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BARNACLES ON TURTLES IN QUEENSLAND WATERS WITH DESCRIPTIONS OF THREE NEW SPECIES

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ABSTRACT

Seventeen species of barnacle are described from five species of turtle. *Tubicinella cheloniae, Stomatolepas dermochelys*, and *Platylepas coriacea* are described as new; *Stephanolepas muricata* is recorded from Australian waters for the first time, and *Lepas hillii, L. anatifera, L. anserifera, Conchoderma virgatum, C. auritum, Balanus trigonus, B. variegatus, Chelonibia testudinaria, C. caretta, Stomatolepas praegustator, S. transversa, Platylepas hexastylos* and *P. decorata* are also recorded. Hosts recorded are *Chelonia mydas, C. depressa, Caretta caretta, Dermochelys coriacea*, and *Eretmochelys imbricata*. A key to the barnacles is given.

The material for this study was collected during the long term turtle research programme being conducted in Queensland waters by one of us (C.J.L.), and the taxonomic analysis was conducted by the other (R.M.).

There have been many reports of barnacles on turtles, but usually within the context of a more generalized taxonomic study (Darwin 1954; Pilsbry 1916; Stubbings 1965, 1967). This study is restricted to barnacles occurring on turtles, and especially barnacles of the family Coronulidae.

Barnacles of the family Coronulidae are obligate epizooans of a wide range of hosts and are commonly called 'turtle' or 'whale' barnacles, though also occurring on sirenians, sea snakes, crustaceans, molluscs, and fish (Ross and Newman 1967). The other two families represented in the collections for this paper (Lepadidae and Balanidae) may be regarded as facultative epizooans.

Seventeen species from five families are recorded from five hosts. Three species are described as new; *Tubicinella cheloniae, Stomatolepas dermochelys*, and *Platylepas coriacea*. Family names follow Newman and Ross (1976).

Register numbers prefixed by 'W' indicate material held in the Queensland Museum. 'U.S.N.M.' prefixes material from the Smithsonian Institution, Washington; 'N.Z.O.I.' the New Zealand Oceanographic Institution in Wellington; 'R.M.N.H.' the Rijksmuseum von Natuurlijke Historie, Leiden; 'B.M.N.H.' the British Museum (Natural History), London; 'Z.S.I.' the Zoological Survey of India, Calcutta; and 'I.R.S.N.B.' the Institut Royal des Sciences Naturelles de Belgique, Brussels.

SYSTEMATICS

Family LEPADIDAE

Lepas anserifera Linnaeus 1767
(Fig. 1)

MATERIAL EXAMINED

W6456–8, 3 specimens, Mon Repos, SE.Q., all ex *Caretta caretta*.

Valves white, furrowed in radiating lines; right scutum with a large umbonal tooth, left with a small tooth; carina contiguous with scuta and terga; peduncle short, dark purple brown, with a pale band at the junction with the capitulum; cosmopolitan, tropical and sub-tropical waters.

Lepas anatifera Linnaeus 1758
(Fig. 2)

MATERIAL EXAMINED

W6453–5, W7375, 21 specimens, Mon Repos, SE.Q., all ex *Caretta caretta*.

Distinguished by its white valves, sometimes bluish tinted, sometimes with a diagonal band(s) of small dirty green squares from umbo to carina;

carina contiguous with scuta and terga; right scutum with a large umbonal tooth, left scutum without a tooth; peduncle dark purple to brown, without a pale band at the junction with the capitulum, may be elongate in older specimens; cosmopolitan, tropical and temperate waters.

Lepas hillii (Leach 1818)
(Fig. 3)

MATERIAL EXAMINED

W6452, 1 specimen, Mon Repos, SE.Q., ex *Caretta caretta*.

Valves smooth, white; no umbonal teeth on scuta; carina well spaced from scuta and terga; peduncle dark purple brown with a broad pale band at the junction with the capitulum; cosmopolitan, possibly fewer specimens occur inshore (Stubbings 1967).

Conchoderma virgatum (Spengler 1790)
(Fig. 4)

MATERIAL EXAMINED

W4636, W7369, 5 specimens, Heron I., SE.Q.; W6496, 2 specimens, Mon Repos, SE.Q.; all ex *Caretta caretta*.

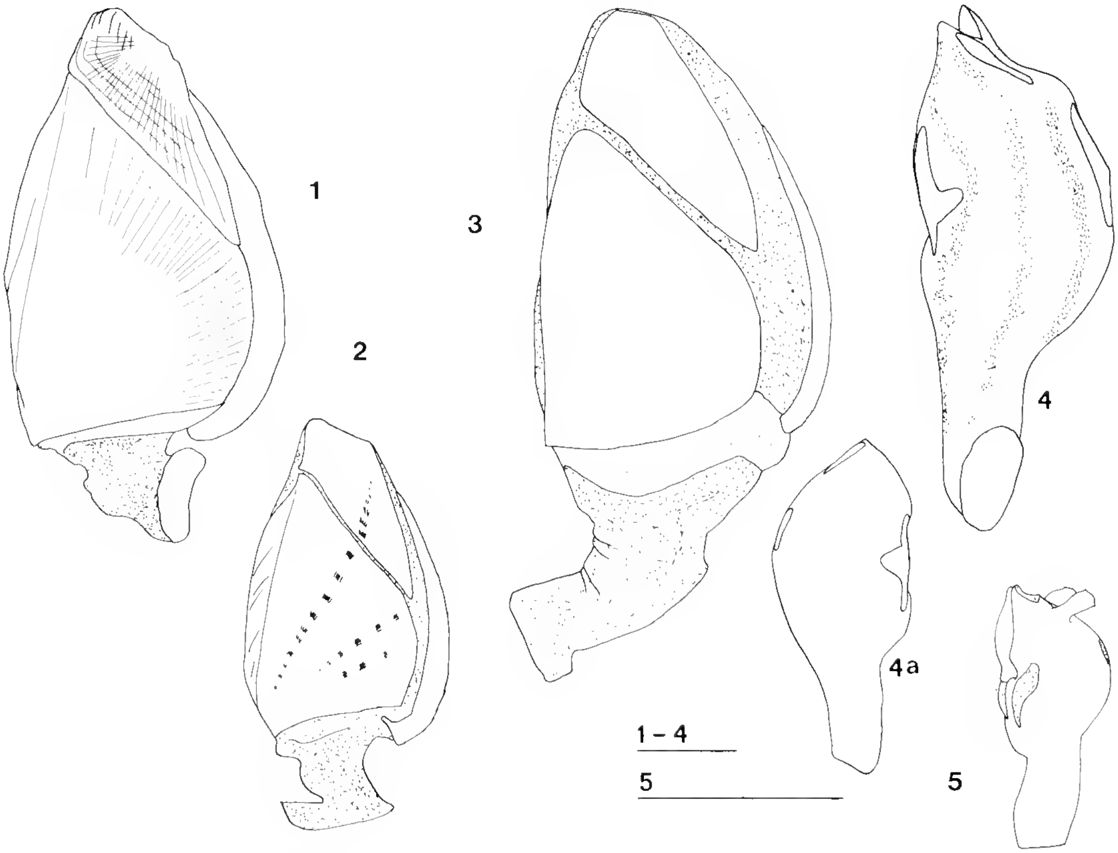
Scutum small, three lobed, carina opposite scuta and as long; terga small, curved, apically divergent; peduncle merges into capitulum, both with three longitudinal purple stripes; cosmopolitan tropical — warm temperate waters (Stubbings 1967).

Conchoderma virgatum chelonophilum (Leach 1818)
(Fig. 4a)

MATERIAL EXAMINED

W7368, 3 specimens, Heron I., SE.Q., ex mouth of *Caretta caretta*.

The largest specimen is 12 mm long, white, capitulum rounded, peduncle distinct; scuta trilobed, carina narrow, opposite scuta, terga very small.



FIGS. 1–5: 1. *Lepas anserifera*, W6456; 2. *L. anatifera*, W6455; 3. *L. hillii*, W6452; 4. *Conchoderma virgatum*, W6496; 4a. *C. v. chelonophilum*, W7368; 5. *C. auritum*, W4637. Scales = 5 mm.

Conchoderma auritum (Linnaeus 1767)

MATERIAL EXAMINED

W4637, Heron I., SE.Q., ex *Platylepas hexastylos* on *Caretta caretta.*

The single specimen recorded here is very small (7 mm) but has the characteristic ear like appendages on the posterodorsal aspect of the capitulum. 'Extremely common from all parts of the world' (Darwin 1851).

Family BALANIDAE

Balanus trigonus Darwin 1854
(Plate 1, fig. 1)

MATERIAL EXAMINED

W6497, W7376, 55 specimens, Mon Repos, SE.Q., ex *Caretta caretta.*

Specimens are up to 11.5 mm basal diameter; steeply conical, deep pink with raised white ribs. The orifice is triangular and the scuta have a characteristic row of pits.

Cosmopolitan in tropical and sub-tropical coastal waters (Stubbings 1967) and recorded from hard substrates to 120 m by Pope (1945).

Balanus variegatus (Darwin 1854)
(Plate 1, fig. 2)

MATERIAL EXAMINED

W7377, W7380, 6 specimens, Mon Repos, SE.Q., ex *Caretta caretta.*

Specimens are up to 9 mm basal diameter, steeply conical, the summits of the radii oblique; colour deep mauve-pink. The spur on the tergum is short and well removed from the basiscutal angle. Harding (1962) includes material from New Zealand and the East coast of Australia in this species.

Family CORONULIDAE

Sub Family CHELONIBIINAE

Chelonibia testudinaria (Linnaeus 1758)
(Plate 1, fig. 3)

MATERIAL EXAMINED

W4902, W4904, 10 specimens, Heron I., SE.Q., all ex *Chelonia mydas;* W3067, W6500, W7370-1, 7 specimens, Mon Repos, SE.Q., W4840, W4846, 5 specimens, Heron I., SE.Q., all ex *Caretta caretta;* W6499, 1 specimen, Mon Repos, SE.Q., ex *Chelonia depressa;* W7373, 1 specimen, Boydong I., N.Q., ex *Eretmochelys imbricata.*

Shell shallow domed cone shape, up to 60 mm basal diameter, massive, smooth; base oval to round; radii with characteristic toothed pattern; adherent to surface of scutes of host, and in no specimen of this collection is there any sign of embedding; cosmopolitan in tropical and warm temperate seas (Pilsbry 1916).

Chelonibia caretta (Spengler 1790)
(Plate 1, fig. 4)

MATERIAL EXAMINED

W3654, 15 specimens, North Reef, N.Q., W4903, 5 specimens, Heron I., SE.Q., W6498, 2 specimens, Wistari Reef, SE.Q., all ex *Caretta caretta;* W7372, 1 specimen, Boydong I., N.Q., W7374, 3 specimens, Wistari Reef, SE.Q., all ex *Eretmochelys imbricata.*

Shell rounded, conical, up to 35 mm basal diameter, rough; radii narrow; orifice eroded; all specimens show evidence of embedding in host tissue (see Pilsbry 1916); an apparently tropical species (Pilsbry 1916; Stubbings 1967).

Sub Family CORONULINAE

Tubicinella cheloniae sp. nov.
(Fig. 6; Plate 1, figs. 5, 6)

Stephanolepas muricata: Nilsson-Cantell, 1932, p. 258, pls. 1-3; Hendrickson, 1958, p. 524, pl. 10; Zullo, 1963 (in part), p. 308, Newman, Zullo, and Withers, 1969 (in part), p. R289.

[non] *Stephanolepas muricata* Fischer, 1886, p. 193, pl. 4, figs. 9-11; Gruvel, 1903, p. 149, pl. 2, figs. 1-3; 1905, p. 279; Pilsbry, 1916, p. 271, 289; Zullo, 1963 (in part), p. 308; Newman, Zullo, and Withers, 1969 (in part), p. R289.

MATERIAL EXAMINED

HOLOTYPE: W7248, Mon Repos, via Bundaberg, SE.Q., ex *Caretta caretta* (recently drowned and washed ashore), – .xii.1968, C. Limpus.

PARATYPES: W6501, 2 specimens, same data as Holotype, W6502, 1 specimen, Mon Repos, via Bundaberg, SE.Q., ex *Caretta caretta.*

OTHER MATERIAL: W7356, 7 specimens, Mon Repos, SE.Q., ex *Caretta caretta.*

DIAGNOSIS

Tubicinella with areas of horizontally flattened upward curving spines projecting from the lateral edges of the compartments; burrowing in chelonians, the orifice below the level of host scutes.

DESCRIPTION OF HOLOTYPE

Shell cylindrical, porose, slightly curved laterally, completely embedded and solidly formed. Orifice slightly larger than basis. Length 19·8 mm, basal diameters 6·6 mm × 8·75 mm, opercular diameters 9·6 mm × 11·7 mm.

Externally each compartment has a median longitudinally ridged area. The ridges correspond to septae between the inner and outer laminae and end in a series of fine teeth that protrude from the convex basal margin of the compartment.

