furthermore, the muscles associated with the elevated

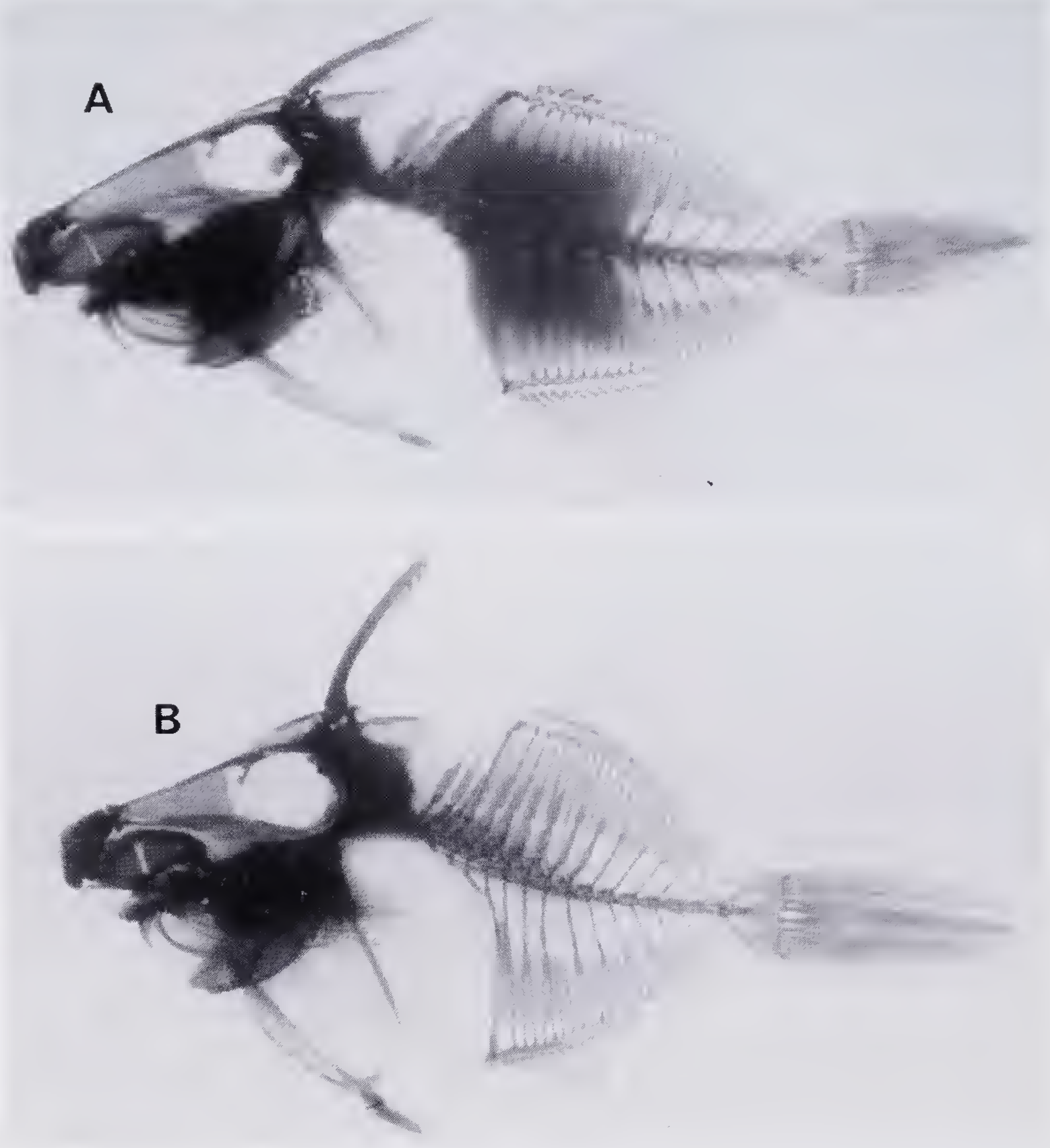

Figure 3 *Paramonacanthus nematophorus* (cleared and stained) showing differences in osteology and musculature between A, male, BPBM 19815, 57 mm SL; and B, female, BPBM 19815, 35 mm SL.

portions of the fins are more likely to clear after treatment with trypsin. Nevertheless, internal gross examination of these deeper-bodied males indicate that they possess apparently normal testes.

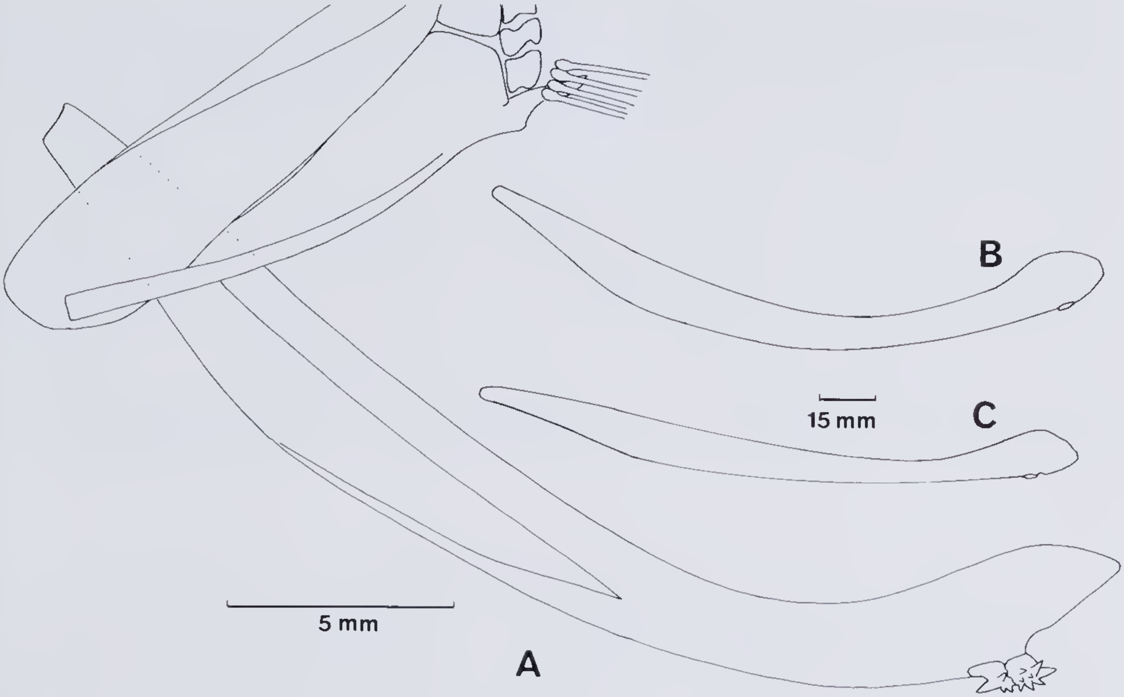

Figure 4 *Eubalichthys mosaicus* showing differences in shape of pelvis (anterior end facing left) between A, juvenile, 53 mm SL (portion of pectoral girdle also illustrated); B, female, 350 mm SL; and C, male, 340 mm SL.

Discussion

The sexual dimorphism outlined above attests to the similarity in body form between the adult female and juvenile, whereas the adult male of some monacanthid species is often more streamlined. This is effected by osteological changes that occur in the male with increasing size. The reduction in height of the predorsal neural spines, inwards movement of the basal pterygiophores of the second dorsal and anal fins, increased size of the interpterygiophore spaces, straighter pelvis, and changes in shape of the head bones all contribute to the male's more elongate shape. Furthermore, as some of these changes occur only in the region beneath the elevated portion of both the second dorsal and anal fins, it can be presumed that there must be a relationship between the shape of the male's body, its elevated fin rays, and the non-clearing musculature associated with these rays. What could be the possible benefits of this to the male?

The second dorsal and anal fins are the primary means of propulsion in monacanthids. However, in those species with obvious sexual dimorphism in the shape of the fins, the method of propulsion also varies between the sexes. Whereas the fins of the female and juvenile propel the fish by moving in an undulatory motion along the length of the fin, underwater observations show that the male can achieve additional propulsion by moving the anterior elevated portions of the fins from side to side in a flapping motion. To achieve this, the muscles controlling the elongate fin rays would have to be capable of producing a greater energy output, which in turn would require a greater vascularization of the muscle tissue. Thus the condition of these muscles could be due to a higher haemoglobin content. (It is noteworthy that both the major blood vessels and the highly vascularized gills also do not clear in trypsin in either sex, remaining a dusky colour similar to the muscle tissue of the male). This finding is also supported by the thicker anterior fin rays and larger ventral flanges, which suggests that these rays have been strengthened for more powerful swimming.

It may be concluded, therefore, that the advantage to the male of its more slender shape and elevated fin rays must be an increase in its swimming ability. Furthermore, those males which have deeper bodies and less elevated fins would appear to be competitively at a greater disadvantage than their more streamlined relatives.

Acknowledgements

Many people too numerous to mention individually contributed to this investigation by providing specimens and/or information on the material in their care. My thanks go to all of them. In particular, I wish to acknowledge the assistance of J.C. Tyler (USNM) and R. Winterbottom (ROM) who provided me with information on the osteology and myology of monacanthids, and J.E. Randall (BPBM) for the many specimens he made available. I am especially grateful to L. Laurenson who volunteered his time to assist with the clearing and staining programme. Technical assistance over the period of the study was provided by N. Sinclair, N. Haig, and K. Smith (all at WAM).

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A history of Western Australian meteoritics

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Abstract

The first documented Western Australian meteorites were a number of irons, the first of which was found in 1884 when agriculture was being established east of the early settlement at York. These became known as the "Youndegin meteorites" after a police station which was the last outpost of civilisation at the time. Some of these large specimens were taken to London to be sold as scrap metal, but fortunately were recognised as meteorites and acquired by various museums around the world.

Despite the sparse population and relatively recent time of settlement by Europeans, a number of factors have led to Western Australia's excellent record of meteorite recovery. Firstly the large regions of arid country enable meteorites to be preserved for long periods of time and recognised against the country rocks; secondly as far as can be ascertained the Aboriginal people of Australia showed little interest in meteorites; and thirdly Western Australians have presented their discoveries to the Western Australian Museum in recognition of their value to science.

The person responsible for laying the foundation for the State's meteorite collection was Dr E.S. Simpson who, as Government Mineralogist from 1922 to 1939, collected and analysed many of the meteorites which today form the basis of the collection. The first catalogue describing Western Australian meteorites was published in 1965. It described 48 Western Australian meteorites, 29 of which were irons. The large number of irons probably resulted from their long terrestrial ages and the ability of people to recognise them. The small proportion of falls to finds (2 in 48) is probably due to the sparse population of the State. Interest in meteoritics was enhanced in the 1960s so that when the 2nd Supplement to the Catalogue was published in 1972, 92 meteorites were recorded, most of the additional discoveries being stones.

The Nullarbor Region in the Eucla Basin has been a 'happy hunting ground' for meteorite collectors. To date, 78 distinct and well-documented meteorite finds are recorded from this region, and since 1971, in excess of 500 individuals and fragments of meteorites have been recorded from the Eucla Basin. The doyen of Western Australian meteorite collectors is undoubtedly Mr A.J. Carlisle, who has lived and worked in the Nullarbor Region for much of his life. Specimens from approximately 80 distinct meteorites have been found by members of the Carlisle family.

Introduction

In September 1990 the 53rd Annual Meeting of the Meteoritical Society was held in Perth. This was an historic occasion because it was the first time in the history of the Society that an Annual Meeting had ever been held outside North America or Europe. Perth was chosen because of the acknowledged excellence of the meteorite collection,

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the opportunity for field trips in Western Australia, and the presence of a group of meteoriticists who were prepared to organise the meeting.

The Annual Meeting was an undoubted success with approximately 250 delegates in attendance and over 160 papers being presented. A unique 20 day Australian Craters Expedition was organised under the leadership of Drs E.M. and C.S. Shoemaker, with a full attendance of 50 delegates. Other field trips were offered after the Meeting. This meeting of the Meteoritical Society, under the Presidency of Dr S.R. Taylor (ANU), has stimulated meteorite research in Australia and will undoubtedly herald a new era in meteoritics in Western Australia, including an enhanced display of meteorites in the Western Australian Museum. It therefore seems appropriate to record the history of meteorites in Western Australia at this time.

The earliest meteorites found in Western Australia were a number of irons, the first of which was discovered in 1884 when agriculture was being established east of the early settlement at York. These were named the "Youndegin meteorites" after a police outpost in the district, although they were actually found some 1300 metres northwest from Penkarring Rock, now known locally as Pikaring Hill (as shown in Figure 1).

The first specimen (designated *Youndegin I*) was found on 5th January 1884 by a mounted policeman named Alfred Eaton, whilst on duty in the Youndegin area. The Curator of the Geological Museum in Fremantle, the Rev. Charles G. Nicolay, requested the Commissioner of Police in Perth to send Mr Eaton back to Penkarring Rock to search for additional specimens, three of which had been observed at the time of the initial discovery. These fragments (*Youndegin II-IV*), together with a considerable amount of weathered iron oxides, indicated that the specimens had lain on the surface for some time and probably represented a single, disintegrated mass. Reverend Nicolay presented *Youndegin I* and *IV* to the British Museum, and this enabled Fletcher (1887) to confirm that the *Youndegin* irons were in fact meteorites. He also carried out a chemical analysis on *Youndegin I*, and identified a cubic form of graphitic carbon in the specimens, which he called "cliftonite". This was the first scientific publication describing a Western Australian meteorite. Further specimens of the Youndegin meteorite were found in 1891 (*Youndegin V*) and in 1892 (*Youndegin VI*). These masses were sold to a London mineral dealer (Gregory 1892), but the specimens were later acquired by the Field Museum of Natural History in Chicago and the Naturhistorisches Museum in Vienna, respectively. An additional mass, *Youndegin VII*, was found in 1929, as were a number of fragments collectively known as *Youndegin VIII*. One of these fragments was made into a horseshoe which hung in a blacksmith's shop in York for many years (Simpson 1938).

Some iron meteorites found later in the same district were not given the name "Youndegin". In 1892, two pieces of Youndegin were found to the east of Pikaring Hill and were given the name *Mount Stirling*. Other meteoritic fragments named *Mooranoppin I* and *II*, were found to the north of Pikaring Hill in 1893 and 1933, respectively (Simpson 1938). The largest mass of the Youndegin meteorites, a 2626 kg iron, was found in 1903, and named *Quairading*, although it was not presented to the

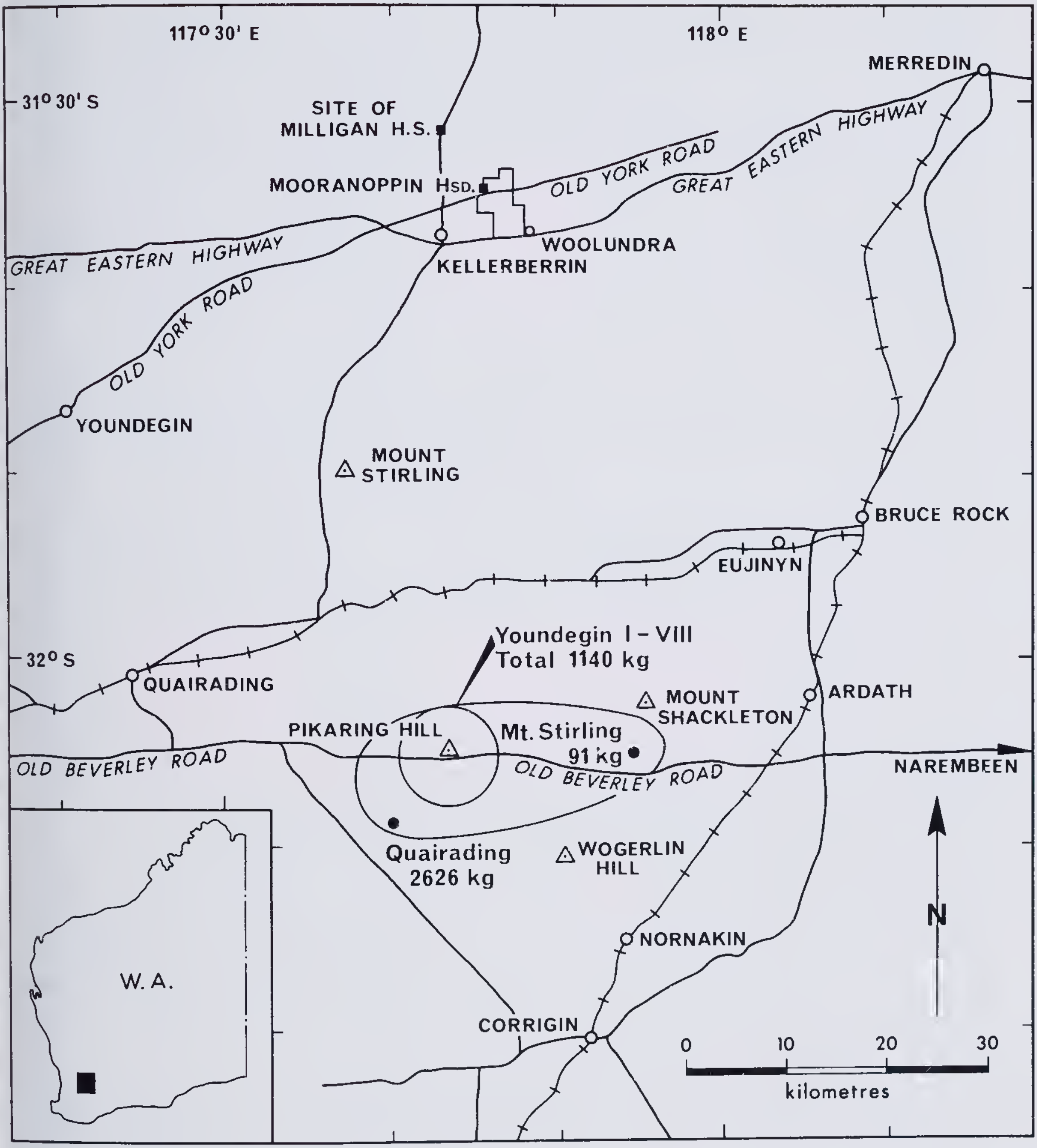

Figure 1 Map of part of Western Australia showing the location of specimens comprising the Youndegin meteorite shower (after Cleverly and Cleverly 1990).

Western Australian Museum until 1954, having been rediscovered during farming operations using a World War II General Grant tank. The most recent member of the Youndegin meteorites, weighing 4.66 kg, was donated to the Quairading District High School in the early 1970's and was identified by De Laeter and Hosie (1985). A detailed examination of the microstructure and chemical composition of the meteorites listed in Table 1 (De Laeter 1973a) showed that they belonged to chemical group IA (Wasson 1974), and were all part of the Youndegin meteorite shower, which probably resulted from the atmospheric disruption of a meteoroid travelling in a south-westerly direction. Cleverly and Cleverly (1990) have recently re-examined the provenance of the Youndegin meteorite shower and delineated a tentative strewnfield (shown in Figure 1), which they believe indicates atmospheric passage in a westerly direction.

It is of interest to compare the elemental concentration in weight percent of nickel and cobalt in the Youndegin meteorites determined by present day analytical methods with the values given by Fletcher (1887) to ascertain the accuracy of the chemical procedures used in the 19th Century. The values given by De Laeter (1973b) vary from 6.47%-7.08% and 0.44%-0.46% for nickel and cobalt respectively, whereas Fletcher (1887) gives corresponding values of 6.46% nickel and 0.55% cobalt for *Youndegin I*. It is apparent that the nickel values compare well, whilst the cobalt abundance determined by Fletcher (1887) is higher than the presently accepted value.

Several thousand specimens from 141 distinct meteorites have been found in Western Australia and described to date. This represents a recovery rate about four times greater than the World average on an aerial basis. More than 50% of all meteorites known from Australia have been recovered from Western Australia (Bevan 1992). A sparse population and relatively short history of settlement by Europeans in Western Australia (from 1829), makes this situation all the more surprising. Furthermore, many of the earliest recoveries of meteorites were sent to the British Museum or sold to other museums. Table 1 indicates that only 4 of the 14 masses of the Youndegin meteorites reside in the State, and only three in the collection of the Western Australian Museum. The absence of a Geological Museum in this State has also been a mitigating factor, for until the 1960s there was little interest in exhibiting meteorites at the Western Australian Museum and until 1985 there was, in fact, no permanent Curator of Meteoritics.

On the other hand, there are a number of factors which have contributed to the excellence of the Museum's collection:

1 The large regions of arid country, which constitute much of Western Australia, enable meteorites to be preserved for long periods of time after falling to the Earth's surface, and to be more easily recognised than in heavily vegetated terrain. The large areas of ploughed farmland also increase the probability of finding meteorites, whilst the vast extent of the Nullarbor Region, with its lack of vegetation and distinctive limestone country rocks, has proved to be an ideal location for finding meteorites.

2 As far as can be ascertained, the Aboriginal people of Australia were not interested in meteorites, either as objects of reverence or for their use as metals, whereas in other countries with ancient civilizations, meteorites have been collected and used for a variety of purposes over many centuries.

3 The excellent record of recovery of meteorites is a tribute to Western Australians who, in the main, have presented their discoveries to the Museum in recognition of their scientific value.

4 The Western Australian Museum Amendment Act of 1973 gives legal ownership of meteorites found in the State to the Crown, whilst the unauthorised export of meteorites from Australia is prohibited by Federal Legislation in the Protection of Movable Cultural Heritage Act (1986).

Table 1: Details of the Youndegin Meteorites

Name	Main Mass Kg	Date of find	Location of main mass
Youndegin I	11.7	1884	British Museum, London: 9.82 kg
Youndegin II	10.9	1884	National Museum, Melbourne: 10.9 kg
Youndegin III	7.9	1884	Western Australian Museum: 5 kg
Youndegin IV	2.72	1884	British Museum, London: 2.7 kg
Youndegin V	173.5	1891	Field Museum, Chicago: 141 kg
Youndegin VI	927	1892	Naturhistorisches Museum, Vienna: 927 kg
Youndegin VII	4.1	1929	Government Chemistry Centre of WA: 3.9 kg
Youndegin VIII	13.6	1891-1929	Private Collections
Mooranoppin I	1.6	1893	Ward-Coonley Collection: 1.1 kg
Mooranoppin II	0.82	1933	Western Australian Museum 0.725 kg
Mount Stirling	92.3	1892	Australian Museum, Sydney: 67.2 kg
	0.68	1892	Australian Museum, Sydney: 0.42 kg
Quairading	2 626	1903	Western Australian Museum: 2 626 kg
Quairading High School Specimen	4.66	1972	Quairading High School: 4.66 kg

Details of the Collection

The first catalogue of Australian meteorites was published by Anderson (1913). Western Australian meteorites listed in this catalogue comprised seven irons, including six specimens of Youndegin. The total number of distinct meteorites in the various Australian collections was 46, including 29 irons. The second Australian meteorite catalogue was published by Hodge-Smith (1939). It lists 20 irons (comprising 27 separately named specimens), one stony-iron and four stony meteorites from Western Australia. All these meteorites are finds, except perhaps for Gundaring which may have been seen to fall on 30 April 1930, although it was not recovered until 20 May 1937 (Simpson 1938). There is sufficient doubt about Gundaring to exclude it as a fall (see Table 2). Simpson (1938) described each of the Western Australian meteorites listed by Hodge-Smith (1939).

The first catalogue of Western Australian meteorites was published by McCall and De Laeter (1965). The number of iron meteorites had by then increased from 20 to 29, the number of stony-irons from one to four, whilst the number of stony meteorites had risen from 4 to 15. Two falls were listed — Gundaring and Woolgorong. Although the number of iron meteorites still dominate the Collection, there are now a significant number of stones. The large number of irons probably resulted from their long terrestrial ages and the fact that they are more easily recognised as meteoritic than are stony meteorites. The small proportion of falls to finds (2 in 48) is undoubtedly due to the sparse population of the State.

Community interest in meteorites was enhanced in the early 1960's, in part by the formation of a Meteorite Advisory Committee, so that when the Second Supplement to the Catalogue was published (McCall 1972), 92 meteorites were recorded, with most of the additional finds being stones. Details of the number and type of meteorites comprising the Western Australian Collection, are given in Table 2. There are presently 28 irons, 8 stony-irons, 101 chondrites and unclassified stones, and four achondrites. Of the total of 141 distinct meteorites currently recognised, only four are falls. These are all stones — Binningup (30th September, 1984), Millbillillie (October, 1960), Wiluna (2nd September, 1967) and Woolgorong (20th December, 1960). There are also three meteorite impact craters associated with meteorites — Dalgaranga, Veevers and Wolf Creek.

The person who was instrumental in laying the foundation for Western Australia's meteorite collection in the first forty years of this century was Dr E. S. Simpson who, for the period 1922 to 1939, was Government Mineralogist and Analyst. Although mostly remembered for his pioneering work on Western Australian minerals, he also collected, analysed and reported details of most of the meteorites found during this period of time, and ensured that they were placed in the Museum's Collection. The present status of the Western Australian Meteorite Collection owes much to the pioneering efforts of Dr Simpson.

During the period 1940 to 1960 a number of meteorites were recovered. These included Dalgety Downs and Mount Egerton (1941), Forrest Lakes (1948), Cocklebiddy (1949), Haig (1951), Duketon and Lake Grace (1956), Wingellina (1958), *Bencubbin II* and Lake Moore (1959), and Woolgorong (1960), in addition to the large '*Quairading*' mass of the Youndegin meteorite (1954).

The most remarkable discovery during this period was undoubtedly the Wolf Creek crater. Recognised from the air in 1947, it was described by Reeves and Chalmers (1949) and Guppy and Matheson (1950). Shale balls, representing the deeply weathered remnants of iron meteorites, were recovered from the site by Cassidy (1954). Taylor (1965) describes unaltered meteoritic material located at the Wolf Creek crater, which is roughly circular in shape with a diameter of 880m. The crater is situated within a roughly circular mound and is 40-55m deep, but is partially filled with wind-blown sand and gypsum (Figure 2).

Figure 2 The Wolf Creek Meteorite Crater which is located some 106 km south of Halls Creek in Western Australia. The diameter of the crater is approximately 880 m and it is 40-55 m in depth

The only other crater known at this time was Dalgaranga, which is approximately 24m in diameter and 3m in depth. It was discovered in 1923 by Mr G.E.P. Wellard, and has stony-iron and metallic fragments associated with it. Simpson (1938) gave a brief description of the crater and details of the chemical analysis of a metallic fragment found in the crater. Subsequently, Nininger and Huss (1960), gave fuller details of the Dalgaranga Crater. Another meteorite crater — Veevers Crater — is located between the Great Sandy and Gibson Deserts. It has a diameter of some 70m (Shoemaker and Shoemaker 1988).

Through the 1960's, interest in meteoritics in Western Australia was revitalised by a group of physicists at the University of Western Australia led by Dr P.M. Jeffery, who was searching for isotopic anomalies in meteorites (e.g. see De Laeter and Jeffery 1965). This research group encouraged G.J.H. McCall, a geologist at the University of Western Australia, to classify the stony meteorites in the Museum's Collection, whilst De Laeter (1973b) undertook a similar task for iron meteorites. An X-ray fluorescence spectrometry technique was established at Curtin University of Technology to measure the nickel, cobalt, gallium and germanium content of the iron meteorites and determine their chemical classification (Thomas and De Laeter 1972).

Owing to the lack of a permanent Curator, the Western Australian Museum formed a Meteorite Advisory Committee to oversee the Collection and to arrange meteorite exchanges with scientists and other Museums. A well known meteoriticist (Dr R.A. Binns), later took over the Chairmanship of the Advisory Committee, and his international contacts proved invaluable in arranging for meteorite exchanges, and in amending the names of some Western Australian meteorites to conform with the guidelines established by the International Meteorite Nomenclature Committee. In 1985 the Western Australian Museum appointed Dr A.W.R. Bevan as the first permanent Curator of Mineralogy and Meteoritics in the State. Previously Dr D. Merrilees, Dr C. Pearson, Dr L.F. Bettenay and Dr K.J. McNamara had acted in the capacity of Curator of Meteoritics to give some oversight to the Collection.

The doyen of Western Australian meteorite collectors is undoubtedly Mr A.J. Carlisle, who has discovered specimens from approximately 80 different meteorites, and donated them to the Western Australian Museum over the last 50 years. The Nullarbor Plain has been a happy hunting ground for meteorite collectors, and Mr Carlisle's collaboration with Mr W.H. Cleverly and Mr M.K. Quartermaine, formerly of the Western Australian School of Mines in Kalgoorlie, has enabled many of these meteorites to be identified and located in the WA Museum. The most remarkable discovery made by Mr Carlisle was the recovery of a small stony meteorite named Lookout Hill. The specimen only measured a few centimetres in diameter and weighed 16.55g. It was covered in red soil, yet was recognised by Mr Carlisle as a meteorite and later confirmed by R.A. Binns to be a CM2 carbonaceous chondrite, the first of its type known from Western Australia.

Western Australian Meteorites

The fall of a meteorite can often be a spectacular event. On the 2nd September, 1967, for example, a stone meteorite fell near Wiluna, a country town in Western Australia. According to witnesses the sky was lit by a flash 'like a welding arc -- white and blue'. One man saw 'an object about 20 feet long throwing out balls of fire'. There were reports of 'a terrific rumbling noise' and 'bangs up to six or seven in number' (McCall and Jeffery 1970). These violent explosive reports are caused by atmospheric shock waves akin to sonic booms which accompany the fragmentation of a meteor into several pieces during its passage through the atmosphere.

At 10.10am on 30th September, 1984, a meteorite fell on to Binningup Beach, 143 km south of Perth. The brilliant fireball associated with the fall, which lasted for only a few seconds, streaked across the morning sky and burst into four or five luminous fragments shortly before disappearing. Two loud bangs, like claps of thunder, accompanied the phenomenon. Two women on the beach at Binningup were startled by a whistling noise and a loud thud in the sand about four metres from where they were lying. Investigating further, a small stony meteorite weighing about half a kilogram was found lying in a shallow depression it had excavated on impact with the soft sand (Bevan *et al.* 1988). To date, the Binningup meteorite is the most recently recovered observed fall in Australia.

In 1916, an iron with an unusual horseshoe shape was found near Mount Magnet. It contains a high concentration of nickel (14.7%), although subsequently the Warburton Range iron was discovered and found to contain 18.1% nickel (McCall and De Laeter 1965). Another unusual iron is Redfields, which is a phosphide-rich meteorite with an unusual structure (De Laeter *et al.* 1973). The high phosphide content has apparently inhibited Widmanstätten pattern development, so that although the nickel content is 6.65%, no taenite is present. Furthermore the meteorite has graphite inclusions, about 1 mm across, distributed throughout the metal, giving it a 'raisin-bread' appearance. The unusual structure of this meteorite is thought to be due to such factors as high carbon and phosphorus content, and relatively rapid cooling.

The discovery of the unique Bencubbin stony-iron in 1930 during ploughing operations, gave Western Australia a large meteorite (weight 54.2 kg), of extreme rarity and scientific importance. This was followed by the discovery of *Bencubbin II* (weight 64.6 kg) in 1959, and a third mass (weight 16 kg) which was found by Mr K. Hogan in 1974 on a neighbouring farm to where the previous finds had been located. Bencubbin is an unclassified meteorite breccia which consists mainly of host silicates and metal in the proportion of 2:3 (McCall, 1968). Rare chondritic clasts and a dark xenolith identified by Weisberg *et al.* (1990), suggest that the Bencubbin components are chondritic and were produced in the solar nebula, or alternatively that the components formed as a result of major impact melting on a chondritic parent body (Barber and Hutchison 1991). This meteorite is the subject of numerous ongoing scientific investigations as detailed in the above references.

Mount Padbury is a mesosiderite which was found by W.C. Martin in 1964. Mount Padbury is a polymict breccia containing large olivine crystals together with achondritic enclaves (McCall 1966). This meteorite, of which 272 kg of fragments were recovered, is the second greatest mass of mesosiderite material ever recovered. The rare Mount Egerton meteorite can be regarded as an achondrite with metallic inclusions. When a section of the metallic phase is polished and etched, it gives a curious 'ruled' etch pattern which is thought to be due to the presence of an iron-nickel silicide mineral, perryite (McCall, 1965)

One of the most impressive meteorites which has been found in Western Australia in recent years is the *Mount Manning* iron. Weighing 701 kg, it was discovered in 1979 near the Mount Manning Range. The meteorite has a fan-like shape, and it has been suggested that it may have performed a delta-wing like flight at a high angle of trajectory through the Earth's atmosphere in a stable aerodynamic configuration. One side of the specimen is smooth, slightly concave with a characteristic fusion crust, whereas the reverse surface is rough, convex and pitted with regmaglypts — which is consistent with the aerodynamic postulate. Measurements of the gallium, germanium and nickel composition of the *Mount Manning* meteorite showed that it belonged to the rare 1C class of irons (De Laeter 1980). However two other meteorites, named *Mount Dooling* and *Gosnells*, which are also Group 1C meteorites, were already in the WA Museum's Collection. The Mount Dooling meteorite was found in 1909 not far from the Mount Manning Range, whereas the *Gosnells* iron was found near Perth in 1960. Further examination showed that *Gosnells* and *Mount Manning* were fragments of the Mount Dooling meteorite, and that the *Gosnells* specimen must have been transported from the Mount Manning region by human agency (De Laeter *et al.* 1972). This is possibly one of the very few examples of a meteorite that may have been transported by aborigines.

Table 2: Number and Type of Western Australian Meteorites

	1913	1939	1965	1972	1991**
IRONS	8	20	29 (1)*	32	28
STONY-IRONS	—	1	4	7	8
STONES	—	4	15 (1)*	53 (4)	105 (4)
TOTAL	8	25	48 (2)	92 (4)	141 (4)
CRATERS	—	1	2	2	3

* The numbers in brackets are designated falls. The falls are included in the given numbers.

** The numbers of distinct meteorites are given in this column whereas the other columns are the numbers listed in the Catalogues.

Nullarbor Meteorites

The Nullarbor Region is a flat area of treeless, limestone desert in the south of the Australian continent. The arid to semi-arid climate of the Region, conducive to the preservation of meteoritic materials, combined with the featureless nature of the Region, has made it an ideal "spotting" ground for meteorites (Bevan and Binns 1989 a and b). Some 78 distinct meteorites, comprising three irons, one stony-iron and 74 stones have been recorded from this Region. In fact since 1971 over 2,500 individual meteoritic fragments have been recovered including some 500 specimens of possible new meteorites. The Nullarbor Region is therefore one of the most prolific areas in the world for the recovery of meteorites.

One of the most remarkable meteorite discoveries occurred in the 1960's when two extremely rare achondrites were found within 30 km of each other in the Nullarbor Region. These two ureilites, named North Haig and Dingo Pup Donga, increased the total known number of ureilites then known throughout the world from three to five. Another unusual meteorite named Coorara was found close to the site of Dingo Pup Donga in 1966 (McCall 1972) . This chondrite contains the high pressure minerals ringwoodite and majorite, which are of importance to our understanding of planetary processes.