The lateral edges of each compartment are smooth on the outer surface. From adjacent edges of contiguous compartments arise a series of large and small, out and upcurving flattened projections, each projection being formed by a contribution from each of the adjacent compartments. These projections at each of the six sutural junctions are arranged approximately in rings up the column of the shell, projections of each ring being united by a fine ridge across the face of the compartments.

The sheath extends approximately 70% the depth of the shell where it ends in a slight ridge. At the orifice the sheath and external wall end in a rough broken edge.

The radii are narrow, smooth at their junction with the compartment whence the projections arise, and transversely ridged laterally. The ridged portion is overlain by a smooth 'secondary covering' (Nilsson-Cantell 1932) arising from the adjacent compartment. This secondary covering contributes to the projections mentioned above.

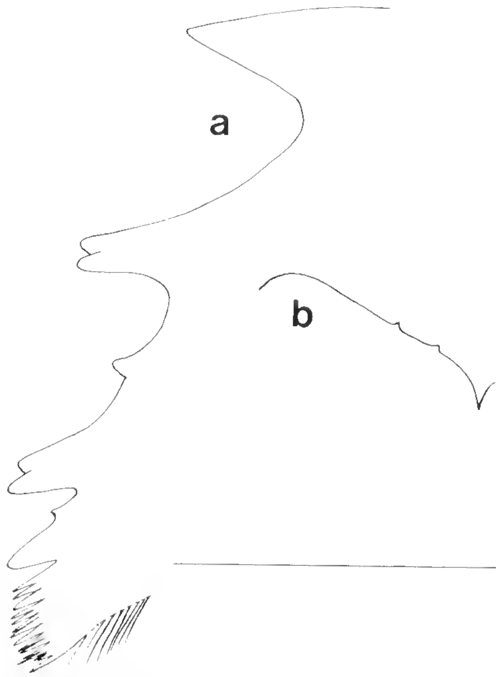


FIG. 6: *Tubicinella cheloniae,* Holotype W7248. a, mandible; b, labrum (half only, fringing hairs omitted). Scale = 0·5 mm.

The alae are thin, and beyond the limit of the sheath, taper into their own compartment.

The valves extend the full length of the opening and are loosely articulated in the heavy opercular membrane.

The labrum is notched, fringed with hairs, and has two teeth on one side of the notch, and none the other. The palp is club shaped, the mesial margin densely clothed in heavily setose spines, the apical and lateral margins more sparsely clothed in long finely setose spines.

The mandible has four teeth, the first and fourth single, the second and third double. There is an accessory tooth between the second and third, and the third and fourth main teeth.

Maxilla I has a straight edge, notched, with two stout spines above the notch, and eight lesser spines below.

Maxilla II has a medial lobe. The smaller of the two outer lobes has a field of long spines mesially on the anterior face. Proximolaterally there is an area of small round papillae (? sensillae) and disterolaterally there is an area of small spines. The larger lobe has a row of long spines along the mesial margin, a dense tuft of long spines apically, and an area of small spines distally on the lateral margin.

The penis is long and annulated with four longitudinal rows of hairs on the distal portion and a fringe of setae apically.

Cirrus I has the anterior ramus twice the length of the posterior (segment numbers 14 and 8). The pedicel is broad and has a fringe of hairs laterally. The segments are protuberant and have strong setal tufts.

VARIATION IN PARATYPES

There is no notable variation in the paratypes except in the irregularity of the development of the projections on the shell.

HOSTS AND DISTRIBUTION

Tubicinella cheloniae has been recorded from the carapace or plastron of *Chelonia mydas, Eretmochelys imbricata,* and *Caretta caretta* from Ceylon, Malaysia, and Australia. It is not possible to distinguish whether Newman, Zullo, and Withers' (1969) record for *Stephanolepas muricata* is that species or *T. cheloniae.*

DISCUSSION

In the collection on which this study is based there are some specimens referable to *Stephanolepas muricata* Fischer (1886), and others referable to *Stephanolepas muricata*: Nilsson-Cantell (1932). In our opinion they belong to two distinct species, and Nilsson-Cantell failed to recognise his material as a new species of *Tubicinella*, here described as *Tubicinella cheloniae* sp. nov.

Nilsson-Cantell believed his own material to be the adult, and Fischer's the juvenile, form of *S. muricata* Fischer, and on the basis of his own material Nilsson-Cantell questions several of Fischer's observations. Comparison of Fischer's type description and figures with material available to us, leaves us in no doubt of the accuracy of Fischer's observations (see following species description).

Nilsson-Cantell gives no grounds for his belief that his material is conspecific with *S. muricata*: his description shows pronounced affinities with *Tubicinella*. While it shows some differences from *T. major* Lamarck we have included this species in *Tubicinella* because of the strong affinity shown by the general facies of the shell and the mode of invasion of the host. It is certainly not congeneric with any other coronulid, and to erect a new genus would not, we feel, adequately reflect the relationship of this species to other members of the family.

Sub Family PLATYLEPADINAE

Stephanolepas muricata Fischer 1886
(Fig. 7; Plate 2, figs. 1–3)

Stephanolepas muricata Fischer, 1886, p. 193, pl. 4, figs. 9–11; Gruvel, 1903, p. 149, pl. 2, figs. 1–3; 1905, p. 279; Pilsbry, 1916, pp. 271, 289; Zullo, 1963 (in part), p. 308; Newman, Zullo, and Withers, 1969 (in part) p. R289.

[non] *Stephanolepas muricata*: Nilsson-Cantell, 1932, p. 258, figs. 1–2, pls. 1–3; Hendrickson, 1958, p. 524, pl. 10, figs. a-c; Zullo, 1963 (in part), p. 308; Newman, Zullo, and Withers, 1969 (in part) p. R289.

MATERIAL EXAMINED

W4845, W4908–10, 8 specimens, Heron I., SE.Q., W7360, 1 specimen, Mon Repos, SE.Q., all ex *Caretta caretta;* W4906–7, W4911–12, 26 specimens, Heron I., SE.Q., W7303, 1 specimen, Moreton Bay, SE.Q., all ex *Chelonia mydas;* W7359, 2 specimens, Boydong I., N.Q., ex *Eretmochelys imbricata*.

DISCUSSION

Shell fragile, not porose, completely embedded in host, orifice approximately twice diameter of basis, larger specimens 4–6 mm greatest diameter.

Externally each compartment with a medial smooth area, lower edge thin, concave, without fine teeth, upper edge broken away; 'spinous' areas laterally, 'spines' formed by convolutions in outer lamina, occurring at similar intervals on all compartments, producing rings of six 'spine' pairs at intervals up shell wall (see Fischer 1886, pl. 4, figs. 10–11).

Sheath projects above outer lamina and breaks off during growth; extends 75% of depth of shell, marked with white lines representing flaking off points as sheath is protruded during growth. Radii narrow and thin; alae thin and extend to lower limit of sheath where they terminate obliquely.

Scuta and terga extend full length of orifice; scutum equals tergum; scutum triangular, tergum rectangular.

Labrum notched; of three specimens dissected one had two teeth each side of the notch, the other two had none. In all cases the labrum was fringed with fine hairs.

Palp club shaped; mesial margin with a dense row of short strongly setose spines; apical and disterolateral margins with a few long sparsely setose spines; lateral margin with a row of short setae.

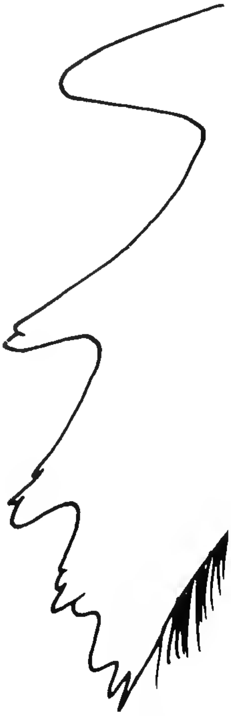


FIG. 7: *Stephanolepas muricata*, W4910, mandible. Scale = 0·5 mm.

Mandible with three major teeth, no interteeth; first tooth single, second double, third multiple, a crenulated lobe at the position of the fourth tooth; inferior angle pectinate in one specimen, composed of one or two broken spines in the other two.

Maxilla I notched, with two large spines above the notch and nine spines below in two specimens, eight in the third.

Maxilla II with a narrow medial lobe; smaller lateral lobe with a dense field of long spines disterolaterally, no small round papillae (? sensillae) proximolaterally; larger lobe with an apical tuft of long spines, a row of similar spines along mesial margin, an oblique field of long spines mesially on anterior surface, an area of small spines and small cresentic spine groups disterolaterally, no small round papillae (? sensillae) apparent.

Penis short and annulated, no rows of hairs, a few fine hairs distally, and a fringe of hairs around orifice.

HOSTS AND DISTRIBUTION

Fischer's (1886) material was from *Eretmochelys imbricata* from Indochina. It is not possible to determine whether Newman *et al.* (1969) recorded the present species or *Tubicinella cheloniae.* The material for this study is the first recorded from Australia, and possibly the first since Fischer. Hosts and localities are listed under 'Material Examined' above. All specimens were taken from the leading edge of the carpal area of the front flippers where they burrow through or between the epidermal scales.

DISCUSSION

Pilsbry (1916) placed *Stephanolepas* close to *Stomatolepas* in a platylepadine series within the Coronulinae. Nilsson-Cantell (1932) on the basis of his misidentification considered *Stephanolepas* in the coronulid series. Hiro (1936) adopted Nilsson-Cantell's opinion and incorporated *Stephanolepas* into the coronulid series along with *Coronula*, *Cryptolepas*, *Xenobalanus*, and *Tubicinella*, leaving *Platylepas*, *Cylindrolepas* and *Stomatolepas* in the platylepadine series. Zullo (1963, 1967) echoed this in his formal elevation of these series to subfamily rank. Newman and Ross (1976) have returned *Stephanolepas* to the subfamily Platylepadinae.

Stomatolepas Pilsbry 1910

It has been almost universally regarded that the only valid name in this genus is *Stomatolepas elegans* Costa 1838, and most records heretofor have been included in this species. The only exceptions have been *Stomatolepas praegustator* Pilsbry (1910, 1916) and Wells (1966), and *Stomatolepas transversa* Nilsson-Cantell (1930 a and b).

We have been unable to ascertain whether the types of *S. elegans* are extant or not, but we have seen the types of *S. praegustator* and *S. transversa.* These latter two species appear to be quite distinct (see following descriptions).

In our collections we have three species of *Stomatolepas; S. praegustator, S. transversa* and a third species which we describe as new under the name *S. dermochelys* while regarding *S. elegans* as a nomen dubium. In support of this we cite the following:

(a) The existence of the types of *S. elegans* is uncertain.

(b) Costa's descriptions of *S. elegans* are inadequate for the identification of his species. His diagnosis includes all 3 species of *Stomatolepas* in our collections.

(c) No host data is given for Costa's material. There is no ground for Pilsbry's (1916) hope that 'this lost species will probably be found again in the throat of sea turtles' since Costa himself did not know the host — or from what part of the host his material came.

'Trovato l'o in Taranto; ma ignoro il corpo sul quale esso viveva: imperciocche io lo debbo alla compaicenza del signor D. Giovanni Membola, giudice de quel circondario, nella cui collezione giaceva indistinto.' I found it in Taranto, but I don't know the body on which it was living: but I am indebted to the kindness of Mr D. G. Membola, guide to the area, in whose collection it lay unrecognised.

'Le prominenze unguiformi della base di ciascuna valvola componente il tubo mi fanno giudicare che impiantate esse fossero ad un corpo molle ed organico, siccome a testugine, a grosso granchio, od a qualche squalo.' The (finger) nail-like prominences* of the base of each valve making up the tube allow me to judge that perhaps it is implanted in a soft organic body, for example a turtle, a large crab, or some shark.

We do not think it adequate or desirable to select a neotype for *S. elegans* in this case until the existence or not of Costa's types is known with certainty. None the less we wish to draw attention to the fact that *Stomatolepas* contains more than

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* Costa has described and figured the shell upside down. The finger nail like prominences in fact surround the orifice.

one species and that the name currently most commonly recorded (*S. elegans*) is of uncertain identity.

Stomatolepas praegustator Pilsbry 1910
(Fig. 8, Plate 2, figs. 4–8)

Stomatolepas pruegustator Pilsbry, 1910, p. 304, fig. 1; 1916, p. 209, pl. 68, figs. 1–1b.
Stomatolepas elegans: Hiro, 1936, p. 314, figs. 1–15; Relini, 1968, p. 225, figs. 7–10; Zullo, 1963, p. 313; Holthuis, 1969, fig. 2.
[non] *Stomatolepas elegans:* Zullo and Bleakney, 1966, p. 162, fig. 2; McCann, 1969, p. 152, figs. 1–5; Holthuis, 1969, p. 44; Brongersma, 1972, p. 53, p. 60; Smaldon and Lyster, 1976, p. 317.