Meteorites are named after the nearest geographical feature to where they are found, but the Nullarbor Region is not well-endowed with such features, so that meteorites from the Region carry such unusual names as Laundry Rock Hole, Mulga (west), Pannikin and Billygoat Donga. Bevan and Binns (1989a) have proposed a grid of 47 named areas in the Nullarbor Region, and each distinct meteorite is given the name of the area in which it is found, and a three digit number which increases integrally in order of recovery.

In 1911 two small iron meteorites weighing 112g and 116g were discovered by Mr H. Kent on that part of the Nullarbor Region known as Premier Downs. They were given the name of *Premier Downs I* and *II* by Simpson (1912) and Simpson and Bowley (1914), respectively. In 1918 a third iron weighing 99g was found in the same area by Mr A. Ewing. Simpson (1938), in describing this meteorite, noted that it had the same "knuckle-bone" appearance as the two previous meteorites, and named it *Premier Downs III*. He pointed out that all three fragments were part of a meteorite shower. Subsequently another similarly shaped iron was found in 1962. Its weight was 108g and it was named *Loongana Station*. Subsequently Mr W.H. Butler found another 66.5g fragment and it was named *Loongana Station West*. In 1965 Mr W. Crowle found three apparently complete irons of weights 94g, 45g and 39g respectively 16 km north of Mundrabilla Siding on the Trans Australian Railway (See Figure 3).

Then in 1966 R. Wilson and A. Cooney discovered two massive iron meteorites some 180m apart in the same vicinity as the *Loongana Station* meteorite. The two meteorites weighed 11.5 tonnes and 6.1 tonnes and were named Mundrabilla 1 and 2, respectively. They were surrounded by innumerable small irons of the type recovered

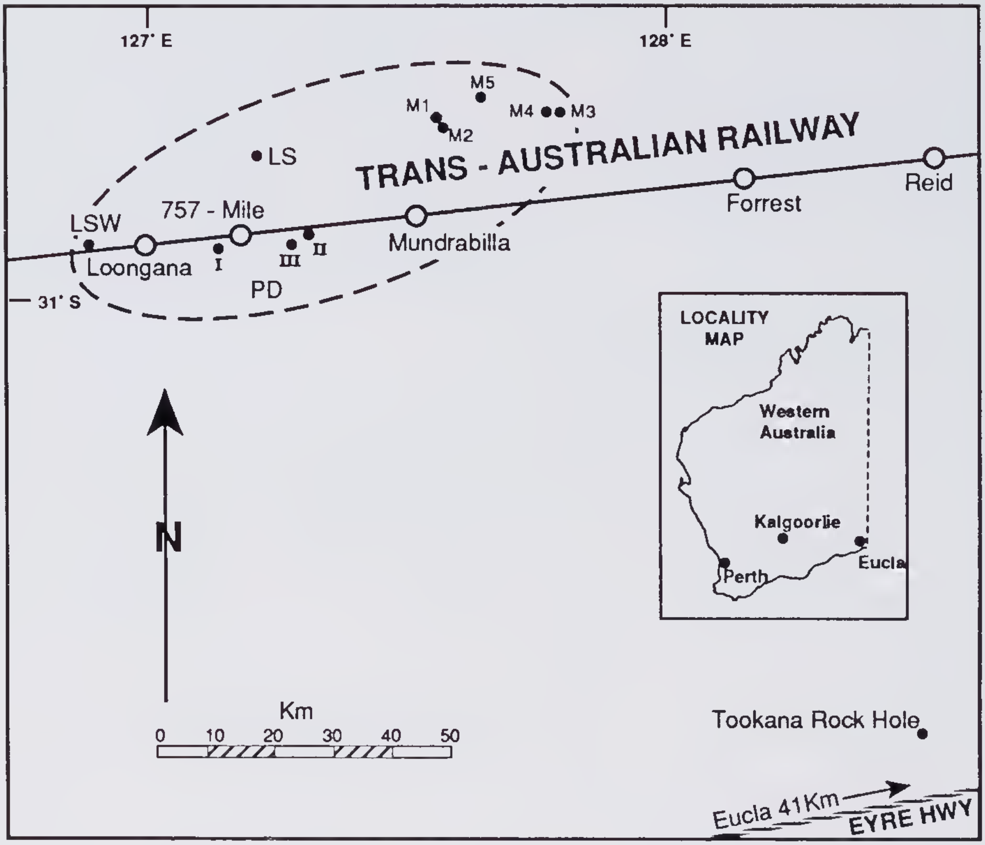

Figure 3 Map of part of the Nullarbor Plain in Western Australia showing the locations of the meteorites comprising the Mundrabilla meteorite shower. The elliptical area contains all the named masses together with many unnamed fragments.

previously in the vicinity. De Laeter (1972) showed that all these meteorites were members of the same shower and were members of Chemical Group 1.

Mundrabilla 2 was sent to the Max-Planck Institut fur Kernphysik at Heidelberg, where several slices were cut using a wire saw. These slices were made available for display in various Museums around the world, and one such slice is on display at the Western Australian Museum. The 11.5 tonne main mass of Mundrabilla 1 is displayed at the Western Australian Museum.

In 1978 Mr A.J. Carlisle discovered about 100 small "knuckle-bone" shaped iron meteorites near Tookana Rock Hole, which is situated 47 km NNW from Eucla on the Eyre Highway (see Figure 3). The heaviest specimen weighed 0.44 kg and the total recovered mass was 3.97 kg. In 1979 Mr Carlisle found another two large specimens of Mundrabilla some 20 km east of the site where Mundrabilla 1 and 2 were found. Both specimens, named Mundrabilla 3 and 4, and which weigh 840 kg and 800 kg respectively, are located in the WA Museum. Chemical analyses showed that all these additional specimens are members of the Mundrabilla meteorite shower (De Laeter and Cleverly 1983). More recent additional recoveries include a 3.5 tonne mass which is now displayed at The WA Museum's Branch at Albany. The "knuckle-bone" fragments from the Mundrabilla shower have presumably been shed in flight due to ablation of the main masses. This is due to the fact that the Mundrabilla meteorites contain a significant amount of troilite, much of which was burnt out in the meteorite's passage through the atmosphere. Thus the characteristic feature of the Mundrabilla meteorites is the deep cavitics which can readily be observed on their surface and which have later been enhanced by terrestrial weathering.

De Laeter (1972) suggested that the Mundrabilla meteoroid travelled in an east-north-east direction, and this is confirmed by the discovery of the additional large specimens. The Tookana Rock Hole material does not fit into this flight path, and it is significant that no large specimen has been found in this location. Perhaps these small specimens were transported from the Mundrabilla area to the Tookana Rock Hole by aborigines or other human agency.

Conclusions

The meteorites which have been recovered from the deserts and farmlands of Western Australia represent a rich store of extra-terrestrial material which have been used extensively by scientists, both within Australia and overseas, to study various aspects of the formation and evolution of the Solar System. Meteorites are survivors in the main from the Asteroid belt which have landed on the Earth's surface, and been discovered by observant men and women, in most cases many years after their fiery descent through the Earth's atmosphere. The excellence of the Western Australian Meteorite Collection is a tribute to those people who, realising that these objects have special significance and represent part of our common heritage, have unselfishly reported their occurrence and assisted in their recovery.

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A new genus of myrmecophilous Chernetidae from southern Australia (Pseudoscorpionida)

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Abstract

A new genus, *Marachernes*, with three new species, *M. bellus* (type species), *M. simulans* and *M. perup*, is described from southern Australia. The relationship of the genus to two other myrmecophiles, *Myrmochernes* Tullgren and *Xenochernes* Feio, is discussed, and the possible gondwanan origin for the group is highlighted.

Introduction

Myrmecophilous pseudoscorpions are not particularly well represented in Australian museum collections, despite the large and diverse ant fauna of the continent (Taylor and Brown 1985). Therefore, the discovery of an undescribed chernetid species from south-eastern Australia which is clearly associated with ants is of special interest. This species is described below, along with two congeneric species from south-eastern and south-western Australia, and all are assigned to a new genus that appears to be related to *Myrmochernes* Tullgren from South Africa and *Xenochernes* Feio from South America.

Materials and Methods

Specimens are lodged in the following institutions: Muséum d'Histoire Naturelle, Genéve (MHNG), Museum of Victoria, Melbourne (MVM), Queensland Museum, Brisbane (QM), Queen Victoria Museum, Launceston (QVM), Tasmanian Museum and Art Gallery, Hobart (TM), and Western Australian Museum, Perth (WAM). Some specimens were fully dissected, cleared and mounted on microscope slides in Euparal. One male of *Marachernes bellus* was dehydrated, mounted and gold-coated for examination in a JEOL JSM-35C Scanning Microscope. Measurements and terminology basically follow Chamberlin (1931); the terminology of the appendages and trichobothria follows Harvey (1993).

Systematics

Marachernes gen. nov.

Type species

Marachernes bellus sp. nov.

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Diagnosis

Marachernes differs from *Myrmochernes* and *Xenochernes* by the presence of 4 flagellal blades (Figs 9, 22, 32), and 1-3 accessory teeth on internolateral mound of male movable chelal finger (Figs 7, 15, 16, 19).

Description

Setae on carapace, tergites, and pedipalpal trochanter, femur and sometimes patella clavate; setae on sternites and pedipalpal chela and sometimes patella slender and acuminate (Figs 5, 20, 30). Venom apparatus present in movable finger terminating in nodus ramosus midway between *st* and *t* (Figs 1, 18, 29). Sense spots present on both chelal fingers. Cheliceral flagellum with 4 blades (Figs 9, 22, 32). Carapace with 1 pair of eye spots; with 2 transverse furrows, posterior furrow closer to posterior margin of carapace than to anterior furrow (Figs 6, 17, 28). Female genitalia with spermathecae consisting of 2 short tubules (Figs 14, 27, 35). Suture line between femur and patella of leg I oblique (Figs 11, 23, 34). Tarsus IV without tactile seta (Figs 10, 24, 33). All tarsi with a proximal slit sensillum. Claws simple; arolium shorter than claws.

Remarks

Marachernes appears to be most similar to *Xenochernes* from Brazil, based mainly upon the shape of the chelal hand. However, specimens of the latter genus have been unavailable to me [despite requests to the institution that apparently holds the type specimens of the only known species, *X. caxinguba* Feio; see also Judson (1985)]. Therefore, direct comparisons with *Xenochernes* are not possible.

Feio (1945) placed *Xenochernes* in the Xenochernetinae, and alluded to the similarity between the cheliceral morphology of *Xenochernes* and *Myrmochernes*, the type of the Myrmochernetidae. Judson (1985) synonymised Myrmochernetidae with the Chernetidae, and in a detailed redescription of *My. africanus* Tullgren (the type and only known species of the genus), also noted the similarity between the African and Brazilian species. I have examined 5♂, 1♀ syntypes of *My. africanus* in the Zoologisches Museum, Hamburg, and specimens from Grahamstown, South Africa, in the Naturhistorisches Museum, Wien (2♀), and the American Museum of Natural History, New York (1♀). Despite its small size and a suite of synapomorphies (e.g. lack of accessory teeth on the chelal fingers, lack of venom apparatus), *My. africanus* appears to be related to *Xenochernes* and *Marachernes*, based mainly on the shape of the chelal hand.

The spermathecae of *Myrmochernes africanus* (Judson, 1985, fig. 9) and *Marachernes* spp. (Figs 14, 27, 35) are quite different. Unfortunately, the spermathecae of *X. caxinguba* are not known.

Etymology

This genus is named for Māra Blosfelds, in recognition of her contributions to the collection of the type species, and combined with *Chernes*, the type species of the family. Gender: masculine.

Key to species in *Myrmochernes* group

1 Cheliceral flagellum with 3 blades; ♂ movable chelal finger without internobasal accessory teeth 2

Cheliceral flagellum with 4 blades (Figs 9, 22, 32); ♂ movable chelal finger with 1-3 internobasal accessory teeth on mound (Figs 7, 15, 16, 19) .... *Marachernes*..3

2 Cheliceral hand with 4 setae, *es* absent (South Africa) .... *Myrmochernes africanus* Tullgren

Cheliceral hand with 5-6 setae, *es* present (Brazil) .... *Xenochernes caxinguba* Feio

3 Pedipalpal patella with clavate setae (Fig. 5); anteromedian area of carapace virtually smooth (Fig. 6); trichobothrium *est* much closer to *esb* than to *et* (Figs 1, 5) .... *Marachernes bellus* sp. nov.

Pedipalpal patella with acuminate setae (Figs 20, 30); anteromedian area of carapace granulate (Figs 17, 28); trichobothrium *est* approximately midway between *esb* and *et* (Figs 18, 20, 29, 30) 4

4 Chelal hand 0.96 (♂), 1.11 (♀) times longer than broad .... *Marachernes simulans* sp. nov.

Chelal hand 1.37 (♀) times longer than broad .. *Marachernes perup* sp. nov.

Marachernes bellus sp. nov.

Figures 1-16, 37-38

Holotype

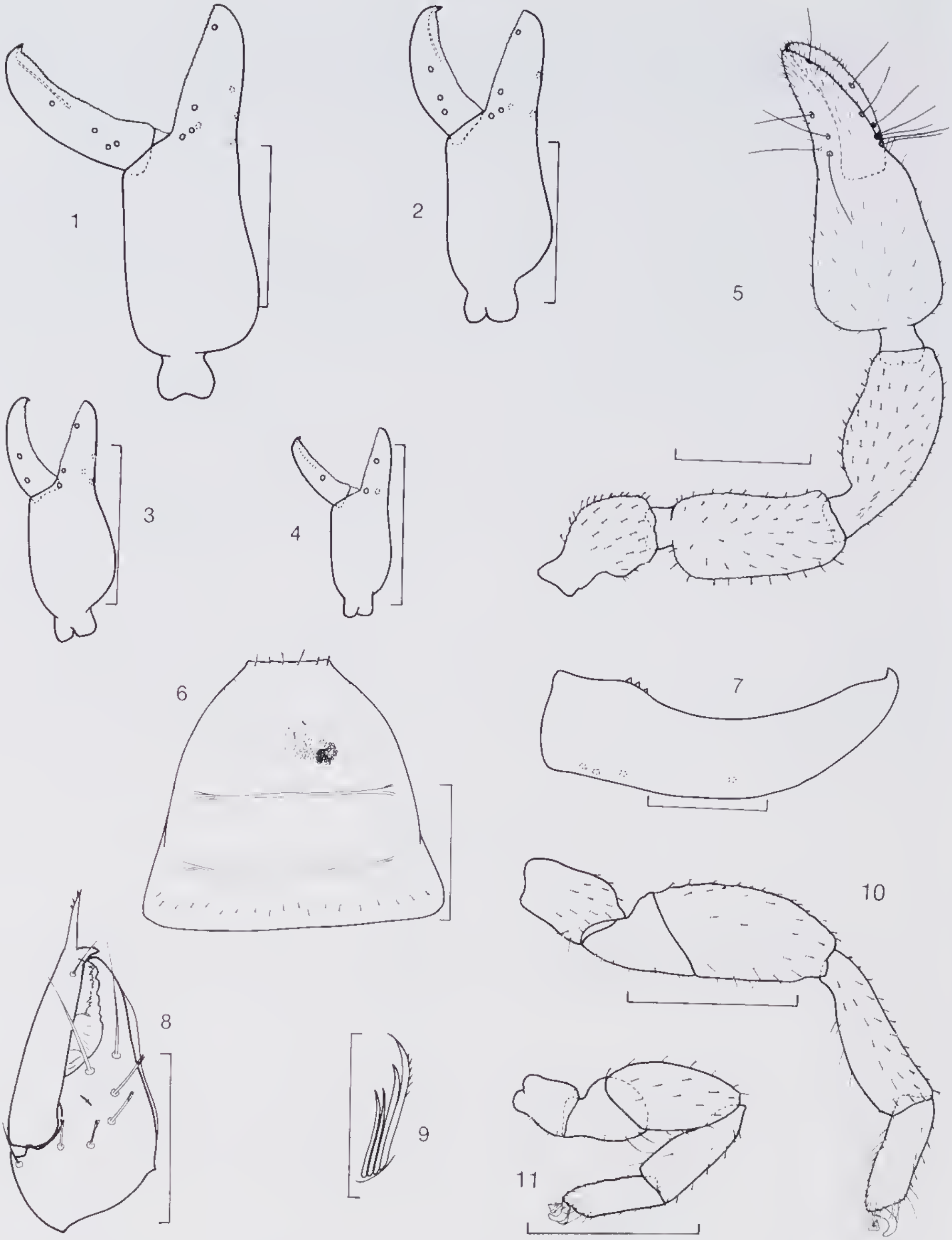
♀, Separation Creek, Otway Ranges, Victoria, Australia, 38°38′S, 143°54′E, under bark of *Eucalyptus* sp. [in association with colonies of *Iridomyrmex* sp. near *foetans* Clark (Hymenoptera: Formicidae)], 19-21 September 1989, M.S. Harvey, M.E. Blosfelds (WAM, 91/1813).