Material Examined

W4848, W7357, 19 specimens, Heron Is, SE.Q., W7358, 75 specimens, Mon Repos, SE.Q., U.S.N.M. 48094, 3 specimens, Tortugas, Florida (Pilsbry's (1910) paratypes of *S. praegustator*), all from gullet of *Caretta caretta;* W7481–6, 51 specimens, Mon Repos, SE.Q., ex *Caretta caretta* from soft skin of neck and base of front flipper.

Hosts and Distribution

Hosts and localities recorded are: *Caretta caretta* from Gulf of Triest, Italy; Tortugas, Florida; and Heron I. and Mon Repos, Australia; and *Lepidochelys olivacea* from Seto, Japan.

Discussion

Hiro (1936) and Relini (1968) suspected there was only one species of *Stomatolepas* — *S. elegans* — and that *S. praegustator* Pilsbry (1910) and *S. transversa* Nilsson-Cantell (1930a, b) were probable synonyms of that species. Stubbings (1965, 1967) refers his material to *S. elegans* without description.

The external morphology of W4848 has been compared with that of U.S.N.M. 48094, Pilsbry's (1910) three paratypes of *S. praegustator*, and we consider them to be conspecific.

The description and figures of Hiro (1936) and Relini (1968) are adequate to allow the inclusion of their material under *S. praegustator*. Examination of Stubbings (1965) material is required to determine its identity. Holthuis' (1969) fig. 2 is after fig. 1 of Hiro (1936) and is therefore included under *S. praegustator*.

The shell is approximately circular in 'dorsal' aspect. Measurements from the 16 specimens in W4848 and the three in U.S.N.M. 48094 combined with data from Hiro (1936) and Relini (1968) give a mean length/breadth ratio of 1·16 (range 1·02–1·38) for a total of 26 specimens.

Some variation in labral tooth number is apparent (0–3 teeth) both between sides and between individuals. The mandible shows some variation around the basic pattern illustrated by Hiro (1936); three examples are shown in Fig. 8. The first tooth is single, the second double, the third treble, and the fourth distinct and double. The inferomedial angle is moderately pectinate. The cirri are all clothed with a dense covering of long fine hairs. The penis is as long as the sixth cirrus, annulated, and with an apical setal fringe.

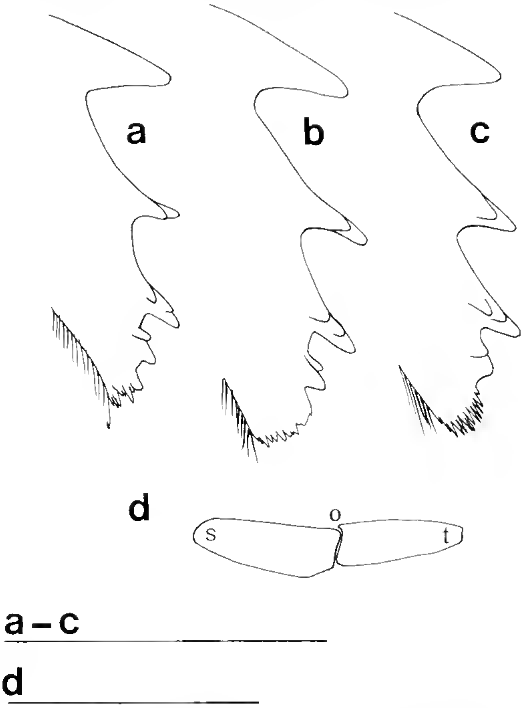

FIG. 8: *Stomatolepas praegustator*, W4848. a–c, mandibular teeth; d, valves (s = scutum, t = tergum, o = orifice); Scales = 0·5 mm, a–c; 5 mm, d.

Stomatolepas dermochelys sp. nov.
(Fig. 9; Plate 3, figs. 1–5)

Stomatolepas elegans: Zullo and Bleakney, 1966, p. 162, fig. 2; McCann, 1969, p. 152, figs. 1–5; Holthuis, 1969, p. 44; Brongersma, 1972, p. 53, p. 60; Smaldon and Lyster, 1976, p. 317.

Material Examined

HOLOTYPE: W6505, Wreck Rock, near Bundaberg, SE.Q., ex *Dermochelys coriacea*, 17.1.1975, C. Limpus.

PARATYPES: W4639, 8 specimens, same data as holotype; N.Z.O.I. Z2278, 14 specimens, Wharama R., North Island, New Zealand; R.M.N.H. 1316, 6 specimens, Ameland, Friesland, Netherlands; R.M.N.H. 1314, 177 specimens, near The Lizard, Cornwall, United Kingdom; all ex *Dermochelys coriacea*.

OTHER MATERIAL. R.M.N.H. 1317, 3 specimens, Hondsbosche, seewering, Zijpe, Netherlands; R.M.N.H. 1318, 30 specimens, High Island, Co. Cork, Ireland.

DIAGNOSIS

Stomatolepas with a length breadth ratio of 1·31 (range 1·10–1·63), penis 2·5 times as long as cirrus VI, cirri IV–VI sparsely setose, and the fourth mandibular tooth a crenulated prominence fused to the shortly pectinate inferomedial angle of the mandible.

DESCRIPTION OF HOLOTYPE

Length 9·1 mm, width 6·9 mm, depth 3·6 mm, orifice larger than basis, shell oval bowl shape. Parities thin and formed as in *S. praegustator:* scales of the outer lamina composed of small oval convolutions; in more superior rows these convolutions distinct and separate, in inferior rows coalesced to form one laterally elongate scale with a crenulated upper margin, upper margin smooth on lowest row: scale rows narrow (5 rows in 250μ at mid-depth): a triangular area bare of scales at middle of bottom edge of each compartment: radial grooves are wide at mid length.

Sheath projects above scaly outer layer in 'finger nail' like projections, extends to 75% of depth of outer layer, and is marked with white curved lines which represent 'flaking off' lines of projecting edge.

Scuta and terga not similar; terga subrectangular, scuta sinusoidal and forming a loose articulation with each other at anterior curve.

Labrum with a wide central notch, two teeth each side, and a fringe of fine hairs.

Palp rounded club shaped, fringed mesially, apically, and disterolaterally with long setose setae.

Mandible with four main teeth and no interteeth: first single, second double, third double, and fourth a crenulated prominence: inferior angle shortly pectinate.

Maxilla I notched with two strong spines above notch and 11 spines below.

Maxilla II with a rounded outer lobe, apically and mesially fringed with setae; inner lobe small rounded and with a row of setae mesially.

Anterior lobe of cirrus I twice length of posterior; rami of other cirri subequal; segments of cirri I–III protuberant and with strong setal brushes; segment numbers in Table 1.

Penis 2·5 times length of cirrus VI, annulated, with a few sparse hairs distally and a fringe of hairs around orifice.

VARIATION IN PARATYPES

The holotype and 42 of the paratypes have an average length/breadth ratio of 1·31 (range 1·10–1·63). There is no notable variation in the morphology of the shell structure.

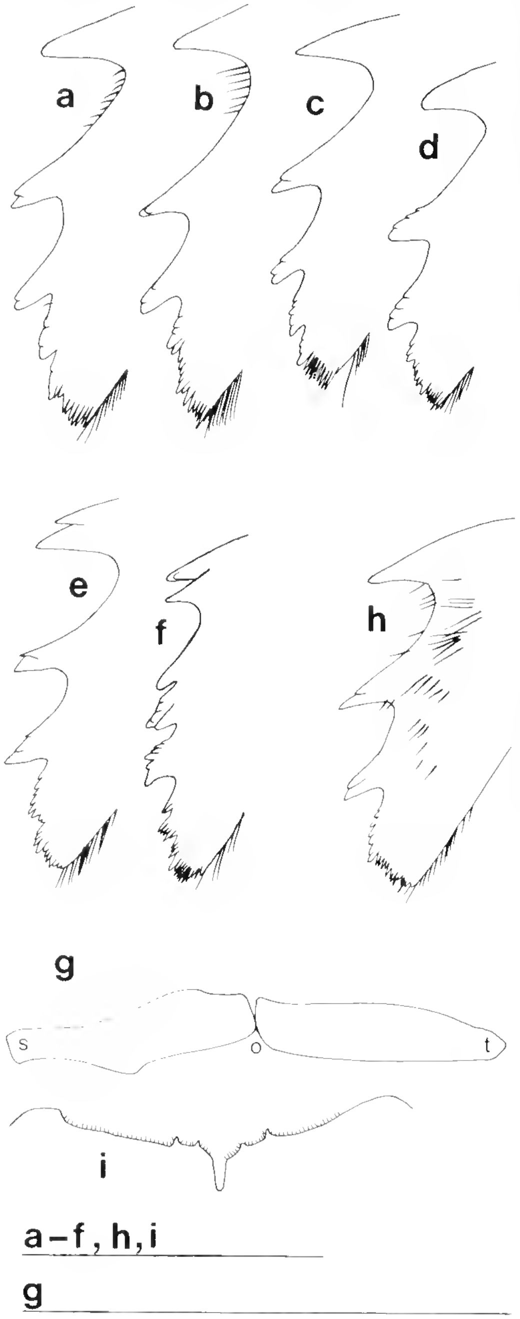

FIG 9: *Stomatolepas dermochelys*, Paratypes, W4639, a–f, mandibular teeth, g, valves (s = scutum, t = tergum, o = orifice); Holotype W6505, h, mandible, i, labrum. Scale = 0·5 mm, a–f, h, i; 5 mm, g.

TABLE 1: Segment Numbers of Cirri in one Species of *Stomatolepas* and three of *Platylepas*

Species	Cirrus* I	II	III	IV	V	VI
S. dermochelys	13:7	8:7	9: 8	15:16	16:17	17:13
P. hexastylos	13:7	10:9	12:11	19:17	22:20	21:19
P. decorata	11:7	9:8	10: 9	14:16	20:22	20:19
P. coriacea	13:7	8:8	10: 7	14:**	16:**	18:17

* (anterior : posterior rami)
** ramus broken

The labrum may bear up to three teeth each side of the notch, and there may be different numbers on each side in the same specimen. The mandibles of the 10 specimens dissected conform to a similar plan. There are three distinct main teeth and no accessory teeth. The first is single (occasionally double) the second double (occasionally multiple), the third treble (occasionally double or multiple). The position of the fourth tooth is always marked by a crenulated lobe closely adjacent to the shortly pectinate inferomedial angle.

All specimens were deeply embedded, there being little free scaly outer wall showing above the ridge marking the host tissue level.

Hosts and Distribution

S. dermochelys has been recorded only from the Leatherback turtle, *Dermochelys coriacea,* from the soft skin at the base of the flippers and tail, and once from the palate (Brongersma 1972, p. 60). Locality records are Norway, Scotland, Ireland, Cornwall, Netherlands, Malaya, Queensland, New Zealand, and Nova Scotia.

Discussion

Material from Queensland, New Zealand, Netherlands, Ireland and Cornwall has been examined in this study. Smaldon and Lyster (1976) considered the Norwegian, Scottish, Malayan, and Cornish specimens to be conspecific. On the basis of their identifications, consideration of the host, and the present examination of other specimens of the Cornish record, Smaldon and Lyster's material is included in this species. The Nova Scotian material is included on the basis of the host, and the shape of the lower scales (Zullo and Bleakney 1966, fig. 2).

S. dermochelys is readily distinguished from *S. praegustator* to which it is most similar by: the length/width ratio, 1·31 (range 1·10–1·63) in *S. dermochelys,* 1·16 (range 1·02–1·38) in *S. praegustator;* the longer penis in *S. dermochelys,* 2·5 times cirrus VI, 1 times cirrus VI in *S. praegustator;* the fourth mandibular tooth, a crenulated lobe in *S. dermochelys,* a distinct bifid tooth in *S. praegustator;* the shape and configuration of the external scales, *S. dermochelys* has 5 scale rows in 250μ at mid depth, *S. praegustator* as 3 rows in 250μ (see plates); and host.

Stomatolepas transversa Nilsson-Cantell, 1930a
(Plate 6, figs. 1–6)

Stomatolepas transversa Nilsson-Cantell, 1930a, p. 2; 1930b, p. 20.

Material Examined

W7468, W7471, 4 specimens, Wistari Reef, SE.Q., W7469–70, 16 specimens, Heron I., SE.Q., all ex *Chelonia mydas,* from midline groove of plastron; I.R.S.N.B., (no number), 5 specimens, Enoe I., Aroe Archipelago, (Nilsson-Cantell's types).

Host and Distribution

S. transversa has been recorded from the median groove of the plastron of *Chelonia mydas* from Aroe Archipelago and Southeast Queensland.

Discussion

The morphology of the external scales of the shell is quite distinct. The transverse scales which carry small upward projections along all of their upper edge in *S. praegustator* and *S. dermochelys* have 1–3 such projections only at their lateral ends on the lateral compartments in *S. transversa.* The rostrum and carina are both very narrow but still have a similar, though cramped, arrangement of the scales.

S. transversa in the most elongate of the three species of *Stomatolepas* and has a length-breadth ratio of 1.75 (range 1.53–2.29).

S. transversa is distinguished from the other species of *Stomatolepas* by its host and position, elongate proportions, and configuration of the external scales.

Platylepas hexastylos (Fabricius 1978)
(Fig. 10; Plate 3, figs. 6–8; Plate 4, figs. 1–4)

Material Examined

W4635, W4844, W4847, W4918, W6503, W7364, 13 specimens, Heron I., SE.Q., W6504, 1 specimen, The Oaks, via Bundaberg, SE.Q., all ex *Caretta caretta:* W7304, 1 specimen, Moreton Bay, SE.Q., ex *Chelonia mydas;* W7365, 4 specimens, Boydong I., N.Q., W7367, 12 specimens, Wistari Reef SE.Q., ex *Eretmochelys imbricata;* W7366, 8 specimens, Mon Repos, SE.Q., ex *Chelonia depressa.*

DESCRIPTION

The present material is in agreement with the descriptions of Darwin (1854), Pilsbry (1916), Kruger (1912), Hiro (1937), and Stubbings (1965). However a detailed description is included here for comparison with other species of the genus.

Shell low, conical, margin multilobed, and orifice small. Major diameter 10–14 mm.

Outer lamina with prominant wear areas around orifice; radii narrow, their free edges not hidden under secondary growth from adjacent compartment, simple septae at their edges; growth lines the predominant sculpturing, septae visible through the wall, becoming more numerous peripherally; line of 'midrib fold' obvious, dividing each compartment into two main lobes, accessory 'folds' also in peripheral margin, these, 'midrib folds', and intercompartmental sutures, appear to enclose host tissue, perhaps as an anchor mechanism.

Sheath massive, with slight depressions between it and outer wall of shell either side of 'midrib', extends halfway to periphery along outer wall, that is about 75% of vertical height of shell; midribs extend only slightly below level of periphery giving slighly convex base; septae visible on inner face of outer wall towards periphery.

Valves subequal, extend full length of orifice.

Labrum notched, a tooth at each lateral angle and two or three teeth either side of notch.

Palp shaped as in Stubbings (1965); setae of mesial margin heavily and coarsely setose for whole length, those of apex and lateral margin longer than former and lightly setose over distal half to two thirds of length.

Mandible in general agreement with descriptions of Stubbings (1965) and Kruger (1912) though the fourth tooth not so well developed as in Stubbings' material.

Maxilla I with 2 strong spines above and 8 lesser spines below notch.

Maxilla II in general agreement with description of Stubbings (1965); the spines, except those of apical cluster, finely setose on distal portions; a small fringe of hairs at basal end of mesial margin of larger lobe; distcrolaterally on larger lobe an area of small cresentic spine groups, laterally on smaller lobe an area of small round papillae (? sensillae); smaller lobe with grooved mesial margin to receive medial lobe.

Anterior ramus of cirrus I twice posterior, segments of cirri I – III moderately to strongly protuberant with strong setal brushes; cirri IV – VI subequal, with four spine pairs per segment at mid length reducing to two at apex and at three base; on each segment distal spine pair longest and strongest, proximal pair shortest and weakest; segment numbers in Table 1.

Penis long and annulated, distal half with four longitudinal rows of fine hairs and a terminal tuft of bristles.

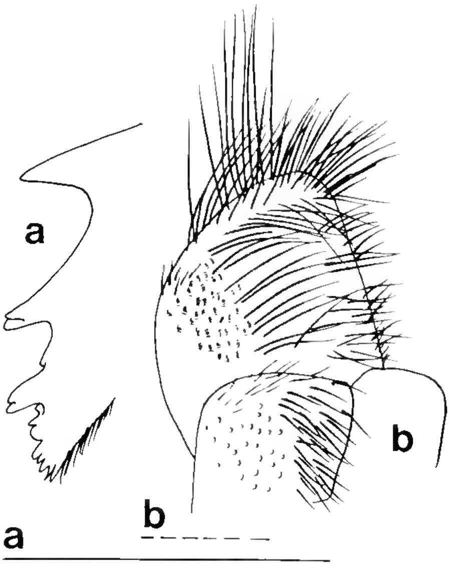

FIG. 10: *Platylepas hexastylos*, W4847, a, mandible; b, maxilla II. Scale a = 0·5 mm, b = 0·1 mm.

HOSTS AND DISTRIBUTION

P. hexastylos is recorded from a variety of chelonian and sirenian hosts from tropical and subtropical waters (Darwin 1854, Pilsbry 1916, Zullo 1963).

Platylepas decorata Darwin 1854

(Fig. 11; Plate 4, figs. 5–8; Plate 6, figs. 7–8)

Platylepas decorata Darwin, 1854, p. 429, pl. 17, fig. 2a,b.

non *Platylepas decorata:* Nilsson–Cantell, 1921, p. 376, fig. 89.

Platylepas multidecorata Daniel, 1962, p. 641, figs. 1–2.

MATERIAL EXAMINED

W4913–5, W4917, W4919–20, 35 specimens, Heron I. Lagoon, SE.Q., ex *Chelonia mydas;* W4916, W4921–2, W7184, W7343, 7 specimens, Heron I. Lagoon, SE.Q., W7142, 12 specimens, Mon Repos, via Bundaberg, SE.Q., all from *Caretta caretta.* W7361–3, 13 specimens, Wistari Reef, SE.Q., ex *Eretmochelys imbricata;* B.M.N.H., no number, 1 specimen, Galapegos Arch., (Darwin material), Z.S.I., 1317/1, 1 specimen, Little Andaman I., (Daniel's paratype of *Platylepas multidecorata*).

DESCRIPTION

Shell subcircular, ring-like, shallow, steep sided, and non-porose; orifice very nearly as large as basis; diameters of shell, 4 mm × 3 mm, height 2 mm.

Outer surface of each compartment sculptured with vertical ridges both double and simple (see Daniel 1962), lower edge dentate with projections of septae; summit of each compartment with prominent wear areas where layers of shell flake off; radii narrow with simple septate margins.

Sheath extends 85% of depth of outer wall; shallow pits between sheath and outer wall either side of 'midrib fold'; inner face of sheath marked with horizontal lines marking layers that flake off at summits; a vertical ridge in middle of sheath marks position of 'midrib fold'; midrib prop extends below sheath a distance equal to height of shell, deepest at inner edge, outer edge of process slopes obliquely up to periphery of shell.

Valves oblong and narrow, scuta longer than terga.

Labrum notched, 7–13 teeth on each side. The teeth extend from notch to lateral angle.

Palp club shaped, protuberant at proximal end of inner margin; rounded apex with a tuft of long spines, finely setose on distal portions; inner margin densely clothed in coarsely setose spines.

Mandible with four distinct main teeth, first and last single, second and third double; an intertooth between second and third, and third and fourth main teeth; also a reduced fifth tooth as a crenulated lobe adjacent to pectinations of the inferior angle occasionally distinct; body of mandible clothed in rows of bristles.

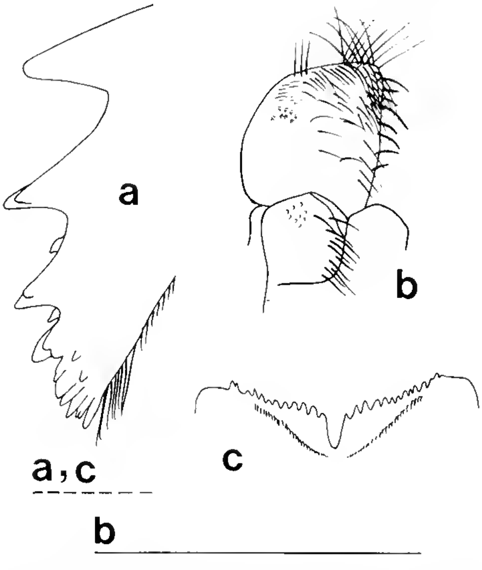

FIG. 11: *Platylepas decorata*, W7142, a, mandible; b, maxilla II, c, labrum (fringing hairs omitted). Scales a, c = 0·1 mm, b = 0·5 mm.

Maxilla I with two large spines above notch and six below.

Maxilla II with a medial lobe; smaller lateral lobes grooved mesially to accept medial lobe, sparsely bristled mesially, an area of small round papillae (? sensillae) laterally; larger lobe with a row of strong spines on mesial edge, an apical tuft of long bristles, and a few bristles laterally; a small area of bristles on anterior face, a small area of small cresentic spine groups disterolaterally.

Anterior ramus of cirrus I twice posterior, segments of cirri I–III moderately protuberant, with strong setal brushes, cirri IV–VI subequal, with four spine pairs per segment, not equally strong, reducing to two or three pairs proximally and distally; segment numbers in Table 1.

Penis long, annulated, with four rows of fine hairs distally and a fringe of hairs at orifice.

HOSTS AND DISTRIBUTION

Hosts and localities are *Chelonia mydas* and *Caretta caretta* from Southeastern Queensland; *Eretmochelys imbricata* from Southeastern Queensland and Palau Is; and unknown hosts from Galapagos Archipelago, Low Archipelago, Little Andaman Island, and the Taumato Archipelago.

DISCUSSION

Darwin's (1854) description of *P. decorata* is incomplete in that no mention is made of mouthparts. He also says of the shell that 'the surface (and this is the chief external character) is marked by five longitudinal ridges, *each* of which . . . is found to be double . . . with minute beads on each side.' Plate 6, figs 7 and 8, shows a scanning electron micrograph of one of Darwin's specimens.

Daniel (1962) notes that *P. multidecorata* differs from *P. decorata* in (among other features) having 'simple ridges in addition to double ridges'. Plate 6, fig. 8 clearly shows that *P. decorata* has both simple and double ridges.

Daniel's diagnostic feature for *P. multidentata* is an elevated ridge on the external surface from mid height to the base of the shell. This feature can be seen in Plate 4, fig. 7. However, it can be seen in Plate 4, fig. 8 that this ridge is calcareous material that fills the sulcus of the infold of the compartment. This is easily eroded in upper parts of the compartment (Plate 4, fig. 8) or overgrown by the enlarging compartment (Plate 6, fig. 7). Daniel further notes that *P. multidecorata* has nine teeth on each side of the labrum where as *P. decorata* has only three. The only source for Daniel's information is Nilsson-Cantell (1921) who records *'P. decorata'* from a sea snake off the West Australian coast. Darwin's material (as seen by one of us, R.M.) is dry and no attempt has been made to rehydrate it. Consequently it is not possible to say how many labral teeth are present, but it is our opinion, based on other characters, that Darwin's material and ours are conspecific. Further comparison of our material with one of Daniel's paratypes leads us to the opinion that they are conspecific. We exclude Nilsson-Cantell's (1921) record from our synonomy, agreeing with Utinomi (1970) that this record is probably a misidentification.

Platylepas coriacea sp. nov.

(Fig. 12; Plate 5, figs. 1–8)

MATERIAL EXAMINED

HOLOTYPE: W7247, Wreck Rock, near Bundaberg, SE.Q., ex *Dermochelys coriacea*, 17.i.1975, C. Limpus.

PARATYPES: W4638, 2 specimens, same data as Holotype. W4640, 7 specimens, Mon Repos, via Bundaberg, SE.Q., W4872, 2 specimens, Alexandra Headlands, SE.Q., all ex *Dermochelys coriacea*.

DIAGNOSIS

Large *Platylepas,* not embedded in host, midribs props, not, or only slightly, projecting below periphery of shell, basis flat, radii wide, found on *Dermochelys coriacea*.

DESCRIPTION OF HOLOTYPE

Shell subcircular, low and non-porose, 22·5 mm × 21·4 mm, 4·5 mm high; orifice subcircular 8·0 mm × 7·2 mm.

Outer surface sculptured with transverse lines of growth increments; midrib folds reach 75% to 90% up compartments towards summits and divide periphery into 12 subequal lobes; septae visible through outer lamina and protrude at periphery.

Radii wide, oblique at upper edge, free edges hidden beneath secondary covering from adjacent compartments.

Sheath shallow, extending only 15% along inner slope of shell, forming dense ring around orifice; deep pits either side of midrib between sheath and outerwall; midrib props extend as far as basis and curve centripetally; midrib fold extends only half depth of prop.

Septae visible on inner face of outer wall as far up as sheath.

Valves subequal extending full length of orifice; terga twisted through 90° along longitudinal axis.

Labrum with three teeth either side of notch and a fourth at each lateral angle; a marginal fringe of fine hairs from notch to beyond fourth tooth.

Palp club-shaped with protuberant inferomesial margin; mesial margin densely clothed in coarsely setose spines; apical and lateral margins more lightly clothed in longer spines plumose over distal portions.

Mandible with four teeth; second and third double, first and fourth single; an accessory tooth between second and third, and third and fourth teeth; inferomedial angle pectinate.

Maxilla I with two large spines above notch and eleven smaller spines below.