Paratypes

Australia: *Victoria*: 16♂, 8♀, 15 tritonymphs, 5 deutonymphs, 3 protonymphs, same data as holotype (WAM, 91/1064-1110); 2♂, 2♀, 1 tritonymph, 1 deutonymph, 1 protonymph, same data as holotype (MVM, K2218-2224); 2♂, 2♀, 1 tritonymph, 1 deutonymph, 1 protonymph, same data as holotype (MHNG); 1♂, 1♀, same data (QM); 1♀, same data as holotype except 28 August 1988 (WAM, 91/1356); 1 tritonymph, 5 km NE. of Wye River, 38°36′S, 143°56′E, under bark of *Eucalyptus* sp., 20 September 1989, M.S. Harvey, M.E. Blosfelds (WAM, 91/1357); 1♂, 4.5 km WSW. of Burton's Lookout, Wonga Road, 38°27′S, 143°30′E, under bark of *Eucalyptus* sp., 1 April 1978, C. Silveira (WAM, 91/1358). *Tasmania*: 1♀, Queen's Domain, Hobart, under bark on eucalypt, 29 January 1927, V.V. Hickman (TM, J3035); 1♀, Trevallyn, Launceston, 1 February 1927, V.V. Hickman (TM, J3034); 1♂, Punch Bowl, Launceston, under bark on eucalypts, 10 December 1926, V.V. Hickman (TM, J3033).

Other material examined

Australia: *Tasmania*: 1 tritonymph, Tatana, under bark of gum (*Eucalyptus* sp.), 30 September 1963, R.N.G. (QVM).



Figures 1-11 *Marachernes bellus* sp. nov., holotype ♀ unless otherwise stated: 1, left chela, lateral. 2, left chela, lateral, paratype tritonymph. 3, left chela, lateral, paratype deutonymph. 4, left chela, lateral, paratype protonymph. 5, right pedipalp, dorsal. 6, carapace (most setae omitted). 7, movable right chelal finger, ventral, paratype ♂. 8, left chelicera, paratype . 9, left flagellum. 10, left leg IV. 11, left leg I. Scale lines = 0.50 mm (Figs 1-6, 10, 11), 0.20 mm (Figs 7, 8), 0.10 mm (Fig. 9).

Diagnosis

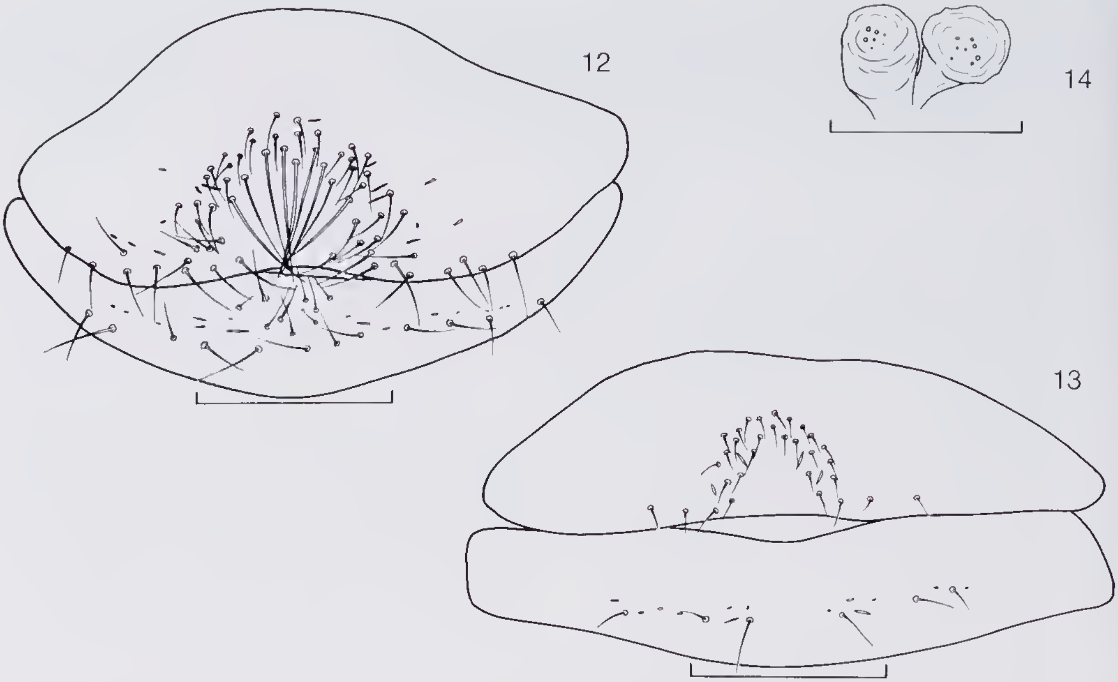
This species is easily distinguished by the clavate setae on the pedipalpal patella (Fig. 5), the virtually smooth anteromedian area of carapace (Fig. 6), and the position of trichobothrium *est*, which is much closer to *esb* than to *et* (Figs 1, 5).

Description

Adult

Colour generally yellow-brown, pedipalps, carapace and legs dark red-brown. Pleural membrane rugose. Pedipalps (Fig. 5): trochanter 1.58-1.67 (♂), 1.57-1.61 (♀), femur abruptly pedicellate, 2.22-2.35 (♂), 2.31-2.45 (♀), patella 2.24-2.47 (♂), 2.24-2.47 (♀), chela (with pedicel) 2.61-2.65 (♂), 2.46-2.60 (♀), chela (without pedicel) 2.29-2.35 (♂), 2.17-2.40 (♀), hand 1.18-1.31 (♂), 1.15-1.23 (♀) times longer than broad, movable finger 0.95-0.98 (♂), 0.93-0.98 (♀) times as long as hand. Pedipalps with coarse granulations on trochanter, femur and patella, chela smooth. Setae on trochanter, femur and patella clavate. Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Fig. 1); *it* closer to *isb* than to tip of finger, *est* much closer to *esb* than to *et*. Fixed finger with 29 (♂), 30-31 (♀) marginal teeth, plus 6 (♂), 6-8 (♀) external and 3 (♂,♀) internal accessory teeth; movable finger with 35 (♂), 31-34 (♀) marginal teeth, plus 4 (♂), 6-8 (♀) external and 3 (♂), 4 (♀) internal accessory teeth; movable chelal finger with 2-3 internobasal accessory teeth on mound (Fig. 7). Chelicera (Fig. 8) with 6-7 setae on hand, *sbs*, *bs*, *bs'* and *bs"* (when present) terminally denticulate; serrula exterior with 24-25 (♂), 23-25 (♀) lamellae; galea with 3 (♂), 4 (♀) small distal or subdistal rami. Carapace (Fig. 6) with 16-19 (♂), 18-19 (♀) setae on posterior margin, 0.97-1.08 (♂), 0.89-0.98 (♀) times longer than broad; anteromedian area virtually smooth. Tergites I-X and sternites IV-X divided. Tergal chaetotaxy: ♂, 19-27: 29-34: 28-33: 41-46: 46-52: 43-49: 43-48: 45-50: 48-50: 43-46: 31-33: 2; ♀, 21-23: 23-34: 28-35: 40-46: 47-54: 44-52: 48-54: 45-49: 49-56: 45-58: 24-29: 2; arranged in 2 indistinct rows. Sternal chaetotaxy: ♂, 61-66: (2-3)13-24[10-12](2-3): (1)11-14(1): 17-20: 24-26: 26-27: 26-29: 27-28: 23-26: 11-13: 2; ♀, 31-47: (3)6-7(3): (1)11-12(1): 19-22: 22-24: 25-28: 26-30: 28-29: 25-26: 12-15: 2. Sternite XI with several tactile setae. Genital opercula of male (Fig. 12): with numerous large setae; several pairs of slit sensilla on anterior operculum, numerous smaller sensillae present on posterior operculum; opercula of female (Fig. 13): anterior operculum with small setae arranged in inverted-U pattern. Male genitalia not unusual; female genitalia as in Fig. 14. Leg I as in Fig. 11. Leg IV (Fig. 10): femur + patella 2.43-2.59 (♂), 2.57-2.74 (♀) times longer than broad.

Dimensions (mm), ♂(♀): body length 2.74-3.14 (2.99-3.34). Pedipalps: trochanter 0.49-0.52/0.30-0.32 (0.47-0.50/0.30-0.31), femur 0.78-0.80/0.34-0.36 (0.74-0.83/0.31-0.35), patella 0.82-0.84/0.34-0.37 (0.74-0.84/0.32-0.35), chela (with pedicel) 1.28-1.31/0.49-0.50 (1.18-1.28/0.48-0.52), chela (without pedicel) 1.12-1.16 (1.04-1.15), movable finger length 0.57-0.61 (0.55-0.59), hand length 0.58-0.64



Figures 12-14 *Marachernes bellus* sp. nov.: 12, genital opercula, paratype ♂. 13, genital opercula, holotype ♀. 14, spermathecae, holotype ♀. Scale lines = 0.20 mm Figs 12, 13), 0.10 mm (Fig. 14).

(0.59-0.60). Chelicera 0.28-0.32/0.14-0.18 (0.31-0.33/0.17-0.18), movable finger length 0.22-0.24 (0.22-0.25). Carapace 0.93-1.04/0.94-1.03 (0.95-1.00/1.02-1.10). Leg I: femur + patella 0.54-0.56/0.21-0.22 (0.52-0.55/0.20-0.21), tibia 0.37-0.39/0.14-0.15 (0.36-0.37/0.14-0.15), tarsus 0.30-0.32/0.10 (0.30/0.10). Leg IV: femur + patella 0.73-0.75/0.29-0.30 (0.72-0.75/0.27-0.28), tibia 0.55-0.56/0.17-0.18 (0.51-0.54/0.17), tarsus 0.36-0.38/0.12-0.13 (0.37-0.39/0.12).

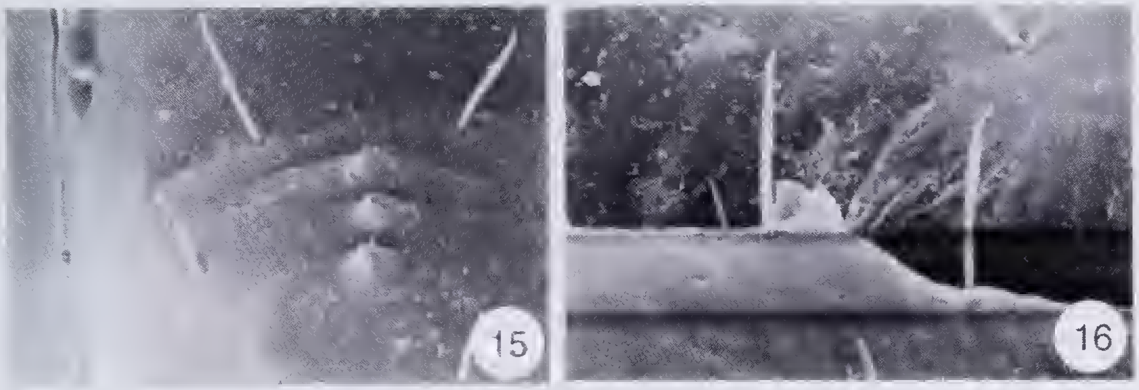
Tritonymph

Colour paler than adults. Pedipalp: trochanter 1.65, femur 2.40, patella 2.27, chela (with pedicel) 2.76, chela (without pedicel) 2.54, hand 1.22 times longer than broad. Fixed chelal finger with 7 trichobothria, movable chelal finger with 3 trichobothria (Fig. 2): *isb* and *sb* absent. Carapace 1.03 times longer than broad; anteromedian area virtually smooth.

Dimensions (mm): Body length 2.63. Pedipalps: trochanter 0.38/0.23, femur 0.60/0.25, patella 0.59/0.26, chela (with pedicel) 0.98/0.37, chela (without pedicel) 0.86, hand length 0.45, movable finger length 0.42. Carapace 0.82/0.80.

Deutonymph

Colour paler than adults. Pedipalp: trochanter 1.61, femur 2.32, patella 2.05, chela (with pedicel) 2.65, chela (without pedicel) 2.32, hand 1.21 times longer than



Figures 15-16 *Marachernes bellus* sp. nov., paratype ♂. 15, movable finger mound, ventral. 16, movable finger mound, mesal.

broad. Fixed chelal finger with 6 trichobothria, movable chelal finger with 2 trichobothria (Fig. 3): *esb*, *isb*, *sb* and *st* absent. Carapace 1.00 times longer than broad; anteromedian area virtually smooth.

Dimensions (mm): Body length 2.26. Pedipalps: trochanter 0.29/0.18, femur 0.44/0.19, patella 0.43/0.21, chela (with pedicel) 0.75/0.28, chela (without pedicel) 0.65, hand length 0.34, movable finger length 0.31. Carapace 0.66/0.66.

Protonymph

Colour very pale. Pedipalp: trochanter 0.93, femur 2.36, patella 1.88, chela (with pedicel) 2.68, chela (without pedicel) 2.32, hand 1.27 times longer than broad. Fixed chelal finger with 3 trichobothria, movable chelal finger with 1 trichobothria (Fig. 4): *eb*, *et*, *ist* and *t* present. Carapace 1.06 times longer than broad; anteromedian area virtually smooth.

Dimensions (mm): Body length 1.66. Pedipalps: trochanter 0.13/0.14, femur 0.33/0.14, patella 0.30/0.16, chela (with pedicel) 0.59/0.22, chela (without pedicel) 0.51, hand length 0.28, movable finger length 0.25. Carapace 0.52/0.49.

Remarks

As discussed below, this species is found in association with colonies of *Iridomyrmex* sp. near *foetans* Clark (Hymenoptera: Formicidae) under the bark of eucalypt trees. Voucher specimens of the ants have been lodged in MVM and WAM. At present, *M. bellus* is known from the Otway Ranges, Victoria, and Tasmania.

Etymology

The specific epithet refers to the beauty of this species (*bellus*, Latin, pretty, lovely).

Marachernes simulans sp. nov.

Figures 17-27

Holotype

♀, Upper Beaconsfield, Victoria, Australia, 38°03′S, 145° 15′E, under bark of tree, 23 April 1979, P. Szigat (WAM, 91/1814).

Paratype

Australia: *Victoria*: 1 ♂, Upper Beaconsfield, 38°03′S, 145° 15′E, under bark of tree, 1 April 1979, P. Szigat (WAM, 91/1815).

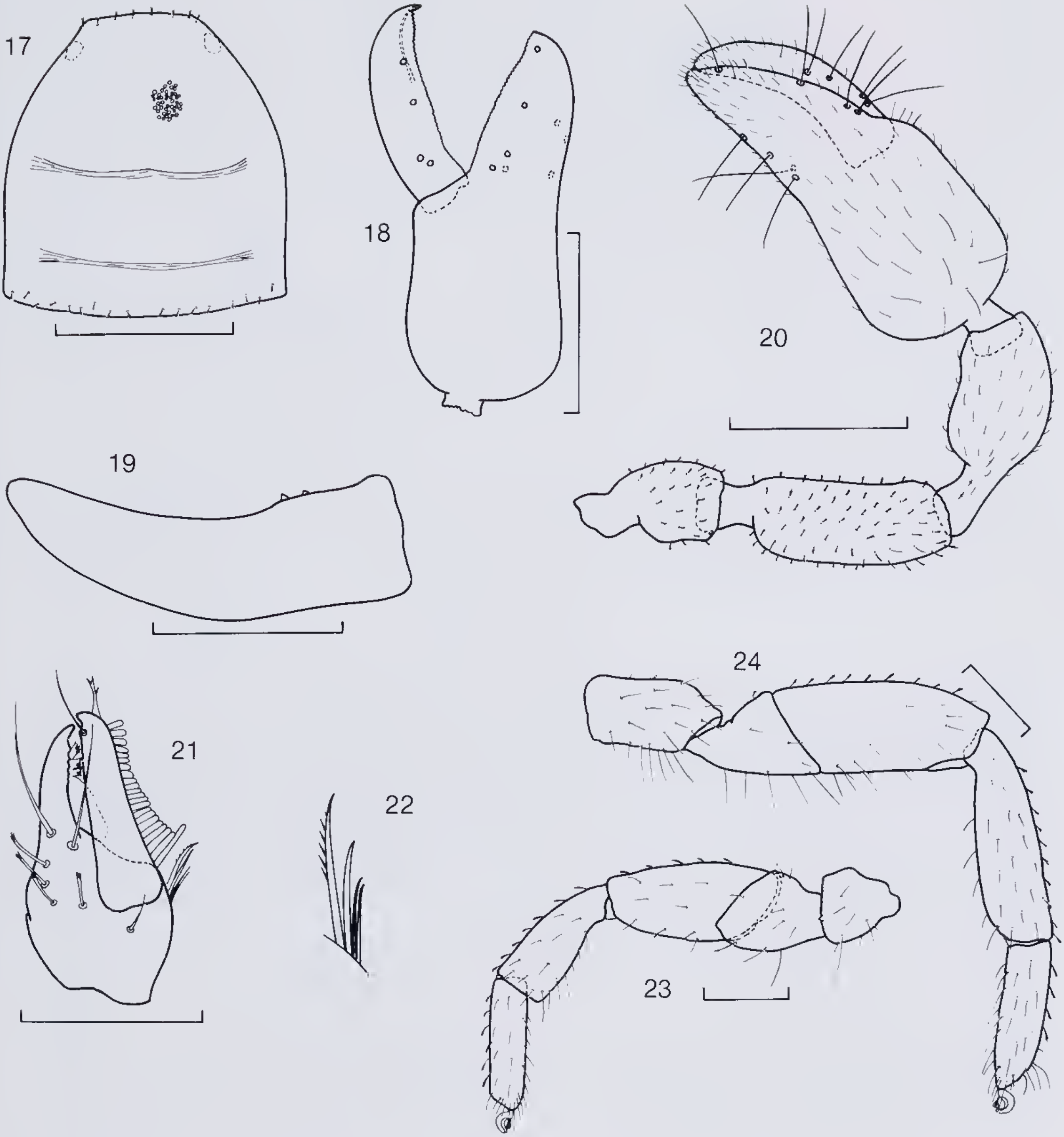
Diagnosis

This species is distinguished from *M. perup* by the broad chelal hand (Fig. 20), and from *M. bellus* by the acuminate setae on the pedipalpal patella (Fig. 18), the rugose anteromedian area of carapace (Fig. 15), and the position of trichobothrium *est*, which is midway between *esb* and *et* (Fig. 16).