Maxilla II with a medial lobe; smaller of lateral lobes grooved mesially to receive medial lobe, densely bristled mesially, with a field of small crescentic spine groups disterolaterally, and a field of small round papillae (? sensillae) proximolaterally; larger lateral lobe moderately clothed along mesial margin with long spines, apex with a

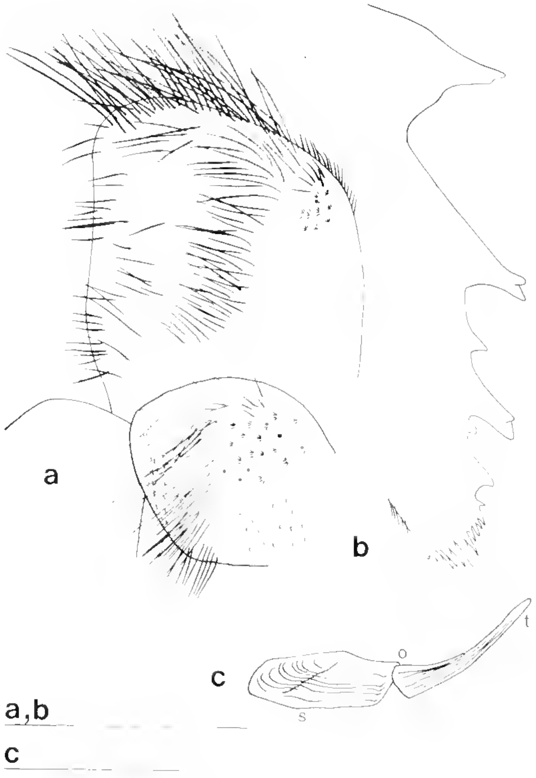

FIG. 12: *Platylepas coriacea*, Holotype W7247, a, maxilla II; b, mandible; c, valves (s = scutum, t = tergum, o = orifice); Scale = 0·5 mm, a, b; 5 mm, c.

dense tuft of spinose spines, a longitudinal field of long spines in middle of anterior face, lateral to distal end of this field a group of small spines and small cresentic spine groups, an area of small spines on disterolateral margin.

Posterior ramus of cirrus I, 75% length of anterior; segments of cirri I–III protuberant with dense setal brushes; cirri IV–VI subequal and with 3 strong and 1 weak spine pair per segment, reducing to 2 strong and 1 weak proximally and distally; segment numbers in Table 1.

Penis long, annulated, with four longitudinal rows of hairs distally and a fringe of hairs around orifice.

VARIATION IN PARATYPES

In general morphology all the available material is very similar to the Holotype. Three paratypes were dissected. One had labial teeth similar to the holotype. The other two had 3/2 at the notch, and in one case no tooth at one lateral angle and two at the other. One specimen lacked the accessory tooth between the second and third main mandibular teeth, and spine numbers below the notch on Maxilla I were 8, 10 and 11.

HOST AND DISTRIBUTION

See Material Examined

DISCUSSION

P. coriacea is distinguished most readily from *P. hexastylos* and *P. decorata* by shell morphology. *P. coriacea* has wide radii, a twisted tergum, no secondary midribs and is not embedded. *P. hexastylos,* which is superficially similar to *P. coriacea,* has narrow radii, flat terga, secondary midribs and is partially embedded. The shell of *P. decorata* is small, ring like and completely embedded. *P. coriacea* appears to be confined to *Dermochelys coriacea*, while *P. hexastylos* and *P. decorata* from the collection available, seem to be excluded from this host.

KEY TO BARNACLES RECORDED ON TURTLES IN QUEENSLAND WATERS
(Excluding *Balanus* species)

1. Barnacles stalked 2
   Barnacles sessile 6
2. Valves very reduced (*Conchoderma*) 3
   Valves well developed (*Lepas*) 4
3. Capitulum and pedicel with three longitudinal purple stripes; no external appendages (Fig. 4) ....*Conchoderma virgatum*
   Capitulum and pedicel concolourous; no appendages ....*C. v. chelonophilum*
   Capitulum and pedicel concolourous; two ear-like appendages posterodistally (Fig. 5) .... *C. auritum*
4. Pedicel with pale or brightly coloured band at junction with capitulum 5
   Pedicel without such a band, capitulum often with diagonal bands of dirty green squares (Fig. 2) ....*Lepas anatifera*
5. Valves smooth; carina well spaced from scuta; no umbonal teeth on scuta (Fig. 3) .... *L. hillii*
   Valves with radiating furrows; carina continguous with scuta; a large umbonal tooth on the right (a small on the left) scutum (Fig. 1) ....*L. anserifera*
6. Shell massive; orifice small compared to base; not or only slightly embedded (Chelonibiinae) 7
   Shell moderately strong to fragile; orifice larger or smaller than base; partially to fully embedded, (except *Platylepas coriacea* on *Dermochelys coriacea*) 8
7. Shell smooth; radii with toothed pattern; not embedded (Plate 1, fig. 3) ....*Chelonibia testudinaria*
   Shell rough; radii narrow; partially embedded in scutes (Plate 1, fig. 4) ....*Chelonibia caretta*
8. Barnacle completely embedded in host, orifice below skin level 9
   Never as above 10
9. Large barnacles in groups of 2–4; embedded in carapace or plastron producing large ulcerous sores; shell tubular, (Fig. 6; Plate 1, figs. 5, 6) .... *Tubicinella cheloniae*
   Small barnacles; embedded in or between dermal plates of leading edge of front flipper; shell bowl-shaped (Fig. 7; Plate 2, figs. 1–3) ....*Stephanolepas muricata*
10. Shell bowl-shaped, orifice larger than basis; externally covered with small scales (*Stomatolepas*) 11
    Shell flat cone shape or ring like; deeply to not embedded; basis larger than orifice and showing six prominent bulges (*Platylepas*) 12
11. Embedded in gullet or soft shoulder skin of *Caretta caretta* and *Lepidochelys olivacea*, external scales as in Plate 2, figs. 4 and 8 ....*Stomatolepas praegustator*
    Embedded in soft skin (and gullet) of *Dermochelys coriacea;* external scales as in Plate 3, figs. 1 and 3 .... *S. dermochelys*

Embedded in median groove of plastron of *Chelonia mydas;* external scales as in Plate 6, figs. 2 and 3 .... *S. transversa*

12. Shell ring-like; almost completely embedded, midrib props deeply penetrating; labrum with 7–13 teeth each side (Fig. 11) .... *Platylepas decorata*
    Shell flat cone shape; not or only partially embedded; labrum with 2–4 teeth each side 13

13. Shell partially embedded; on chelonians other than *Dermochelys coriacea;* mandible and maxilla II as in Fig. 10 .... *P. hexastylos*
    Shell not embedded; on *Dermochelys coriacea;* mandibles and maxilla II as in Fig. 12 .... *P. coriacea*

11. Embedded in gullet or soft shoulder skin of chelonians other than *Dermochelys coriacea;* mandibles and valves as in Fig. 8 .... *Stomatolepas praegustator*
    Embedded in soft shoulder skin of *Dermochelys coriacea;* mandibles and valves as in Fig. 9 .... *S. dermochelys*
    Embedded in median groove of plastron of *Chelonia mydas;* rostro-carinally elongate .... *S. transversa*

12. Shell ring-like; almost completely embedded, midrib props deeply penetrating; labrum with 7–13 teeth each side (Fig. 11) .... *Platylepas decorata*
    Shell flat cone shape; not or only partially embedded 13

13. Shell partially embedded; on chelonians other than *Dermochelys coriacea;* mandible and maxilla II as in Fig. 10 .... *P. hexastylos*
    Shell not embedded; on *Dermochelys coriacea;* mandibles and maxilla II as in Fig. 12 .... *P. coriacea*

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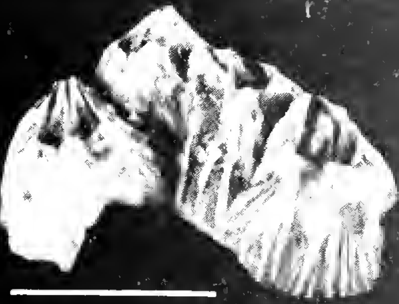
PLATE 1

FIG. 1: *Balanus trigonus* Darwin, W6597
FIG. 2: *Balanus variegatus* (Darwin), W7380
FIG. 3: *Chelonibia testudinaria* (Linnaeus), W3067
FIG. 4: *Chelonibia caretta* (Spengler), W3654
FIGS. 5, 6: *Tubicinella cheloniae* sp. nov., Holotype, W7248.

Scale lines = 10 mm.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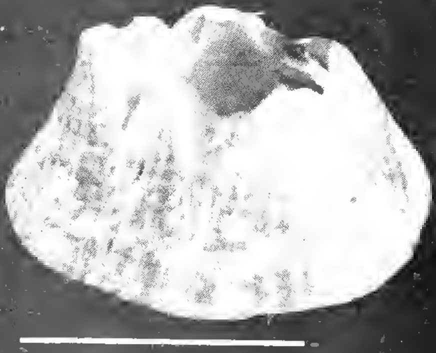
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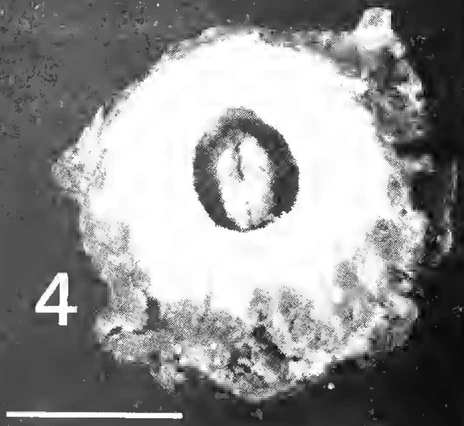
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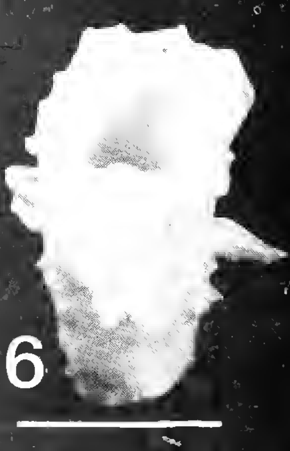
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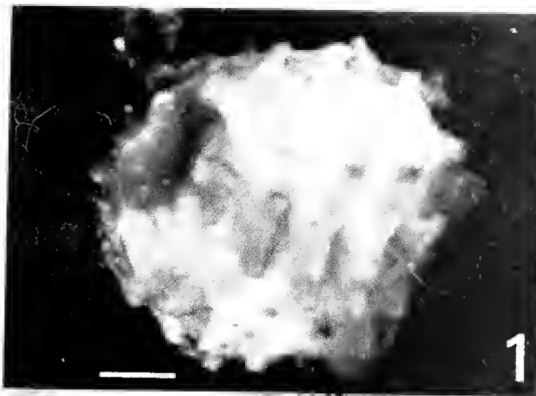
PLATE 2

FIGS. 1–3: *Stephanolepas muricata* Fischer, W7359; 1, whole animal with investing layers of host tissue, membranous basis to the left; 2, exterior of a lateral compartment; 3, sheath of a lateral compartment.

FIGS 4–8: *Stomatolepas praegustator* Pilsbry, W7358, aspects of a lateral compartment; 4, exterior; 5, alar edge; 6, sheath; 7, radial edge; 8, detail of growth of exterior scales.

Scale lines: Fig. 1 = 1 mm; Figs. 2–8 = 0·05 mm.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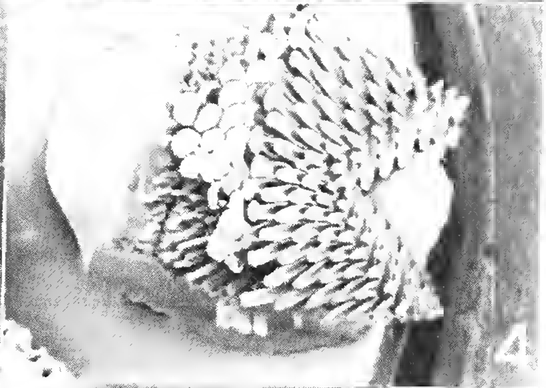
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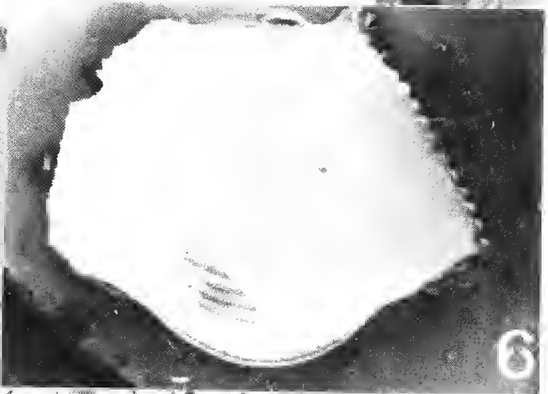
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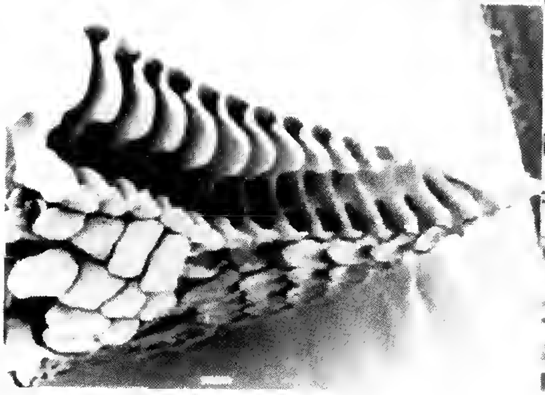

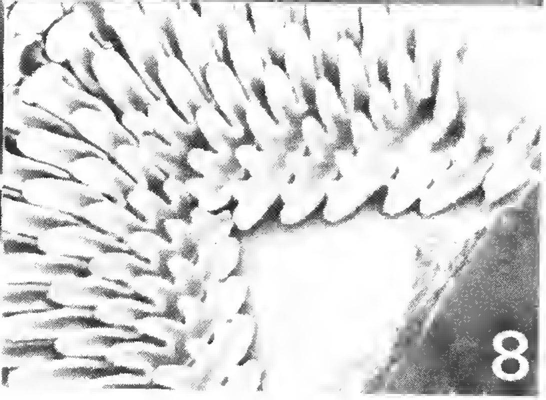
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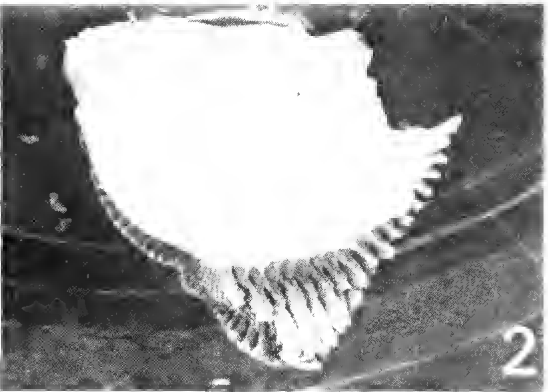
PLATE 3

FIGS. 1–5: *Stomatolepas dermochelys* sp. nov., Paratype, W4639; 1, exterior of carina; 2, sheath of a lateral compartment; 3, detail of growth of exterior scales; 4, radial edge; 5, alar edge.

FIGS 6–7: *Platylepas hexastylos* (Fabricius), W7365; 6, basal aspect, and 7, opercular aspect of whole shell.

FIG. 8: *Platylepas hexastylos* (Fabricius), W4847, exterior aspect of rostrum.

Scale lines: Figs. 1–5, 8, = 0·05 mm; Figs. 6, 7 = 1 mm.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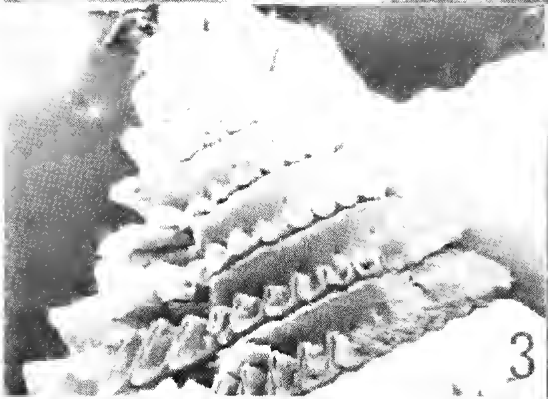
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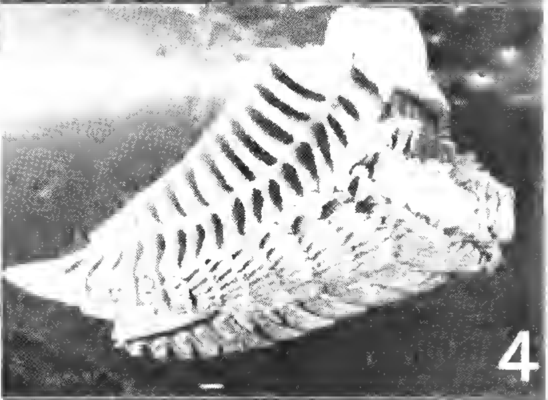
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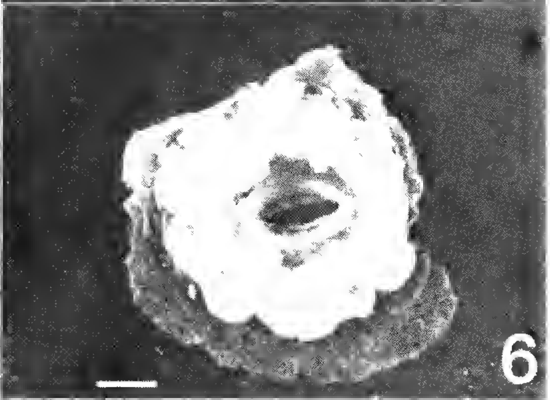
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PLATE 4

FIGS. 1–4: *Platylepas hexastylos* (Fabricius), W4847; 1, basal aspect of carina; 2, oblique basal aspect a lateral compartment showing midrib; 3, opercular aspect of rostrum; 4, basal aspect of a lateral compartment showing an 'accessory' fold at the top right.

FIG. 5: *Platylepas decorata* Darwin, W7363.

FIGS. 6–8: *Platylepas decorata* Darwin, W7142; 6, alar aspect of a compartment showing triangular shape of midrib 'prop'; 7, exterior aspect of compartment; 8, opercular aspect of rostrum.

Scale lines: Figs. 1–4, 6–8, = 0·05 mm; Fig. 5 = 1 mm.


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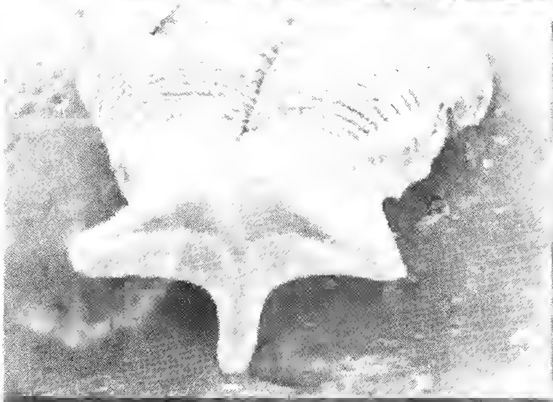


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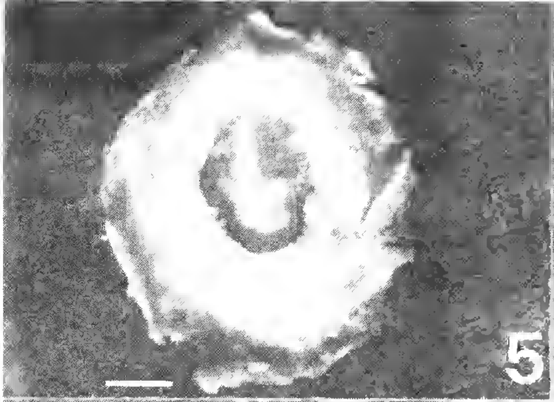
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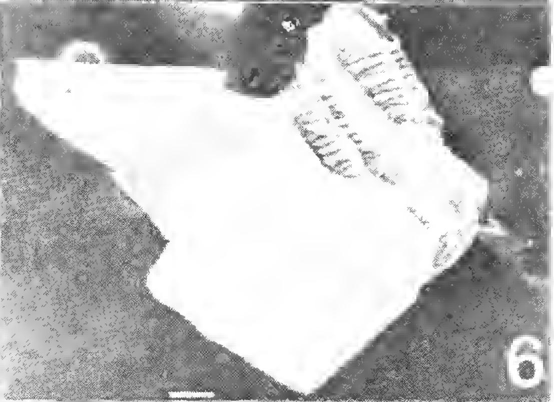
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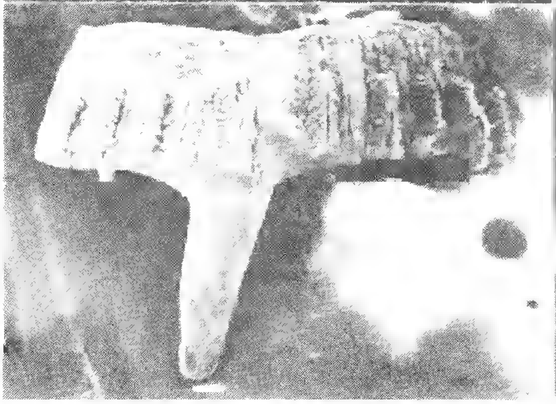


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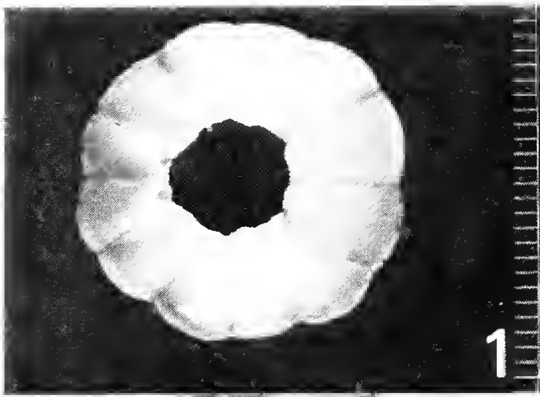
PLATE 5

FIGS. 1–2: *Platylepas coriacea,* sp. nov. holotype, W7247; 1, opercular aspect; 2, basal aspect.

FIGS. 3–8: *Platylepas coriacea,* sp. nov., paratype, W4640; 3, exterior aspect of rostrum; 4, interior aspect of a lateral compartment; 5, detail of peripheral edge and growth lines; 6, oblique basal aspect of a lateral compartment showing ala, and 'pits' behind sheath; 7, 8, exterior oblique views of alar.

Scale lines: Figs. 1–2, 1 div. = 1 mm; Figs. 3–8, = 0·05 mm.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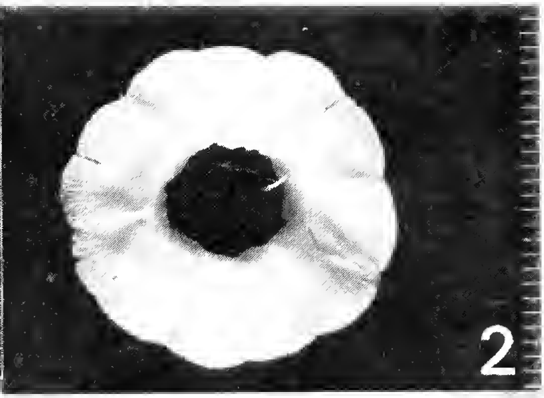
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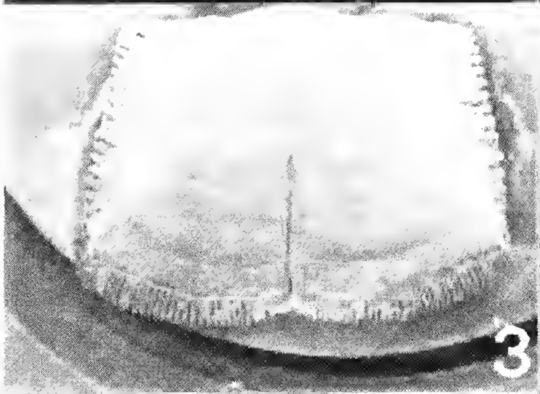
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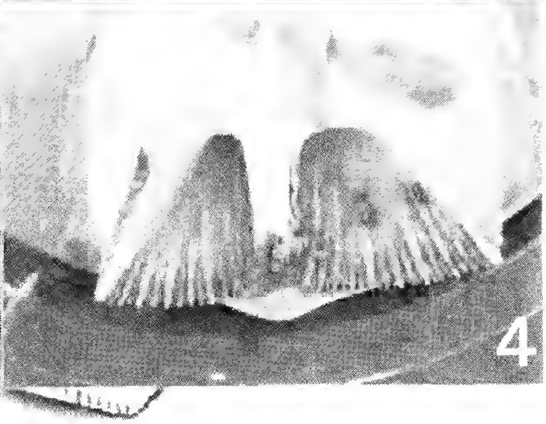
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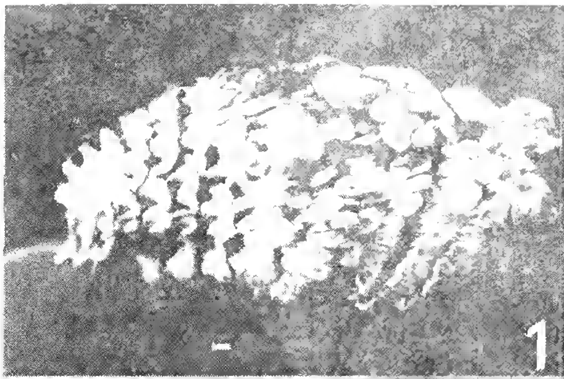
PLATE 6

FIGS. 1–2: *Stomatolepas transversa*, Nilsson-Cantell, Paratype, I.R.S.N.B. (no number); 1, carina; 2, fragment of a lateral compartment.