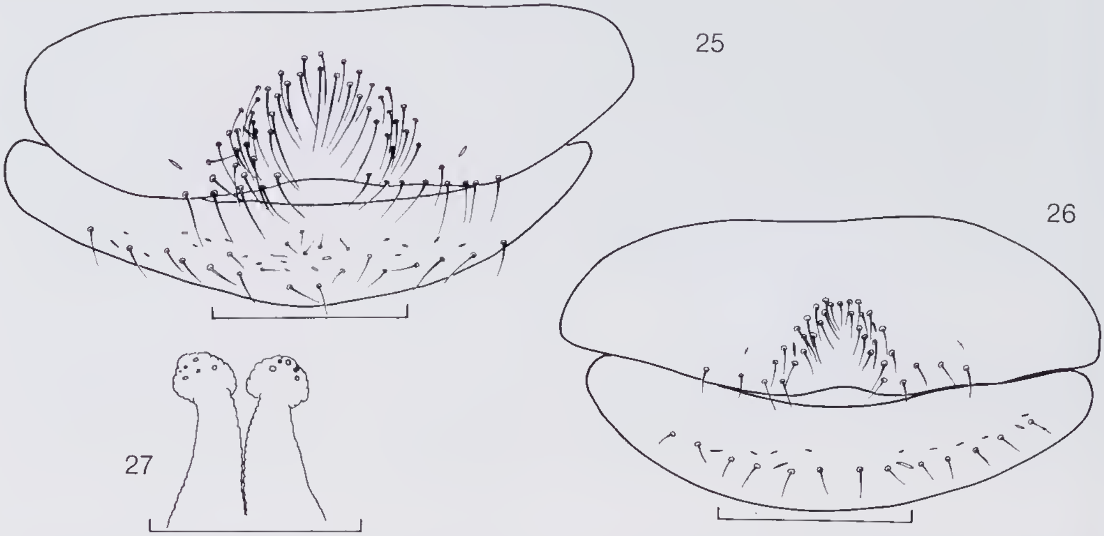
Description

Adult

Colour generally yellow-brown, pedipalps and carapace dark red-brown. Pleural membrane rugose. Pedipalps (Fig. 20): trochanter 1.77 (♂), 1.79 (♀), femur abruptly pedicellate, 2.64 (♂), 2.83 (♀), patella 2.40 (♂), 2.43 (♀), chela (with pedicel) 2.29 (♂), 2.43 (♀), chela (without pedicel) 2.06 (♂), 2.30 (♀), hand 0.96 (♂), 1.11 (♀) times longer than broad, movable finger 1.18 (♂), 1.16 (♀) times longer than hand. Pedipalps with coarse granulations on trochanter, femur and internolateral margin of patella; chela and remainder of patella smooth. Setae on trochanter and femur clavate, on patella acuminate. Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Fig. 18): *it* closer to *isb* than to tip of finger, *est* approximately midway between *esb* and *et*. Fixed finger with 35 (♂), 33 (♀) marginal teeth, plus 4 (♂), 8 (♀) external and 2 (♂, ♀) internal accessory teeth; movable finger with 35 (♂), 35 (♀) marginal teeth, plus 3 (♂), 5 (♀) external and 1 (♂), 2 (♀) internal accessory teeth; movable chelal finger with 1 internobasal accessory tooth on mound (Fig. 19). Chelicera with 7 setae on hand, *sbs*, *bs*, *bs'* and *bs"* strongly denticulate; serrula exterior with 23 (♂), 22 (♀) lamellae; galea of with 3 small rami, of damaged. Carapace (Fig. 17) with 19 (♂), 17 (♀) setae on posterior margin, 1.04 (♂), 1.13 (♀) times longer than broad; anteromedian area of carapace not smooth. Tergites I-X and sternites IV-X divided. Tergal chaetotaxy: ♂, 45: 56: 56: 60: 70: 73: 68: 69: 67: 52: 26: 2; ♀, 34: 52: 49: 63: 68: 67: 73: 66: 64: 59: 26: 2; arranged in 2 indistinct rows. Sternal chaetotaxy: ♂, 64: (3)22[9](3): (1)17(1): 30: 36: 36: 38: 41: 36: 13: 2; ♀, 35: (3)13(3): (1)12(1): 23: 34: 33: 40: 40: 34: 14: 2. Sternite XI with several tactile setae. Genital opercula of male (Fig. 25): with numerous large setae; 3 slit sensillae on anterior operculum, numerous smaller sensillae on posterior operculum; opercula of female (Fig. 26): anterior operculum with small setae arranged in inverted-U pattern. Male genitalia not unusual; female genitalia as in



Figures 17-24 *Marachernes simulans* sp. nov., holotype ♀ unless otherwise stated: 17, carapace (most setae omitted). 18, left chela, lateral. 19, movable right chelal finger, ventral, paratype ♂. 20, right pedipalp, dorsal. 21, right chelicera, paratype ♂. 22, left flagellum. 23, left leg I. 24, left leg IV. Scale lines = 0.50 mm (Figs 17, 18, 20), 0.20 mm (Figs 19, 21, 23, 24).



Figures 25-27 *Marachernes simulans* sp. nov.: 25, genital opercula, paratype ♂. 26, genital opercula, holotype ♀. 27, spermathecae, holotype ♀. Scale lines = 0.20 mm (Figs 25, 26), 0.10 mm (Fig. 27).

Fig. 27. Leg I as in Fig. 23. Leg IV (Fig. 24): femur + patella 2.73 (♂), 3.40 (♀) times longer than broad.

Dimensions (mm), ♂(♀): body length 2.88 (2.80). Pedipalps: trochanter 0.46/0.26 (0.43/0.24), femur 0.74/0.28 (0.65/0.23), patella 0.72/0.30 (0.68/0.28), chela (with pedicel) 1.17/0.51 (1.12/0.46), chela (without pedicel) 1.05 (1.06), movable finger length 0.58 (0.59), hand length 0.49 (0.51). Chelicera 0.31/0.16 (0.29/0.16), movable finger length 0.22 (0.23). Carapace 0.89/0.86 (0.90/0.80). Leg I: femur + patella 0.51/0.20 (0.50/0.19), tibia 0.34/0.13 (0.32/0.12), tarsus 0.30/0.09 (0.30/0.08). Leg IV: femur + patella 0.71/0.26 (0.68/0.20), tibia 0.52/0.17 (0.48/0.14), tarsus 0.37/0.11 (0.35/0.10).

Etymology

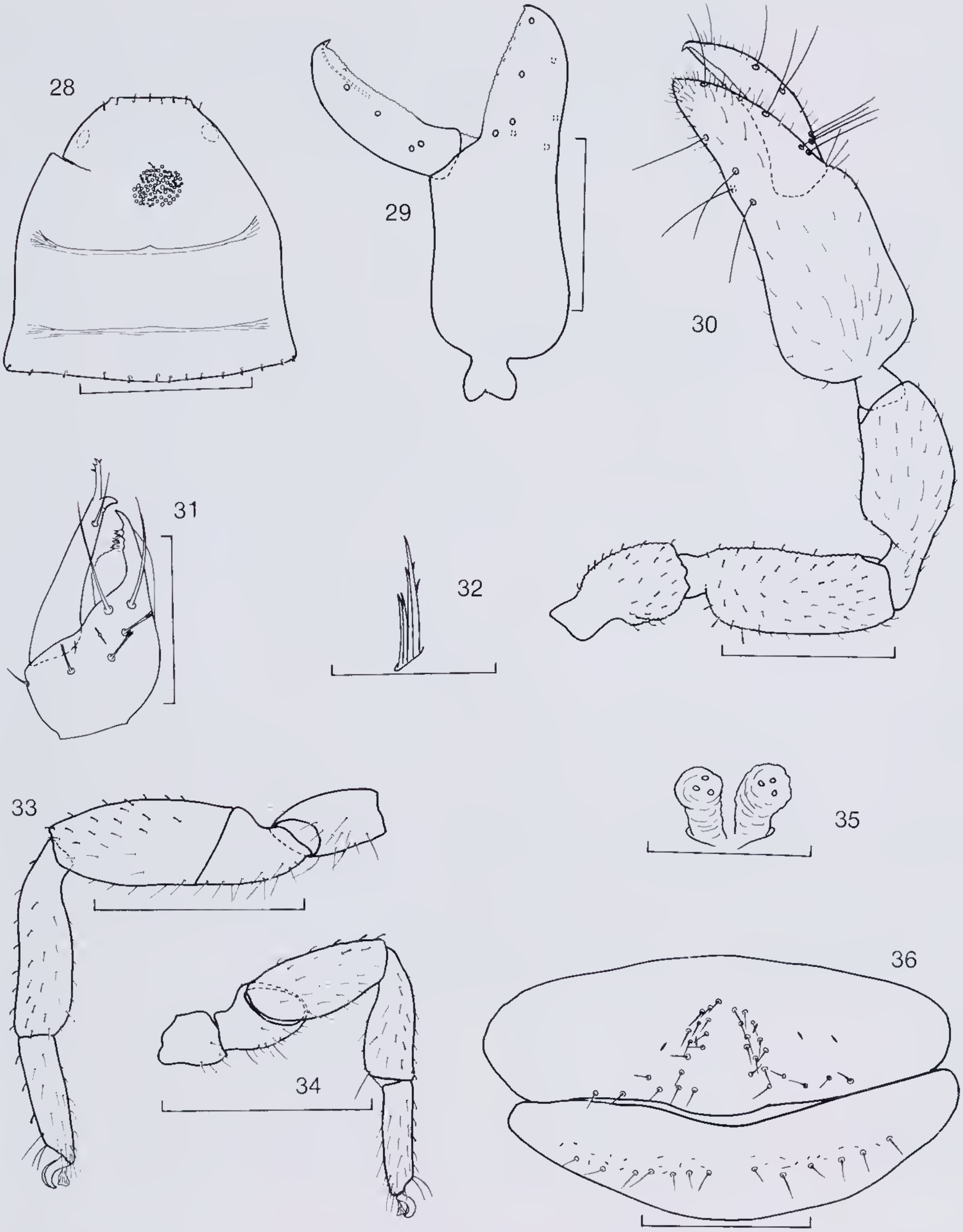
The specific epithet refers to the similarity between this species and *M. perup* (*simulo*, Latin, imitate, copy).

Marachernes perup sp. nov.

Figures 28-36

Holotype

♀, Perup Nature Reserve, ca. 40 km E. of Manjimup, Western Australia, Australia, 34°06′S, 116°40′E, from jarrah (*Eucalyptus marginata*) logs, 17 March 1989, S. Griffin (WAM, 91/1111).



Figures 28-36 *Marachernes perup* sp. nov., holotype : 28, carapace (most setae omitted). 29, left chela, lateral. 30, right pedipalp, dorsal. 31, left chelicera. 32, right flagellum. 33, left leg IV. 34, left leg I. 35, spermathecae. 36, genital opercula. Scale lines = 0.50 mm (Figs 28-30, 33, 34), 0.20 mm (Figs 31, 36), 0.10 mm (Figs 32, 35).

Diagnosis

This species is distinguished from *M. simulans* by the narrow chelal hand (Fig. 30), and from *M. bellus* by the acuminate setae on the pedipalpal patella (Fig. 28), the rugose anteromedian area of carapace (Fig. 26), and the position of trichobothrium *est*, which is midway between *et* and *esb* (Fig. 27).

Description

Adult female

Colour generally dark yellow-brown, pedipalps and anterior portion of carapace dark red-brown. Pleural membrane rugose. Pedipalps (Fig. 30): trochanter 1.87, femur abruptly pedicellate, 2.96, patella 2.48, chela (with pedicel) 2.80, chela (without pedicel) 2.56, hand 1.37 times longer than broad, movable finger 0.98 times as long as hand. Pedipalps with coarse granulations on trochanter and femur; patella and chela smooth. Setae on trochanter and femur clavate, on patella acuminate. Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Fig. 29); *it* closer to tip of finger than to *isb*, *est* approximately midway between *esb* and *et*, *it* midway between level of *et* and *est*. Fixed finger with 35 marginal teeth, plus 5 external and 1 internal accessory teeth; movable finger with 32 marginal teeth, plus 4 external and 1 internal accessory teeth. Chelicera with 6-7 setae on hand, *sbs*, *bs* and *bs'* terminally denticulate; serrula exterior with 23 lamellae; galea with 2 distal and 4 sub-distal rami. Carapace (Fig. 28) with 16 setae on posterior margin, 0.98 times longer than broad; anteromedian area of carapace virtually smooth. Tergites I-X and sternites IV-X divided. Tergal chaetotaxy: 37: 39: 45: 51: 57: 53: 54: 53: 47: 42: 16: 2; arranged in 2 indistinct rows. Sternal chaetotaxy: 34: (2)14(2): (1)10(1): 23: 26: 33: 31: 29: 26: 8: 2. Sternite XI with several tactile setae. Genital opercula (Fig. 36): anterior operculum with small setae arranged in inverted-U pattern. Genitalia as in Fig. 35. Leg I as in Fig. 34. Leg IV (Fig. 33): femur + patella 3.00 times longer than broad.

Dimensions (mm): body length 2.66. Pedipalps: trochanter 0.43/0.23, femur 0.68/0.23, patella 0.67/0.27, chela (with pedicel) 1.15/0.41, chela (without pedicel) 1.05, movable finger length 0.55, hand length 0.66. Chelicera 0.28/0.16, movable finger length 0.22. Carapace 0.85/0.87. Leg I: femur + patella 0.47/0.15, tibia 0.32/0.12, tarsus 0.29/0.08. Leg IV: femur + patella 0.63/0.21, tibia 0.49/0.13, tarsus 0.32/0.09.

Etymology

The specific epithet is a noun in apposition taken from the type locality.

Biology and Biogeography

Sporadic collections of *Marachernes* specimens have been taken over the past few years in southern Victoria. In September 1989, whilst collecting specimens from under bark of eucalypt trees at Separation Creek, it became apparent that the pseudoscorpions (*M. bellus*) were only found in close proximity to the ants (*Iridomyrmex* sp. near *foetans* Clark) that were found in large aggregations under the bark. The pseudoscorpions were immobile when collected (during daylight hours), and none were seen feeding on the ants or their larvae. One pseudoscorpion was found firmly clenched in the mandibles of an ant, which was presumably feeding on the pseudoscorpion. The only known specimens of the other two *Marachernes* species, *M. simulans* and *M. perup*, were taken from under the bark of a tree and of a eucalypt log, respectively; it is not known whether ants were in close proximity.

Members of the *Iridomyrmex foetans* species group are confined to wet forests (Andersen 1991), and may parallel the Bassian distribution of *Marachernes* species. However, only a single species of *Marachernes* has been found in association with ants, and more data are needed to confirm the myrmecophilous nature of other members of the genus.

As discussed above, *Marachernes* appears to be most similar to *Myrmochernes* from South Africa and *Xenochernes* from Brazil, which tends to indicate a gondwanan origin for this group of genera. The collection and study of further pseudoscorpions living in association with ants (and other social insects, such as termites) in the southern hemisphere may help to elucidate relationships between these genera.

Acknowledgements

Māra Blosfelds' collecting prowess provided a long series of specimens of the type species, and accommodation was kindly provided by Robin Wilson. Julianne Waldock furnished the scanning micrographs. Norman Platnick (American Museum of Natural History, New York), Jürgen Gruber (Naturhistorisches Museum, Wien), Gisela Rack (Zoologisches Museum, Hamburg), Tim Kingston (Queen Victoria Museum, Launceston) and Elizabeth Turner (Tasmanian Museum and Art Gallery, Hobart) loaned material for this study. Other specimens were donated by Charles Silveira and Sandra Griffin.

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A new genus and two new species of millipedes from the Cape Range, Western Australia (Diplopoda, Polydesmida, Paradoxosomatidae)

William A. Shear*

Abstract

Two new species of millipede, *Boreohesperus capensis*, gen nov., sp. nov., and *Antichiropus humphreysi*, sp. nov. (Polydesmida, Paradoxosomatidae) are described from cave and epigean localities on the North West Cape, Western Australia. The former represents the first record of the Tribe Australiosomatini from Western Australia.

Introduction

The millipede fauna of Western Australia was last examined in a more or less comprehensive way by Attems in 1911. He recorded 17 diplopod species in four families, all of them described as new. Seven of these species were paradoxosomatids, and six of them were placed in his new genus, *Antichiropus.* He also described as new *Orthomorpha triaina,* which we now know to be a synonym of *Akamptogonus novarae* (Humbert and de Saussure), a synanthropic species, probably from eastern Australia but now established in New Zealand, Hawaii, and California, USA (Jeekel 1981; Hoffman 1980). Verhoeff described *Helicopodosoma,* with two new species (1924; Attems 1937; Jeekel 1968). More recently, as a result of an intensive effort to explore the caves of the semi-arid North West Cape region, additional paradoxosomatid taxa have come to light. Living in these caves as troglobites are three species of a new genus in the tribe Antichiropodini (Humphreys and Shear, in press). Also taken in the caves were several specimens of paradoxosomatids unmodified for cave life, obviously inhabitants of the surface, but which found the conditions of the caves congenial. These consisted of members of two species, one of which represents a new genus, and the second a new species of *Antichiropus.*

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Systematics
Family Paradoxosomatidae Daday
Subfamily Australiosomatinae Brölemann
Tribe Australiosomatini Brölemann
Boreohesperus, gen. nov.

Type Species

Boreohesperus capensis, sp. nov.

Etymology

From the Latin, *Boreus*, god of the North, and *hesperus*, the west. The gender is masculine.

Diagnosis

Differing from other members of its tribe in the simple structure of the male gonopod, with a short femorite, long solenomerite bent over and coiled in nearly a complete circle at its apex, and shorter, simple, rodlike tibiotarsus.

Description

Twenty segments. Pore formula normal. Segments about as long as broad, strongly constricted between prozonite and metazonite, unsculptured, smooth and shining. Pleural keels present only on second segment. Paranota absent, segments cylindrical. Sternites sparsely setose; sternite of fifth segment modified in males. Legs and antennae normal. First legs of males incrassate, with strong ventral femoral tubercle; other anterior legs of males unmodified. Gonopod coxae robust, prefemora short, densely setose, articulation with acropodite distinct. Acropodite long, quite straight. Femorite about one-third of acropodite length. Femoral process absent; articulation at end of femur moderately distinct. Tibiotarsus (*tt*, Figure 1) long, thin, unbranched. Solenomerite (*s*, Figure 1) without processes, twisted 360 degrees around its lengthwise axis, apical third abruptly deflected mesally and ventrally, curving in nearly a complete circle.

Distribution

Known only from the Cape Range, Western Australia.

Included species

Only the type.

Remarks

Boreohesperus is placed in the Tribe Australiosomatini with some hesitation, on the basis of the short femorite and the presence of a distinct tibiotarsus. The nonseminiferous branch is regarded here as a tibiotarsus in spite of the fact that it departs the acropodite on the anteriolateral, not posterior surface; this is a reflection of the extreme coiling of the gonopod in this genus, as the drawing shows. The presence of only two acropodite branches suggests a relationship to a group of genera from eastern and southern Australia, to wit: *Dicladosoma* (Victoria), *Phyllocladosoma* (Queensland, New South Wales), *Somethus* (South Australia, Tasmania, Victoria), and *Oncocladosoma* (South Australia). In *Dicladosoma* Brölemann, 1913 and *Phyllocladosoma* Jeekel, 1968, the tibiotarsus is by far the largest of the two branches (Attems 1937; Jeekel 1968). *Somethus* Chamberlin, 1920 and *Oncocladosoma* Jeekel, 1985 retain femoral processes and have the tip of the solenomerite uncate, not coiled (Jeekel 1985). Further, in all these genera the femorite is much shorter than in *Boreohesperus.*

In the Antichiropodini, well represented in Western Australia, the homologies of the gonopod branches remain in confusion, but in at least one group of genera in the tribe, including *Antichiropus* and *Helicopodosoma,* the gonopod solenomerite is strongly coiled as it is in *Boreohesperus. Antichiropus* species (Attems 1911, 1937) usually have two or three short processes of indeterminate identity at the base of the long, coiled solenomerite, a long femorite and no tibiotarsus (unless the tibiotarsus has fused for most of its length with the solenomerite). *Helicopodosoma* (Attems 1937) evidently lacks all processes; the gonopod is a simple rod with a coiled tip. The new genus (Humphreys and Shear, in press) is strongly modified for a troglobitic existence, with elongated segments, legs and antennae, and lacks all pigment.

If the assignment of *Boreohesperus* to the Australiosomatini holds up, it represents the first record of that tribe in Western Australia.

***Boreohesperus capensis,* sp. nov.**

Figure 1

Holotype

Male, Cave 324 (22°22'34"S; 113°51'25"E), Cape Range, North West Cape, Western Australia, 27 August 1989, M. East (WAM 91/1408).

Paratypes

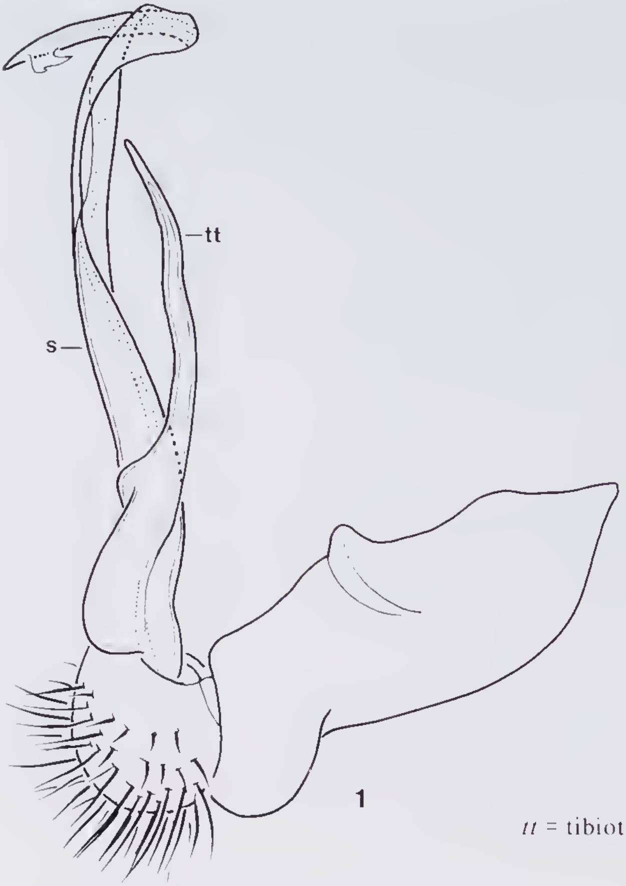
Female, same collection data as male (WAM 91/1409). 2 males, Cave 203 (22°26'14"S; 113°54'39"E), 19 July 1989, W. F. Humphreys (WAM 91/1410-1411). Male, surface near Cave 106, 21 June 1989, M. S. Harvey (Australian Museum). Male, Cave 222, 10 July 1989, E. Bowra (American Museum of Natural History). Male, Cave 225 (21°56'31"S; 114°05'39"E), near entrance, 30 June 1989, M. East (Zoologische Museum Amsterdam).

Diagnosis

See Diagnosis of the genus.

Description

Male. About 18-20 mm long, 1.9 mm wide. Segments as described for genus; second segment with pronounced pleural keel, anterior angle of keel strongly projecting. Third segment with low projection in usual position of paranota, subtended by few indistinct striae. Subsequent segments without pleural keels or paranota, pores, when



tt = tibiotarsus; *s* = solenomerite.

Figure 1 Left gonopod of *Boreohesperus capensis*, lateral view.

present, opening flush on surface of segment. Legs and antennae robust. First legs with usual modifications. Sternum of fifth segment with anterioventrally projecting process between coxae of anterior pair of legs; process roughly trapezoidal in posterior view, with notch in apex; anteriorly, apex set with fine setae.

Gonopods (Figure 1) with coxa nearly three times as long as broad, coxa with strong anterior ridge which in situ rests on anterior margin of gonopod socket. Prefemur short, subglobose, articulation with acropodite distinct. Femorite about one-third to one-fourth of acropodite length, twisted, enlarged at base. Tibiotarsus not exceeding solenomerite, slender, acuminate, curved mesally, appearing to arise posteriolaterally because of twist in femorite. Solenomerite twisted 360 degrees or more on its long axis, apical part coiled in nearly a complete circle, tip with small, laminate subterminal process.

Colour dark brown at low magnification, appearing black in the field.

Female. Structure in nonsexual characters as in male. About 20-22 mm long, 2.0 mm wide.

Distribution

Caves in the Cape Range of the North West Cape, Western Australia, in addition to the type localities as follows (all specimens in WAM): Cave 328 (22°01'21"S; 113°55'39"S) 28 August 1989, M. East (male). Cave 68, 26 June 1989, R. Wood (male). Cave 162 (22°09'00"S; 113°59'51"E), 20 June 1989, M. S. Harvey (male). Cave 232, 10 July 1989, M. Bowra (male). Surface at 22°03'S; 114°02'E, 26 June 1989, W. F. Humphreys (male). Cave 18 (22°05'24"S; 113°59'30"E), 26 June 1989, B. Vine (juvenile). Near Cave 21 (22°14'00"S; 113°58'18"E) on surface, 10 July 1989, A. J. Humphreys (female). Surface near Cave 161 (22°12'33"S; 113°58'14"E), 2 August 1989, E. Pryor (female). Cave 107 (22°07'00"S; 113°59'54"E), 30 June 1989, B. Vine (female). Surface near Cave 203 (22°26'14"S; 113°59'54"E), in litter among rocks below a fig tree, 19 July 1989, B. Jones (2 females, juvenile). Cave 177 (22°06'19"S; 113°57'48"E), 7 July 1989, M. East (female). Cave 111 (22°55'08"S; 114°00'17"E), 5 July 1989, R. Wood (2 females). Cave 21 (22°14'00"S; 113°58'18"E), 10 July 1989, A. J. Humphreys (female).

Notes

This species has commonly been found in caves, often near the entrance, as well as on the surface. The species shows no troglobitic adaptations, and its presence in caves is probably accidental, though cave entrances may present attractive refuges in the dry enviroment of the Cape Range. The details of distribution remain unknown, as little surface collecting has been done on the North West Cape Peninsula.

The females (and even juveniles) of this species may be separated at a glance from the females of the following species by the strongly projecting triangular anterior corner of the pleural keel of the second segment. However, at present we have only one syntopic record, from Cave 225.

Tribe Antichiropodini Brölemann

Antichiropus Attems

Antichiropus Attems, 1911, 3:168. 1937, p. 266. Jeekel, 1968, p. 29. 1982, 8:121-124. 1985, 19:34.

Species of the genus *Antichiropus* are among the most distinctive of Australian Paradoxosomatidae. The gonopod has a comparatively long femorite (as in most antichiropodines), but the solenomerite is nearly as long and strongly coiled, in most species in at least a complete circle.

Attems (1911) named seven species and subspecies from Western Australia, and Jeekel (1982) added one from South Australia. The New Guinea species (Silvestri 1895) placed in the genus by Attems (1937) were re-examined by Jeekel (1956, 1964). *Strongylosoma luxuriosum* Silvestri was assigned to *Hoplotessara*; Jeekel (1956) speculated that this represented a mislabelled Australian collection. *Strongylosoma maculatum* Silvestri was assigned to *Dendrogonopus* (Jeekel 1964). *Hoplotessara* (Australiosomatini) and *Dendrogonopus* (Aschistodesmini) differ from *Antichiropus* at the tribal level.

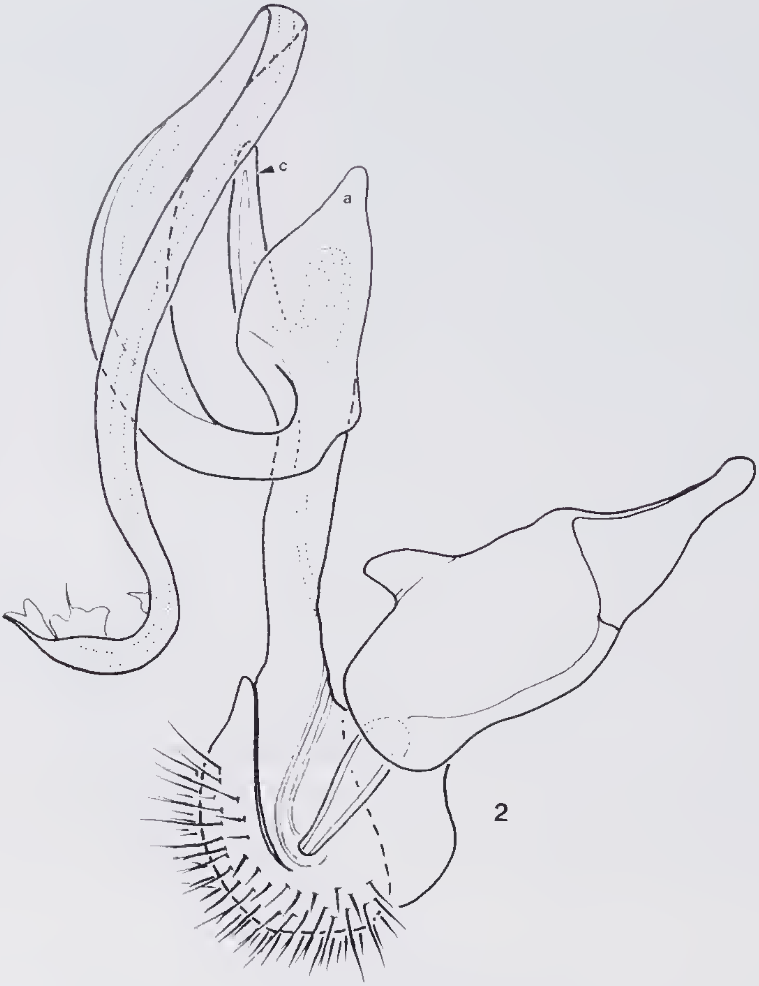


Figure 2 Right gonopod of *Antichiropus humphreysi*, mesal view.

Antichiropus humphreysi, sp. nov.

Figure 2

Holotype

Male, Cave 225 (21°56'31"S; 114°05'39"E), Cape Range, North West Cape, Western Australia, 10 July 1989, R. Young (WAM 91/1412).

Paratypes

Female, same collection data as holotype (WAM 91/1413). Male, same collection data as holotype (WAM 91/1414). Male, same collection data as holotype, but 30 June 1989 (Zoologische Museum Amsterdam).

Diagnosis

Easily distinguished from the other species of *Antichiropus* by the enormous development of the coiled solenomerite, far exceeding that of any previously described species.

Description

Male. About 18 mm long, 1.8 mm wide. Segments somewhat longer than broad, strongly constricted between metazonite and prozonite, unsculptured, smooth and shining. Second segment with weak pleural keel; third and fourth metazonites with low swellings representing paranota, subsequent segments without paranota, pores opening flush on surface. Labrum with pronounced transverse oval depression set with setae. First legs strongly incrassate, with prominent basoventral femoral tubercle. Fifth sternum with large lobe between anterior leg pair; lobe with evenly curved distal margin of hyaline cuticle, anterior surface with bilaterally paired setose swellings near base.

Gonopod coxae (Figure 2) twice as long as broad, with very pronounced shelf on anterior surface, in life lodging under anterior border of gonopod socket. Prefemur subglobose, nearly as massive as coxa, articulation with acropodite distinct, with posterior articular lip. Femorite long, about two-thirds acropodite length, distally thickened, flaring, with acute subtriangular terminus (femoral process?). Process *a* (see notes below) prominent, smoothly tapering to bluntly rounded tip. Solenomerite very long, estimated twice as long as remainder of acropodite if uncoiled; curving first posteriorly, then laterally, widening, then turning anteriorly, finally dorsally in shallow, sigmoid curves. Tip of solenomerite complex, with two subterminal processes, actual apex evidently bifid.

Colour dark brown, somewhat lighter than the foregoing, with prozonites lighter brown still.

Female. Structure in nonsexual characters as in male. About 20 mm long, 2.0 mm wide.

Etymology

It is a pleasure to name this distinctive species for William F. Humphreys, who has led the biological exploration of the Cape Range caves.

Distribution

So far this species has been collected in only one cave, Cave 225. There it is syntopic with *Boreohesperus capensis*. The cave is in a very dry, shallow rock-shelter halfway up the wall of a gorge, 200 m from C-222, the only known location for one species in the new genus of Antichiropodini (Humphreys and Shear, in press).

Notes

The identities of the gonopod processes in *Antichiropus* remain obscure; the lettering of Figure 2 follows the scheme of Attems (1937) and Jeekel (1982). As in *A. minimus* and *whistleri*, process *b* seems to be missing. Without much to go on, the positions of the three basic processes suggest that a is simply a prolongation of the femorite consequent to making the sharp retrorse angle into the solenomerite, that b is the tibiotarsus, and that c is a prefemoral process.

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Biological observations of the Australian green carpenter bees, genus *Lestis* (Hymenoptera: Anthophoridae: Xylocopini)

Terry F. Houston*

Abstract

Opportunistic observations of the nests, provisions, life histories, forage plants, colony structure and nest associates of *Lestis bombylans* and *L. aeratus* are recorded and discussed. *L. aeratus* is recorded from South Australia for the first time.

Complex burrow systems with a single entrance occurred commonly and were inhabited by varying numbers of adults of both sexes (up to 10 females and 25 males). While some of these groups may have consisted of newly emerged siblings (with an older female, perhaps the mother, sometimes present) at least one group appeared to be an overwintering aggregation. In another nest, two females constructed brood cells independently. Nests appeared to be perennial when sufficient stem was available for extension of the burrow systems.

In south-eastern Queensland, cells of *L. bombylans* were constructed at the rate of one every two days and development from egg to adult required about 65 days.

Females are polylectic and form firm, somewhat tetrahedral provision masses. Pollen-collecting observed in the absence of brood cells probably served to sustain groups of overwintering adults.

The mite *Sennertia leei* occurred as a commensal in some nests, consuming unused provision, and its hypopi were carried by the adult bees.

Introduction

Lestis is an endemic Australian genus of large, attractive, metallic green bees (Figures 1, 2). There are probably only two valid species, *L. bombylans* Fabricius and *L. aeratus* Smith, but a critical revision of the genus is required (Hurd and Moure 1963, Michener 1965).

The genus is recorded only from eastern Australia, ranging from Cape York to Victoria (occurring chiefly on and east of the Great Dividing Range) but extends also into southern South Australia (a fact which has not previously been recorded in the literature).

The bees are reasonably abundant and yet little has been recorded of their habits. The observations presented here were made opportunistically over an eleven year period (1968-78) and, although fragmentary, significantly extend our knowledge of these fine bees. As there seems little chance that I will undertake further studies of the bees, it seems desirable that my field notes should be published and made available to other workers.