FIGS. 3–6: *Stomatolepas transversa*, Nilsson-Cantell, W7471; 3, carina; 4, carino-lateral; 5, view of ala; 6, view of radius.

FIGS. 7–8: *Platylepas decorata* Darwin, B.M.N.H. (no number); 7, a lateral compartment; 8, detail of 7 showing sculpturing.

Scale lines: Figs. 1–8, 1 div. = 0·05 mm.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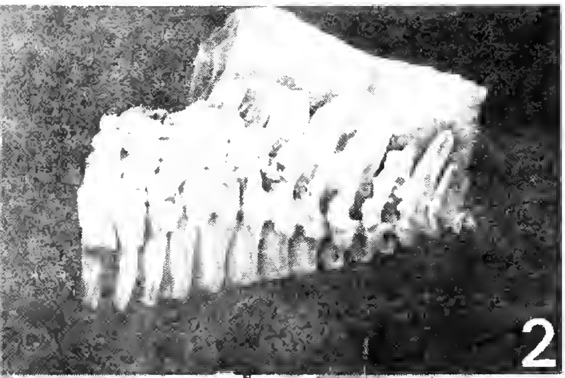
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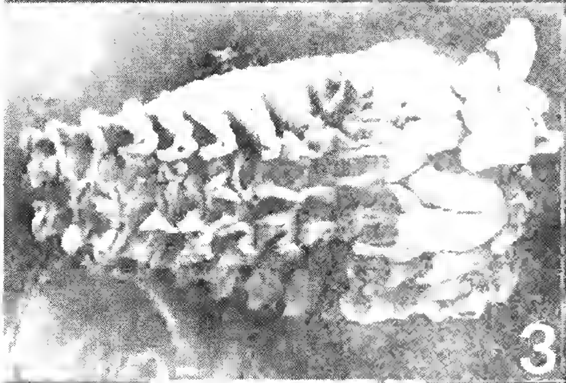
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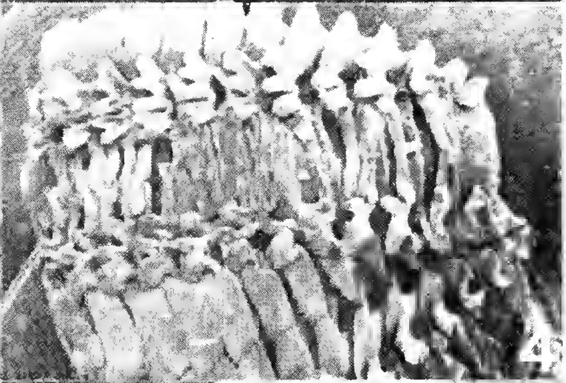
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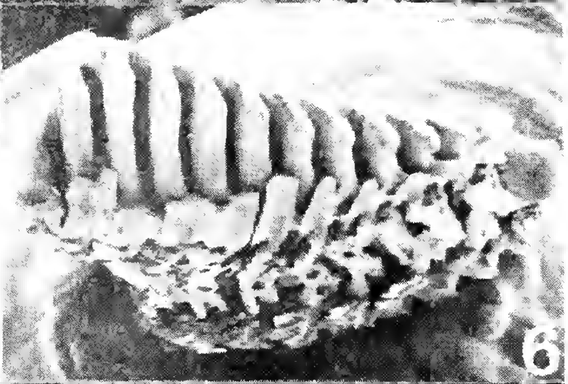
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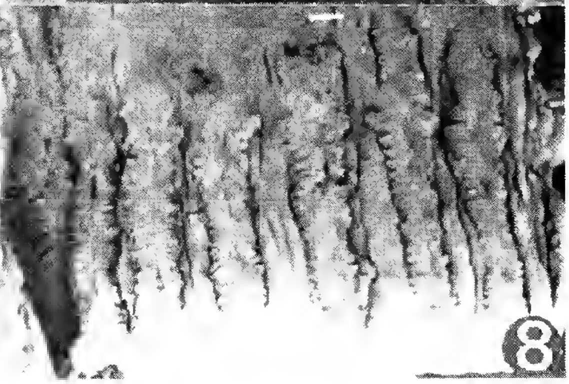
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Mem. Qd Mus. **19**(3): 225–9. [1979]

THE WOLF SPIDERS OF AUSTRALIA (ARANEAE: LYCOSIDAE): 9. *PARDOSA SERRATA* (L. KOCH 1877)

R. J. McKay
Queensland Museum

ABSTRACT

A redescription of *Pardosa serrata* (L. Koch) is provided with notes on the life history, habitat, and burrow.

The Australian species of the genus *Pardosa* are inadequately known, and compared to other continents, Australia has very few described species (McKay 1973, p. 378). A revision of the Australian species would be most desirable, but at present insufficient material is available to make this possible, and it appears likely that most Australian species placed in the genus *Pardosa* may be accommodated in other genera. I have followed Simon (1909) in assigning *Lycosa serrata* L. Koch to *Pardosa*, despite the fact that the labium is equal to or only slightly wider than its length, and the combined length of the tibia and patella of the fourth leg is greater than the length of the corresponding metatarsus, due to the similarity of the male palp with those of the better known Holarctic species of the genus *Pardosa*.

Pardosa serrata (L. Koch 1877)
(Fig. 1A–F, 2A–D)

Lycosa serrata L. Koch, 1877, pp. 930–2, pl. 80, Figs. 5, 5a, 6, 6a, Sydney, New South Wales; Rainbow, 1911, p. 272; Mascord, 1970, p. 106, pl. 49, Nos. 193, 194; Main, 1976, pp. 142–3.

Pardosa praevelox Simon, 1909, pp. 191–2, Station 114, Buckland Hill near North Fremantle, Western Australia.

Geolycosa serrata, Roewer, 1954, p. 243; McKay, 1973, p. 380.

MATERIAL EXAMINED

HOLOTYPES: *Lycosa serrata* L. Koch: Location of holotype unknown. *Pardosa praevelox* Simon: Location of holotype unknown.

OTHER MATERIAL

Western Australia: Attadale, 5.v.1959, A. R. Main, WAM 68–515, 26.ii.1960, W. Lane, WAM 68–964–990, 22.i.1960, W. Lane, 68–991–1000, 13.viii.1960, W. Lane, WAM 68–1001–1007, 11.vi.1960, W. Lane, WAM 69–1008–1–11, 22.i.1960, BYM, WAM 68–1012–1050, 25.v.1966, W. Lane, WAM 68–1051–1056, 5.v.1959, A. R. Main, WAM 69–99, 1.iv.1960, BYM, W. Lane, WAM 69–368–375, 1.iv.1960, W. Lane, WAM 69–376–384, 13.xii.1960, W. Lane, WAM 69–385–393, 23.iii.1960, W. Lane, WAM 69–401, 5.viii, 1960, W. Lane, WAM 69–402; Balga, 4.iv.1973, G. W. Kendrick, WAM 73–221; Brentwood, 6.xii.1966, BYM, WAM 69–394–400, 23.iv.1969, RJM, WAM 69–672; Bullsbrook, 26.vii.1959, BYM, WAM 69–916; Burnabinmah Station, 25.v.1968, JG, WAM 69–819; Cape Freycinet, 25.i.1971, HB, WAM 71–786; Caversham, 26.vii.1952, BYM, QM S18; Cheyne Beach, Albany, at Bluff Creek, 27.v.1959, A. R. Main, WAM 68–516; Collie, 23.x.1960, BYM, WAM 71–1431; Coogee, 5.ix.1952, BYM, WAM 71–508; Cottesloe, 21.ix.1952, BYM, WAM 70–195–196; Cunaring Hill, south, 3.v.1959, BYM, WAM 68–514; Dianella, 15.iii.1973, L. D. Cooke, WAM 73–223; Fitzgerald River Reserve, 12.vii.1970, RJM, R. Prince, WAM 70–207, 13.vii.1970, RJM, WAM 71–5–10; Gingin, vii.1954, E. Lindgren, WAM 71–1433; Golden Bay, Mandurah, 21.i.1971, RJM, WAM 71–810; Goomalling area, 18.vi.1952, BYM, WAM 69–907, 17.vi.1952, BYM, WAM 70–194; Great Northern Highway near Yandanooka, vii.1957, BYM, HB, WAM 69–85; Harrismith east, 11.vi.1952, BYM, WAM 70–191; Hyden at The Humps, 20.vi.1952, BYM, WAM 71–1425–1427; Kingoonya 16 km SE., 1955, BYM, WAM 69–834; Kondinin 35 km E., 9.vi.1952, BYM, WAM 69–1030; Margaret River, xi.1931, Walleliff, MCZ Harvard; Murchison River at Gie Gie Camp, 2.xii.1968, RH, WAM 69–699–719; Narembeen, 8.vi.1952, BYM, WAM 69–908–910; Narrogin, 12.vi.1952, BYM, WAM 69–1011; Nedlands, iii.1952, BYM, WAM 69–913; North Irwin River, 14.vii.1968, L. V. Shields, WAM 71–901; Pingrup 27 km E. at Greenshields Soak, 30.iii.1970, T. Evans, WAM 71–1421; Point Peron at Lake Richmond, 14.iv.1968, RH, WAM 70–197; Reabold Hill, 20.iv.1969, M. Archer, E. Jeffreys, WAM 73–151; Red Hill Road, 12.x.1952, BYM, WAM 71–1026; Rossmoyne, 1.v.1969, RJM, WAM 69–881, 13.xi.1968, RJM, WAM 68–857, iii.1968, RJM, WAM 69–83–84, 4.iv.1971, RJM, WAM 71–1847; Rottnest Island, viii.1956, A. R. Main, WAM 68–859, 5.iii.1959, RJM, WAM 69–453; Tammin, iv.1946, BYM, WAM 69–912, 12.vii.1952, BYM, WAM 69–914; 25.ii.1952, BYM, WAM 71–1027–28; Tarin Rock Reserve, 23.v.1971, A. Baynes, WAM 71–1428–30, 26.v.1971, WAM survey party, WAM 71–1432; Toolibin, 12.vi.1952, BYM, WAM 70–190; Triggs Island, 8.v.1971, Mr. Mellows, WAM 71–1423–24; Walebing south, 18.viii.1953, BYM, WAM 69–833; Wanneroo, 12.iv.1969, RH, WAM 69–831–832, 26.iv.1969 at Badgerup Swamp, RH, WAM 69–1038–39, WAM 71–393–394; Wilson near Canning River, 29.iv.1969, H. Lingius, WAM 69–882; Wongan Hills, 28.vi.1970, A. Baynes, WAM 70–189; Wubin 3 km south, 7.xii.1968, RJM, JG, WAM 69–790; Yalgoo, 29.vii.1957, HB, WAM 68–856; York 11 km W., 4.vii.1964, HB, WAM 68–858; Yorkrakine Rock, 12.vii.1952, BYM, WAN 9–911.

South Australia: Gawler Ranges at Kokotha Sands, 13.x.1976, D. C. Lee, 1 ♀M, SAM ARA 535; Moonarie Gap, Wilpena Pound Range at the flats east of the Gap, 22.viii.1970, W. D. L. Ride, HB, 2 ♀M, WAM 637–38.

New South Wales: Malabar, 16.ii.1966, R. Mascord, 3 ♀PIJ, A.M.

DESCRIPTION (after L. Koch 1877)

Female: Carapace dark red-brown with yellow-brown hair; a white lateral band divided in its posterior half by a longitudinal brown stripe; a white median longitudinal stripe, narrow at the posterior margin and broadening at the fovea to form three stripes on the cephalic part; the median stripe is broader than the lateral ones and reaches the PL eyes where it constricts into a fine white line which continues down the centre of the face to the AM eyes; the lateral stripes are wavy and terminate at the PL eyes; on each side of the face is a white diagonal stripe; mandibles dark red-brown, covered with yellow hair; maxillae and labium yellow-brown; sternum black-brown with yellow to white hair. Abdomen black-brown above, covered with yellow-white dots; at the base is a black longitudinal stripe, wider posteriorly, and forming serrations on either side with white borders; behind this serrated stripe and connected to it is a black longitudinal band reaching to the spinnerets and crossed throughout its length by white angular lines; on either side of this black band is a row of large white spots; sides of abdomen covered with yellow-white hair and black dots; ventral surface yellow-white. Legs reddish-brown with white hair; on the femora anteriorly, posteriorly, and above, a continuous black longitudinal stripe. Spinnerets yellow-brown, covered with grey-brown hair (Fig. 1A).

Anterior row of eyes straight; AM slightly larger. PM not large, barely larger than the PL eyes, and from these and each other, equidistant. Anterior row of eyes narrower than second row.

Male: Similar to female in coloration and pattern except for the posterior half of the longitudinal stripe on the abdomen which is more deeply serrated. The AM slightly further apart than from the AL.

VARIATION: Specimens from dark substrates are much darker in colour than those from pale or white beach sands. Three promarginal teeth on the chelicerae, the middle on largest; three retromarginal teeth of equal size. The eye diameters and interspaces of four specimens are given as a percent of the total width of the first row of eyes in Table 2. Measurements of leg segments of a male (WAM 71.1423, C.L. 7.0) given in Table 1.