Specimens taken during the course of my observations have been deposited in the collections of the South Australian Museum, Adelaide, and the Western Australian Museum, Perth.

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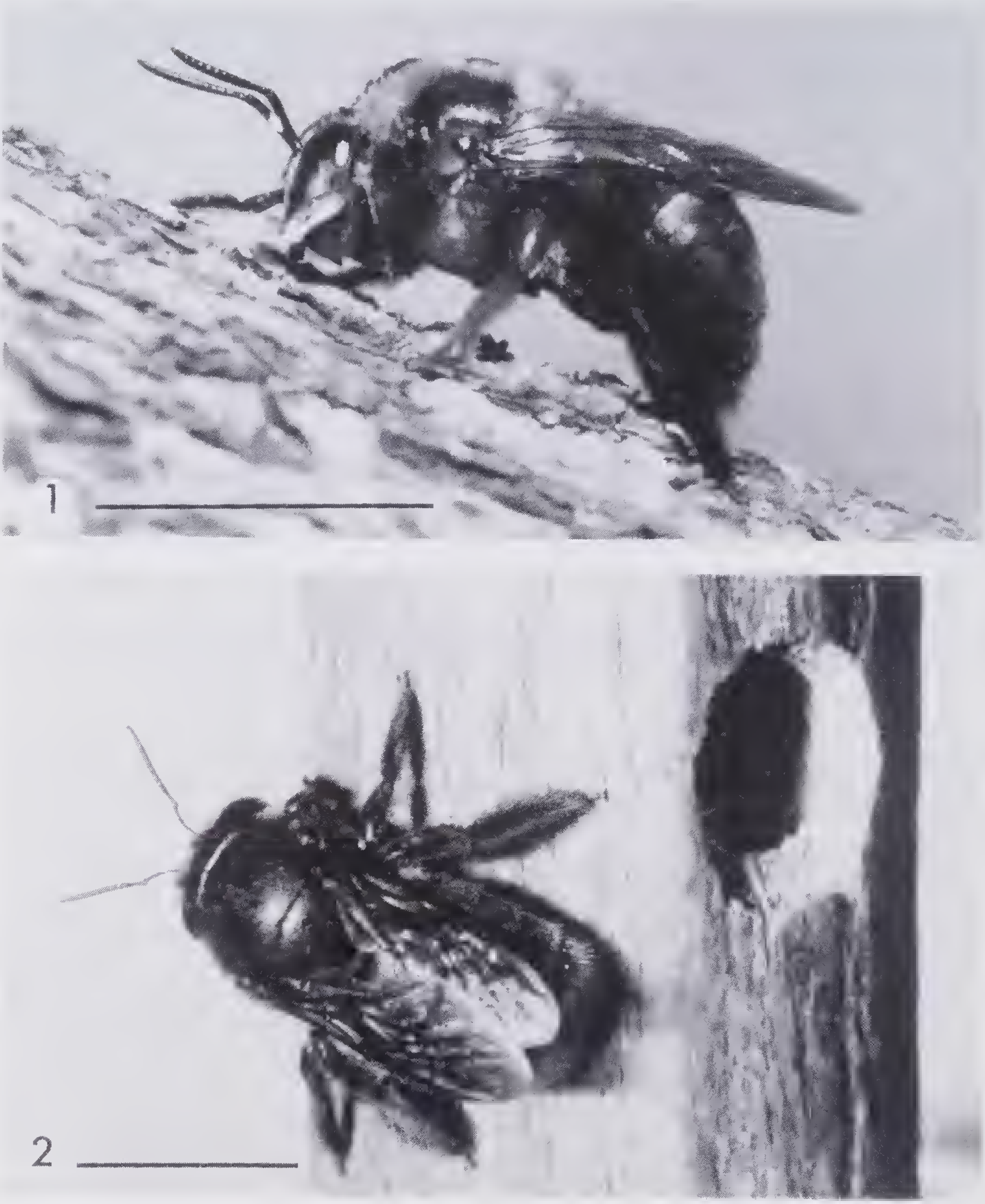


Figures 1-2 Adults of *Lestis: (1) male of L. bombylans* (note the numerous hypopi of the mite *Sennertia leei* clinging to the thoracic pubescence, especially close to the head); (2) female of *L. aeratus* near the entrance to its nest in a dead flower scape of *Xanthorrhoea*. Scale lines = 1 cm.

Summary of literature

Hurd and Moure (1963) listed all prior biological references to *Lestis* and summarized the known nesting substrates. Smith (1851) gave the first account of the nests of *Lestis*, stating that the bees nested in the hollow stems of "Zamia or the grass trees" (perhaps confusing *Xanthorrhoea* with the cycad *Macrozamia*). Froggatt (1896) also recorded *bombylans* (as *bombiliformis*) nesting in dry flower scapes of *Xanthorrhoea*. Hacker (1918) reported that, near Brisbane, *L. bombylans* made its nests in dead stems or branches of *Xanthorrhoea*, *Leptospermum* and *Casuarina* and females were said to defend their nests by blocking the entrance holes with their heads. Hacker figured one nest with a simple burrow along the length of a branch, a lateral entrance hole, and five closed brood cells in two linear series, three at one end of the burrow and two at the other. Rayment (1935) briefly described the nesting activity of *L. bombylans* in the dry flower scapes of *Xanthorrhoea*. His description of the nest was essentially similar to Hacker's. Rayment noted also that nests of '*L. aerata*' had been found in twigs of *Casuarina* in Victoria. McKeown (1945) briefly described and figured the nest of *L. bombylans* and Michener (1965: 243) recorded some forage plants for this species.

Observations and Discussion

Geographic Distribution

Lestis has been reported as occurring from northern Queensland to Victoria (east to the Grampian Ranges) (Hacker 1921, Hurd & Moure 1963, Michener 1965). However, specimens in Australian collections suggest a patchy and chiefly coastal distribution from the tip of Cape York, Qd, south to Victoria and east to Kangaroo Island, South Australia. The range does not extend west of the Great Dividing Range and Carnarvon Gorge National Park, 290 km south-west of Rockhampton, Queensland, is the most inland record. I have seen no specimens from Tasmania despite Smith's (1854) record of *L. aeratus* from 'Van Diemens Land'.

The individual distributions of the two species have not been clearly established. Cockerell (1930) considered *aeratus* to range from northern Queensland to Victoria and *bombylans* to be restricted to Queensland. However, Rayment (1954) recorded the latter also from Sydney. Clarification of the distributions must await a revision of the species and is beyond the scope of this paper.

L. aeratus is extant on Kangaroo Island but is probably now extinct on mainland South Australia. Its former occurrence there is attested by the following old specimens in the South Australian Museum: 1 ♀, Aldinga, 28.7.[18]96, W.F.[?] Kimber; 1♂, Aldinga; 1 ♀, Naracoorte, 29.9.[18]88, R.D., Rev. A. Burgess; 1♂, 1♀, Naracoorte. Extensive searches of likely habitat near these and other mainland localities (including southern Yorke and Eyre Peninsulas) during 1970-78 revealed no sightings of *Lestis* nor any signs of their work.

An intensive search for adults and nests of *L. aeratus* was made on Kangaroo Island during two visits in 1970 and 1978. The localities where they were found are listed in

Table 1. These localites are distributed peripherally on the western two thirds of the island. No trace of the species was found on the eastern third of the island or in its central region despite the occurrence there of some seemingly suitable habitat and nesting substrate.

Floral relationships

Very few records of flower visiting are available for *Lestis* but they do suggest that the bees are polylectic. Michener (1965) recorded *bombylans* visiting flowers of four genera, *Hibbertia* (Dilleniaceae), *Baeckea* and *Melaleuca* (Myrtaceae), and *Leucopogon* (Epacridaceae), and collecting pollen from the first two of these genera. Eight females of *bombylans* collecting pollen from *Hibbertia* were captured by me near Noosa, Queensland, in January. Females buzzed quite audibly as they raked through the dense clusters of stamens, a phenomenon reported for other bees that collect pollen from flowers with 'shaving-brush' clusters of stamens (Buchmann 1985).

Records for *aeratus* are 1♂, 2♀ from flowers of *Leptospermum* and 2♀ from flowers of *Leucopogon* on Kangaroo Island, South Australia, in October. Microscopic examination of both provisions and larval faeces from six cells in three nests and adult faeces from a fourth nest revealed four quite different unidentified kinds of pollen grains in one cell and a fifth, myrtaceous kind in all the remaining samples.

Nesting sites

Nine inhabited nests of each species and a few abandoned ones were observed. Details of nests and their contents are presented in Table 1.

The bees select standing, dead, dry, pithy wood in which to nest. I observed single nests of *L. bombylans* in trunks of *Acacia* and *Tristania suaveolens* and seven in branches of a single *Banksia* tree. All nests of *L. aeratus* were in flower scapes of *Xanthorrhoea*. Other plants utilized for nesting are *Casuarina* and *Leptospermum* (Hacker 1918, Rayment 1935). The range of nesting stem diameters was 17-70 mm in *bombylans* and 28-50 mm in *aeratus*. Nest entrances occurred 90-295 cm above the ground in *aeratus* and 120-270 cm in *bombylans*.

Generally, nests occurred singly. However, three separate nests of *aeratus* (two of them abandoned and one of these occupied by an ant colony) were found in a single flower scape of *Xanthorrhoea* near Rocky River Homestead on Kangaroo Island. At Woy Woy near Sydney, one *Banksia* branch contained two nests and another contained three nests of *bombylans*. In all cases the nests were occupied and the entrances were about 17-20 cm apart.

Nest architecture

Entrances to nests occurred laterally in stems or branches (not terminally) and consisted of a neat round hole (Figure 2) of diameter 7-8 mm (*bombylans*) and 8-10 mm (*aeratus*). Where nests occurred in horizontal or oblique branches, the entrances were

Table 1: Details of *Lestis* nest and their contents. All localities for *L. aeratus* are on Kangaroo Island, South Australia. Symbols: E, egg; pA, pharate adult; pP, prepupa; ˜ in the 'cells' column means no live stage present and in the immatures column means immature dead.

Nest #	Collection date and locality	No. of blind ends	Total length (mm)	No. of cells	No. of immatures	No. of adults	
						♀	♂
L. aeratus							
1.	4-8.x.1970 Cape Borda	2	318	0	0	3	2
2.	4-8.x.1970 Stokes Bay	2	204	0	0	2	0
3.	4-8.x.1970 Seal Bay	6	587	0	0	3	0
4.	ditto	5	628	0	0	9	12
5.	22.x.1970 Cape Borda	2	402	0	0	2	25
6.	8-20.iii.1978 Rocky River	6	720	0	0	5	7
7.	ditto	9	733	1	1pP˜	0	0
8.	14.iii.1978 Murray Lagoon	2	251	0	0	3	3
9.	20.iii.1978 Ravine de Casoars	3	400	1	1E˜, 2pA	2	3
10.	ditto	2	188	3	1L˜, 2pA	1	0
L. bombylans							
1.	10.ix.1968, nr Mooloolaba, Qd	2	155	5	3E, 1L	2	0
2.	20.xi.1968 Tambourine, Qd	6	423	0	0	5	1
3.	27.i.1971 Woy Woy, N.S.W.	10	795	1	0	8	4
4.	ditto	5	273	1	1pA	3	1
5.	ditto	3	215	1˜	0	10	3
6.	ditto	2	217	4˜	0	0	0
7.	ditto	7	272	1˜	?	4	3
8.	ditto	8	418	1?	1L	7	3
9.	ditto	8	454	0	0	5	1

always on the undersides. Entrance chambers broadened strongly within, extending no more than 1 cm before opening into the primary shaft.

Previous accounts of nests have noted only a single, simple burrow extending above and below the entrance. Seven nests found by me were of this form (Figure 3) but the majority (12 nests) had branched burrows (Figures 9-11). In all cases, the burrows extended along the grain of the wood (except for curved sections where burrows adjoined).

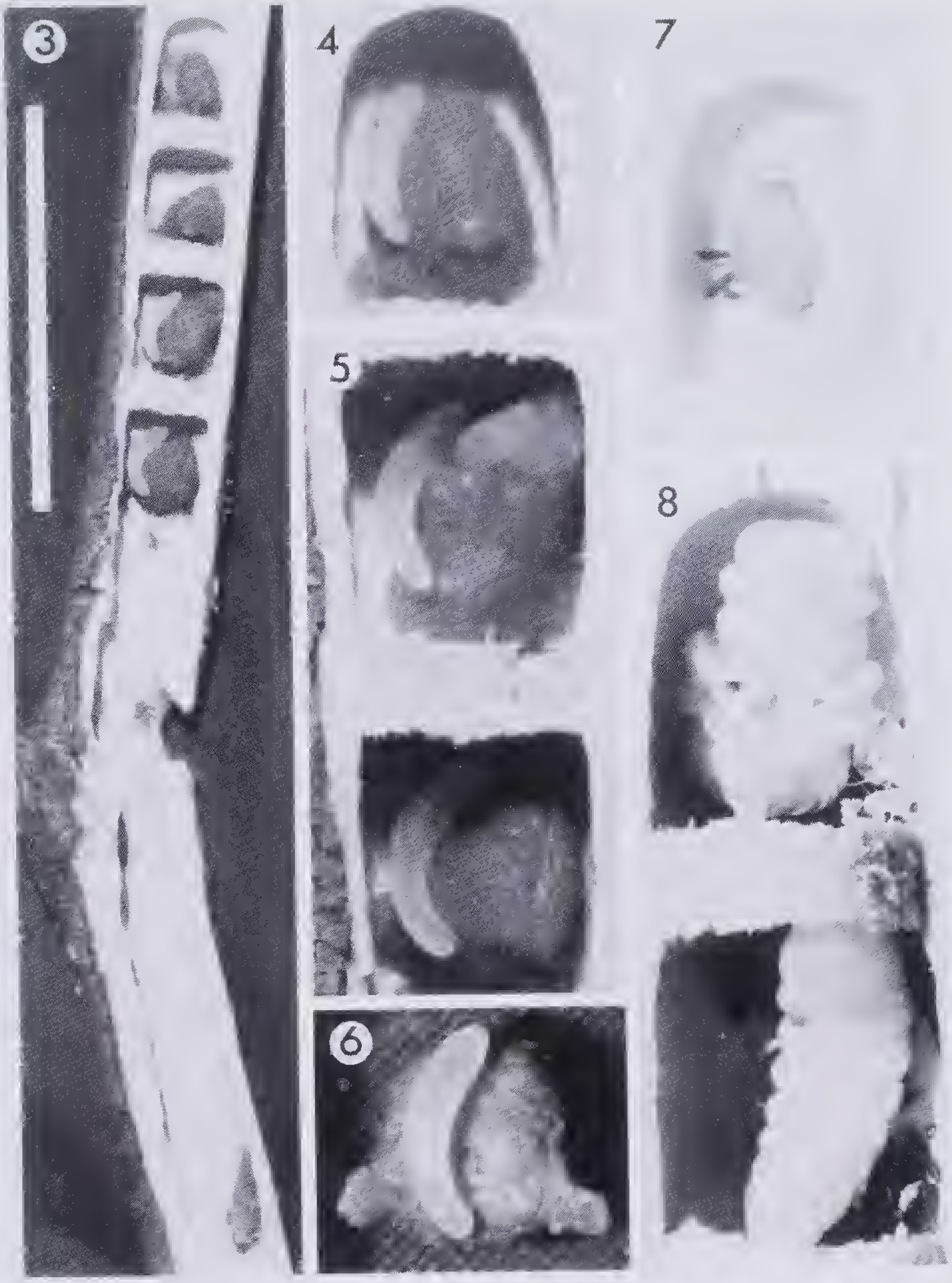
Presumably all nests are initiated as simple, double-ended burrows but, given adequate stem thickness, extensions may be added. Primary, secondary and tertiary burrows were recognized (Figure 9). Primary burrows were always double-ended but secondary and tertiary burrows were either single or double-ended. Both ascending and descending single-ended extensions were encountered. A measure of the complexity of burrow systems is given by the number of blind ends present (Table 1) and the most complex nest found was *bombylans* nest #3 with ten (Figure 9). In this instance, burrow lengths totalled 795 mm.

Internal openings (ports) connecting older burrows with newer ones were larger than nest entrances and usually elliptical. The largest measured had a greatest diameter of 25 mm. Secondary ports (openings into secondary burrows) usually occurred in close proximity to the nest entrances and tertiary ports were similarly close to secondary ports. Rarely did a burrow arise more than halfway along an ascending or descending portion of a parent burrow.

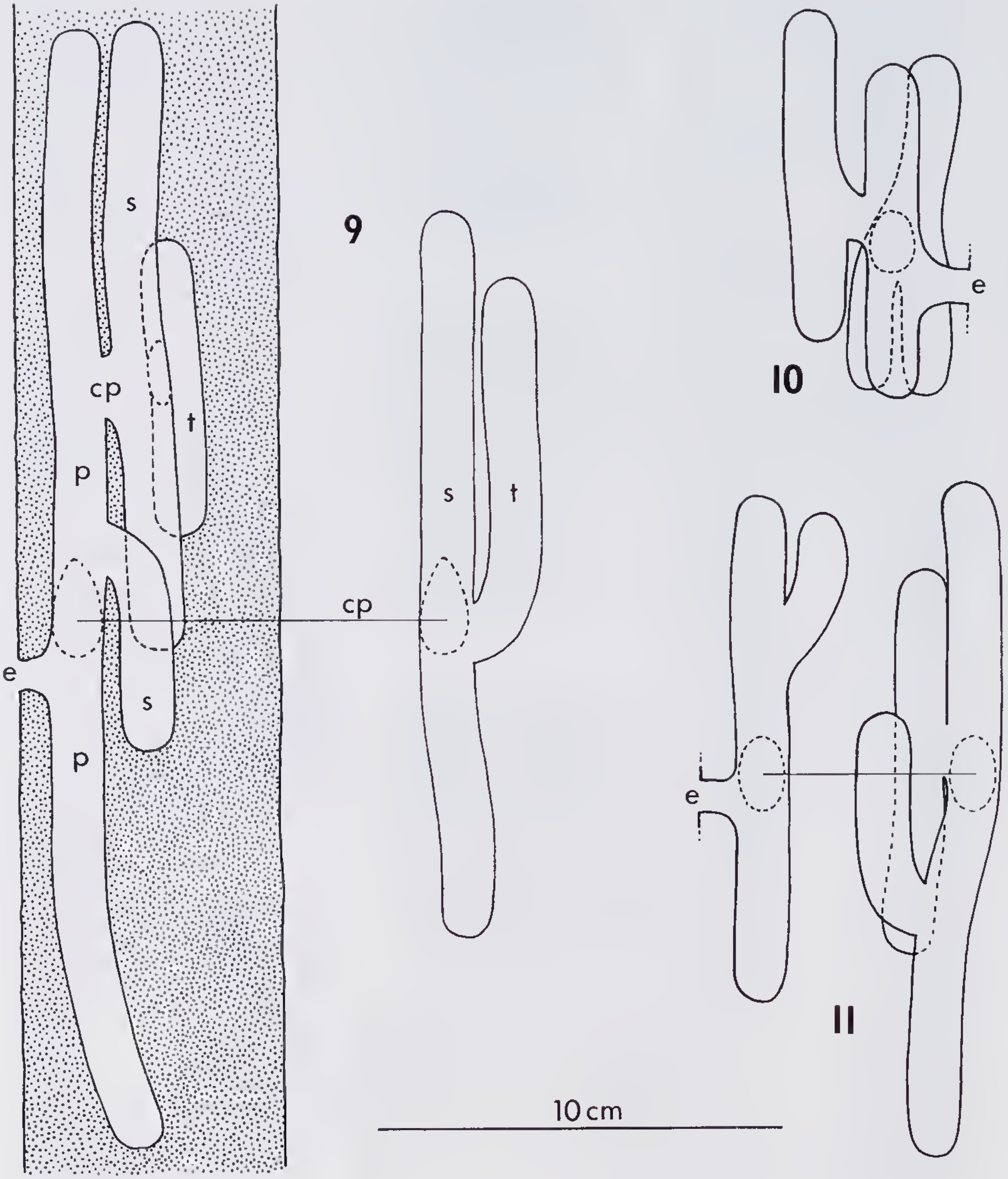
Burrows were round in section with a diameter of 11.0-12.5 mm in *bombylans* and 12.0-14.5 mm in *aeratus*. In complex nests, burrows often lay closely parallel and walls between them were sometimes paper thin. In a few cases, perforations occurred between closely juxtaposed burrows. Where three *aeratus* nests had been built in one stem, the burrows of adjacent nests interdigitated without contact and it was clear that during nest excavation females had deviated from straight paths to avoid one another's burrows.

The distal halves or two-thirds of burrows usually exhibited regular series of swellings. Where cells occurred, they coincided with the swellings and their caps with the constrictions. Some newly excavated burrows lacked swellings while others (still without cells) had them. One freshly provisioned but uncapped cell occurred in a swelling. These observations suggest that females first excavate cyclindrical burrows then excavate the swellings prior to commencement of provisioning. Scraping particles of wood from the walls to form cell partitions most probably accentuates swellings ahead of completed cells.

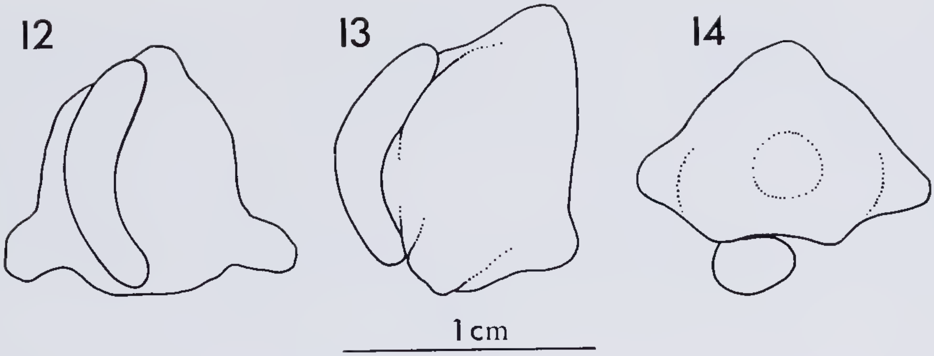
As will be seen from Table 1, cells were found in seven of the eight occupied nests of *bombylans* but only three of the nine occupied nests of *aeratus*. The greatest number of cells in any one nest was five in *bombylans* nest #1. Four closed cells occupied the upper section of this nest and one open cell being provisioned occurred in the lower section. Above the lowermost cell was a swelling and space adequate to accommodate a sixth cell. Evidence of up to six cells being built in series was provided by pollen-stained swellings with traces of cell caps in *aeratus* nests #8 and #9.



Figures 3-8 Nest, provisions and immatures of *Lestis bombylans* (nest # 1): (3) longitudinal section of nest (note unformed, incomplete provision in lower end of burrow; scale line = 5 cm); (4) first (uppermost) cell with first-instar larva on provision; (5) third and fourth cells with eggs on provisions; (6) egg on provision; (7) first cell with near-mature larva feeding on provision (note dark faeces); (8) first and second cells with pupa and prepupa.



Figures 9-11 Nest burrow complexes of *Lestis bombylans* in profile (diagrammatic; all from Woy Woy, N.S.W., in dead branches of *Banksia*; nests ## 1, 5, 7, respectively, Table 1). Branch substrate shown stippled in Figure 9. Horizontal lines associate parts of nests drawn separately by their connecting port. Legend: **cp** =connecting port; **e** = nest entrance; **p** = primary, s = secondary and **t** = tertiary burrows.



Figures 12-14 Three views of provision masses of *Lestis bombylans* bearing eggs: 12, 13 adaxial views; 14 axial view from proximal end (based on Kodachromes of nest #1 contents; see Figure 5 for orientation in cell; egg may have been displaced sideways through handling in 12 and 14).

Cells were barrel-shaped. Their caps, which were composed of cemented particles of wood or pith, were slightly concave with a distinct spiral pattern on the inner surface and smooth and strongly concave on the outer surface. They formed partitions between adjacent cells and were spaced at intervals of 16 mm in *bombylans* and 19 mm in *aeratus*.

Provisions

Newly completed provisions of both species consisted of firm moist masses of pollen, somewhat tetrahedral in shape and resting on four tubercles, one facing the cell base and three facing the cap (Figures 3-6, 12-14). The surface bearing the egg or young larva was gently concave (Fig. 14). Rayment (1935) and McKeown (1945) described the provision as spherical with the egg atop.

One incompletely provisioned cell contained a large 'scale' of moist pollen fitting flush against its base and side wall (Figure 3) so it appears that the bees accumulate pollen and nectar together in a compacted state during at least the late stages of foraging and then mould the provision prior to oviposition.

Immatures and development

The egg, typically large as in other xylocopines and measuring 9 mm in length in *bombylans*, rested on the flatter side of the provision lengthways in the cell (Figures 3, 5, 6). McKeown's (1945) figure (p. 201) incorrectly indicates a small egg *ca.* 3 mm long.

Some indication of the duration of the immature stages was gauged from the occupants of four cells in *bombylans* nest #1 which was kept intact and observed periodically in the laboratory. The immatures seemed to be about two days out of phase with their neighbours suggesting that the cells had been completed at intervals of two days. All eggs had hatched within a week of the nest being found. The larval feeding phase occupied 16-19 days with defaecation commencing on the 12th day. At this stage the larva was large enough to curl around and support the reduced, spherical provision mass (Figure 7) and the dry, dark red, rod-like faeces fell harmlessly to the floor of the cell. The prepupae and pupae orientated themselves with their heads towards the bases of their cells (Figure 8), not the caps as is usual amongst bees (two pharate adults of *aeratus* were found similarly orientated in their cells). Orientation of prepupae and pupae towards cell bases was figured for some *Xylocopa* species (Gerling *et al* 1983) and may be a xylocopine norm. Pupation occurred 13 days after the completion of feeding and adults began emerging from the pupal cuticle 25-27 days later. The total time from oviposition to emergence of the adult would have been a little over 65 days.

The pharate adults reorientated correctly with their heads against the cell caps and commenced picking at them with their mandibles. In *aeratus* nest #9 two pharate adults were found on top of a mass of loose frass (pith, faeces and exuviae).

Adult behaviour

Little was observed of female behaviour and nothing at all of males outside of nests.

When nests were being opened, an occupant female sometimes blocked the nest entrance with the dorsum of the metasoma and stubbornly resisted being dislodged with a probe. Such disturbance also resulted in some females emitting a loud buzzing sound (produced by vibration of the flight muscles) in short intermittent bursts or continuously for several minutes.

Adults were difficult to remove from burrows, even after the latter had been opened lengthwise, and tended to retreat to any part of the nest that afforded them more protection.

Occasionally, when an adult was grasped in forceps, it spurted liquid faecal material. Ejection of faecal fluid for distances up to 30 cm was also observed to occur from entrances of undisturbed nests of *bombylans*. Congealed drops of faecal material adhered to the lower rim of several nest entrances of both *Lestis* species suggesting that projectile defaecation is of common occurrence.

Nest occupancy and sociality

As will be seen from Table 1, most nests found were inhabited by both sexes and by more than one female. Even nests with just a single primary burrow (two blind ends) sometimes had more than one female. As nests were found and collected during the day, some of their adult inhabitants may have been out foraging and the figures in Table 1 may not fully represent nest populations. Up to nine females occupied nests of *aeratus*, up to ten in *bombylans*.

The degree of wing wear (as an indicator of relative age) was noted for all adults taken by me from nests. By far the majority of adults had entire wing margins and several bore one to a few nicks. Adults with well worn wings and therefore likely to be relatively old were seldom encountered with never more than one per nest complex.

One female from *bombylans* nest #1 had tattered wings while the wings of another were almost entire (for dates of these and the following records see Table 1). Dissection revealed that both females had well-developed ovaries with some enlarged oocytes, 5-6 mm long, and spermathecae containing sperm. As the nest contained two incomplete cells, it appeared that these females were nesting independently in opposite ends of the single burrow.

A female of *bombylans* collected while entering nest #3 loaded with pollen also had tattered wings. Her nest companions had entire wing margins and one male was obviously freshly emerged.

All five females in *bombylans* nest #2 had entire wing margins or (in one) only a few small nicks indicating that they were young females and they may have been progeny of the nest.

A female of *aeratus* collected while foraging at flowers on 4 October had extremely frayed wings and had presumably overwintered in this state.

Most nests were occupied by one or more males up to a maximum of 25 in *aeratus* nest #5. Not all of the males and two females of nest #5 could have been progeny of the nest: only 12 or 13 burrow swellings which could be equated to previous brood cells were discernible in the burrows and the total length of the burrow was quite insufficient to accommodate 27 brood cells. Consequently, some of these adults must have come from elsewhere. The wings of five males bore a few to several nicks indicative of some flight activity while those of the remainder were entire.

It was interesting to note that the walls of nest #5 were stained yellow with pollen, particularly closer to the entrance, suggesting that the females had been bringing in and unloading pollen shortly prior to collection of the nest. As no cells were present, the pollen may have provided nutrition for the large adult population.

The walls of many older burrows were dark-stained (usually a sooty grey), presumably by mould growing on pollen and nectar soiling, whereas newly excavated burrows were quite clean and pale. This contrast revealed where some old burrows had been extended. For example, the upper extremities of the primary and secondary burrows of *aeratus* nests #1, #3 and #4 had been extended upwards from 25-130 mm and these extensions lacked the swellings of the older, stained burrows. This suggests that successive generations may reuse burrows. However, old burrows probably cannot be refurbished for cell construction as their diameters would increase beyond acceptable limits as females scraped particles from the walls for construction of cell caps (Stark *et al* (1990) reported that females of *Xylocopa sulcatipes* competing for dominance will break into and reseal each others brood cells but did not reveal whether material from the old partition is reused or new material was scraped from burrow walls).

Evidence of recent burrowing occurred in many nests with two or more females and it seems clear that nesting proceeds in the presence of groups of adults.

To see if there was any indication of social behaviour in *Lestis*, I dissected eight females of *bombylans* collected while foraging for pollen at flowers of *Hibbertia*, 8 km south of Noosa, Queensland, on 18 January 1969. All females carried sperm in their spermathecae. Their ovaries varied from slender with no obvious oocytes to moderately enlarged with two or more oocytes up to 5.5 mm long. The females with the smallest ovaries all had very worn wing margins suggesting that they were old. However, two other females with very worn wings had moderately developed ovaries.

Phenology

A survey of specimen data in museum collections revealed only a sketchy picture of the phenology of *Lestis.* Adult females had been collected in all months except July with the greatest concentration in August-October. Males were far fewer but were also collected throughout much of the year. Specimen labels seldom indicated the circumstances of capture (whether from flowers or nests).

Similarly, only a sketchy picture of nesting phenology can be obtained from the available evidence. I found females of *bombylans* extending burrows and constructing cells in September in south-eastern Queensland and in late January near Sydney. Rayment (1935) recorded nest-building for *bombylans* in early October (locality not stated). Given an egg-adult development time of 65 days, successive generations of adults could appear in November, January and April. My nests ## 3-9, collected in late January, strongly suggested a recent emergence of adults and the earliest stages of cell construction (newly excavated burrows and one cell receiving pollen).

The nests of *aeratus* collected in October are presumed to have contained groups of over-wintering adults as months of wintery conditions had preceded their collection and while burrows were being extended, cell construction had not commenced. If cells were built around early November, successive generations of adults might appear in January and March. March nests (## 6-10) provided evidence of an emergence of young adults at that time. Assuming no further breeding occurs through the cool months of April-August, *aeratus* (at least in the southern extremity of its range) could produce two generations per year and *bombylans* (at least in the Brisbane-Sydney region) could produce three. However, many more observations are required to obtain a reliable picture of the phenology of the two species.

Associated organisms

Only one intranest associate of *Lestis* was found. A mite, tentatively identified as *Sennertia leei* Fain (Chaetodactylidae) by B.M. O'Connor, was encountered in three nests of *bombylans* and two of *aeratus.*

In *bombylans* nest #2, which contained no brood cells, nymphs and adults (but no hypopi) of the mite were found crawling about the tunnel walls. When a particle of pollen provision was placed in a tunnel the mites immediately converged on it and began feeding. They were then transferred to a glass vial with the provision and eggs appeared within three days.

The one closed cell in *bombylans* nest #3 was infested with the mites and contained a loose, powdery mass of pollen grains, mites and mite exuviae. No trace of a bee immature was found and it appeared that the mites had demolished a provision mass.

One male and five female *bombylans* adults in nest #9 carried hypopi. The mites were clustered on the frons, vertex, occiput, anterior of the scutum, the propodeum, base of metasoma and beneath the wing bases of the bees (Figure 1).

Mite larvae, nymphs and adults were also observed wandering in burrows of *aeratus* and a few hypopi were observed on prothoracic and scutal pubescence of adults of this species.

The foregoing observations suggest that *Sennertia leei* is a scavenger in nests of *Lestis*, feeding on larval provision. Whether the mites infest only cells where the bee immature has failed to develop remains to be answered. Clearly the mite is transported to new nests on the bodies of the bees.

Sennertia leei hypopi (misidentified as *S. bifilis* (Canestrini)) were recorded from adults of *bombylans* and *aeratus* by Rayment (1954).

Conclusions

It would be unwise to attempt to make comparisons at the species level between my observations of *Lestis* and those of earlier authors because of uncertainties as to the authenticity of their identifications. Generally though, my observations confirm and extend the observations of earlier observers with few points of divergence.

Whereas all previous reports of nests have described only a single nest burrow (extending above and below the nest entrance), this study has shown that nests are often more extensive and complex where stems are sufficiently thick. It shows, too, that previous reports of spherical provisions (Froggatt 1896, McKeown 1945) are inaccurate and were presumably based on observations of partly consumed provisions.

Generally, groups of adults within burrow systems consist mostly of young individuals (presumably progeny of the nests) and occasionally include single older females (presumably their mother). However, in some cases, at least, adults congregate in burrow systems other than their natal ones and such groups may overwinter together. More than one female may build cells in a burrow complex but no evidence of cooperative behaviour was noted.

Much remains to be learned about *Lestis* biology. Nothing at all has so far been recorded of male behaviour and mating. Virtually nothing is known of the social structure of colonies or the interactions that occur between adults in nests. Only the sketchiest details of flower preferences, foraging behaviour, voltinism and nesting phenology are known.

However, what is known of the bees is consistent with the known habits of other Xylocopini as revealed by recent literature (Watmough 1974, Gerling *et al* 1983, Michener 1988). No known feature of the bees' biology can be deemed to be exclusive to *Lestis*.

The only known nest associate of *Lestis*, the mite *Sennertia leei*, was originally described from adults of *L. bombylans* (Fain 1982). It lives as a commensal in nests of both *bombylans* and *aeratus*, feeding on larval provision. Other *Sennertia* species have similarly been recorded as commensals in nests of Xylocopini (Abrahamovich & de Alzuet 1990; de Alzuet & Abrahamovich 1990).

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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.

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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.

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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.

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