The female epigynum is longer than broad with a scarcely evident median guide that does not join the broad inverted horseshoe-shaped terminal guide (Fig. 1E). Internal genitalia of a female from Caversham, W.A. illustrated in Figure 1F. The male palp (Figs. 1B, C, D, Triggs Island, W.A.) is very characteristic of the species, having a broad inverted horseshoe-shaped embolic guide and a short curved somewhat trough-shaped median apophysis situated over the membranous secondary conductor. See McKay (1974) p. 17, fig. 4, for terminology.

TABLE 1: MEASUREMENTS OF LEG SEGMENTS OF MATURE MALE *PARDOSA SERRATA* IN MM

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1	6·1	2·3	5·8	6·1	2·9
2	6·0	2·3	5·2	6·1	3·1
3	5·9	2·2	4·9	6·5	3·4
4	7·9	2·4	6·7	8·8	4·1

TABLE 2: EYE DIAMETERS AND INTERSPACES OF *P. SERRATA* CONVERTED TO PERCENT OF THE TOTAL WIDTH OF THE FIRST ROW OF EYES

Regd No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM	AL:PM	CLYP
SAM ARA 535	♀M	7·2	20	18	51	41	17	8	33	18	14	29
WAM 68–857	♀M	7·9	21	19	45	38	12	6	40	14	14	24
QM. S18	♀M	7·2	22	17	42	35	13	8	40	16	16	24
WAM 71–1423	♂M	7·0	23	18	45	35	13	5	40	15	15	26

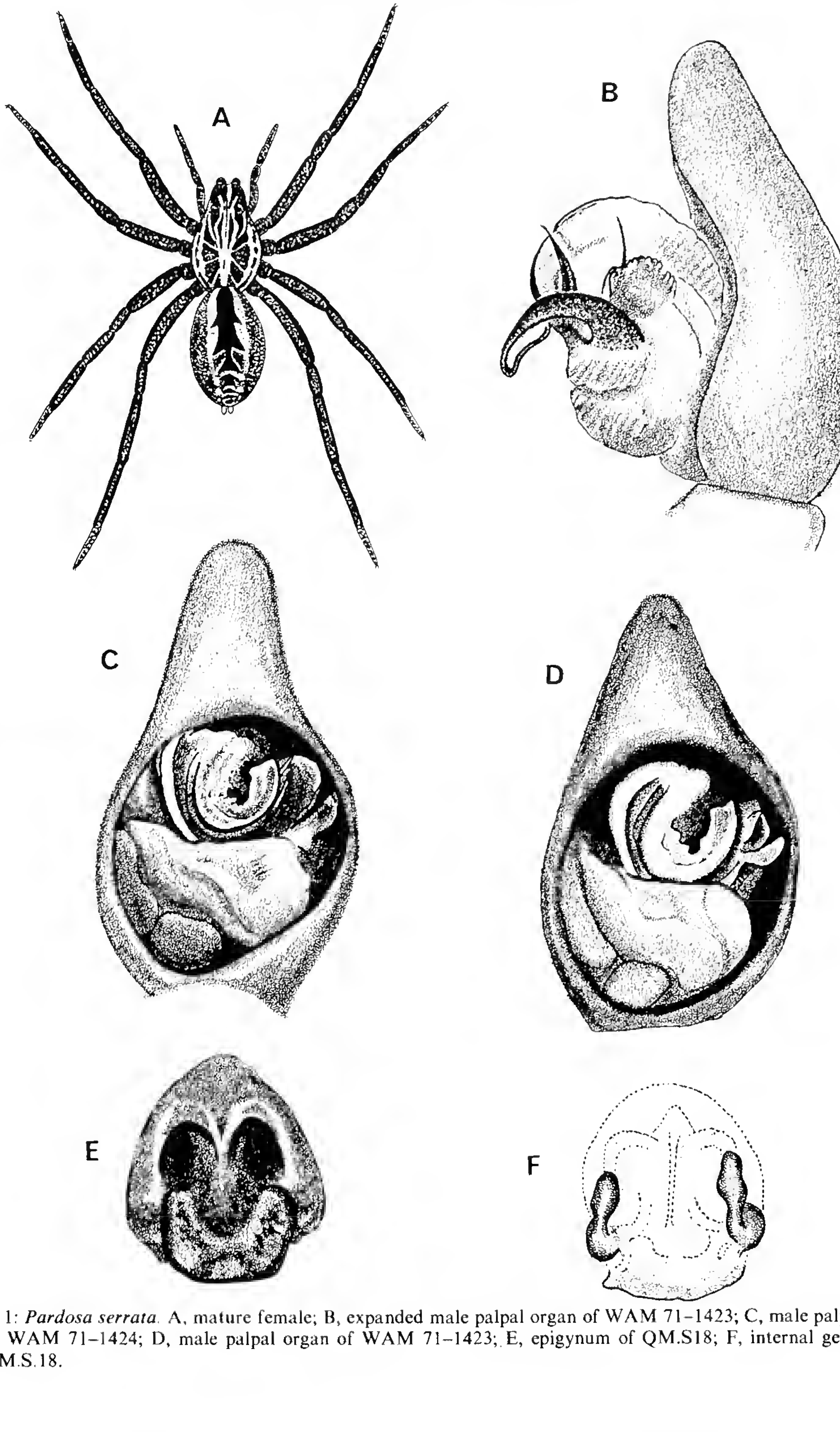

FIG. 1: *Pardosa serrata.* A, mature female; B, expanded male palpal organ of WAM 71–1423; C, male palpal organ of WAM 71–1424; D, male palpal organ of WAM 71–1423; E, epigynum of QM.S18; F, internal genitalia of QM.S.18.

SIZE RANGE: Mature females 3·3 to 7·7 mm. Mature males 3·6 to 6·6 mm.

DIAGNOSIS: This species is distinctive in coloration, the ventral surface of the abdomen is pale and the median longitudinal stripe on the cephalic part of the carapace is divided into three white stripes, the central one extending over the face to reach the first row of eyes. The female epigynum is of characteristic shape, as is the male palpal organ (see above).

LIFE HISTORY

Mature females may be found throughout the year. In Western Australia the mature males are found from early January to late May, and are most abundant during February to mid April. Copulation takes place on warm or humid nights, during late March to mid April. Mature males seeking females may be very numerous at night just prior to thunderstorms during March and April. The males die after mating, and if retained in the laboratory following copulation, they cease to feed, become uncoordinated, and rapidly die in a bout of frenzied activity once stimulated. Gravid females remain in the burrow and only leave to capture prey. The eggs are laid during mid July to early September and on warm sunny days females may be observed at the burrow entrance head downwards sunning the egg cocoon by turning it slowly with the last pair of legs. Females with egg-cocoons have been collected from mid July to early November and are most abundant during August. The young hatch during late August to November and are most common during September when females bearing young are to be collected from the burrow. By November no young remain with the female and many mature females are to be found in an emaciated condition, frequently dying, within the burrow. Some females persist throughout the summer months to copulate the following season. The juveniles may be found running during late September to late November and are most commonly observed following light rains. The juveniles dig burrows with the onset of summer and mature during February to March.

Pardosa serrata was found to be active in the burrow at ground temperatures of 12°C but below 10°C become comatose (observations during July 1970, Fitzgerald River, W.A.).

HABITAT

Although this species may be found on clay soils or lateritic gravels they are most abundant on sandy soils, especially coastal heathlands, and may on occasions be quite numerous on coastal interdune flats. Most specimens were collected from the Swan Coastal Plain, Western Australia, on leached sandy soils with a scrub vegetation of *Banksia, Xanthorrhoea* and *Melaleuca.* At the Fitzgerald River this species was most common on

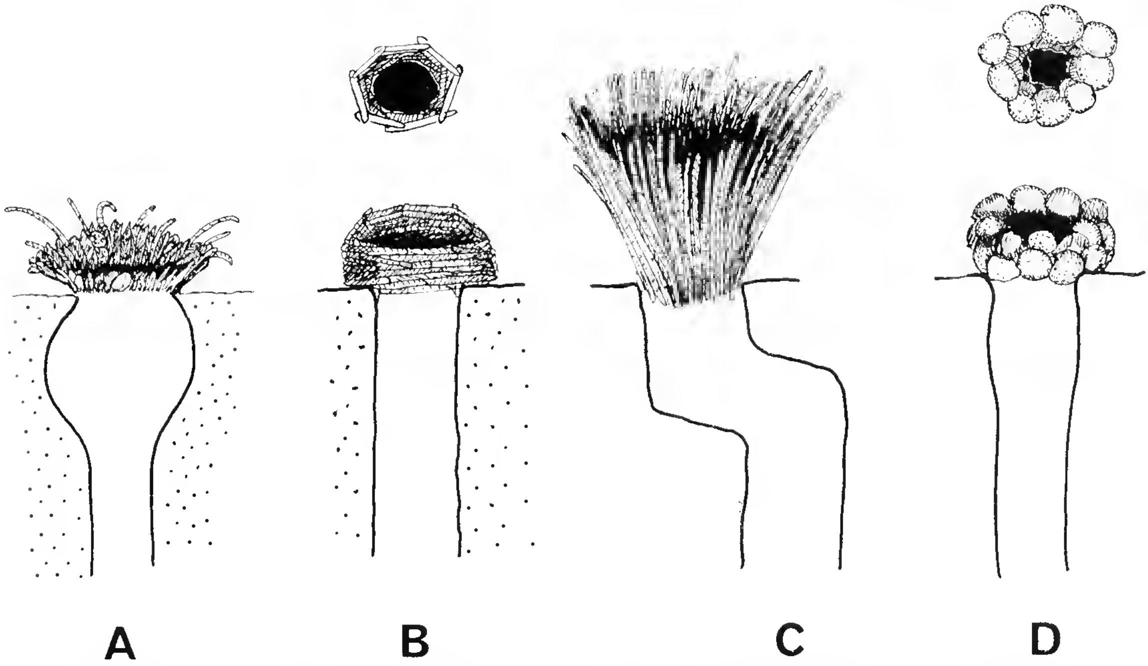

FIG. 2: Burrows of *Pardosa serrata.* A, collar type; B, log-cabin type; C, palisade type; D, pellet or turret type.

sandy soils bearing *Gahnia* clumps, and on the south west coast populations were frequently associated with Peppermint trees *Agonis flexuosa.*

BURROW

The burrow is invariably protected at the entrance by a turret or palisade constructed from a variety of materials. The burrow is usually vertical and descends to a depth of between 10 and 20 cm. Occasional burrows have an enlarged chamber below the entrance (Fig. 2A) or may have an abrupt bend some 4 cm below the surface (Fig. 2C).

The construction of the palisade varies according to available materials and the following types have been observed:

1. Collar type: A low collar of twigs, grass cuttings (on suburban lawns), grass seeds, or debris, bound together by silk (Fig. 2A).
2. Log-cabin type: elaborately constructed of short (5 to 10 mm) lengths of grass stem or twigs laid horizontally and overlapping to form a complete wall bound with silk (Fig. 2B).
3. Palisade type: a well constructed or loosely constructed wall of grass stems, *Acacia* or *Casuarina* litter arranged vertically as a tube or funnel (Fig. 2C).
4. Pellet or turret type: A wall of small *Eucalyptus* nuts, rabbit dung, or sheep pellets stacked on top of each other, and bound with silk (Fig. 2D).

At Fitzgerald River, W.A., the log cabin type and the palisade type of burrow were found to occur together. The log cabin type was constructed from short pieces of twig, with or without occasional small nuts, bound together to form a wall 2 to 3 cm high. One burrow was constructed by pulling long (5 to 6 cm) flexible grass stems around the entrance to form a bound circular wall; each strand was bound into place by silk, and in some sections reinforced by short pieces of grass or twig laid horizontally. The palisade type was constructed from grass stems arranged vertically to form a low funnel-like entrance some 3 to 5 cm high. Mature females were collected from both types of burrow.

Penultimate females retained under laboratory conditions within large glass jars part filled with sand were provided with a crude burrow formed by forcing a rod into the packed moist sand and various turret building materials. Both the palisade type (grass leaves) and the log cabin type (short pieces of grass stem and twig) were built by spiders collected from a dry suburban lawn at Rossmoyne near Perth, W.A.; the turrets were poor representatives of the elaborate palisades found in the field however. A study of these constructions under laboratory conditions using a variety of building materials would be a most interesting ethological experiment.

Most burrows were found in open flat areas where the turret or palisade may prevent sand from blowing in, or provide protection from predators or flash floods. The adaptive value of such elaborate structures have been little studied (see Gwynne and Watkiss 1975).

DISCUSSION

This species is characterised by its distinct colour pattern and the structure of the male palp. The original description of *Pardosa praevelox* leaves little doubt that this nominal species is a junior subjective synonym of *Lycosa serrata* L. Koch. Mature males of the New South Wales and South Australian populations have not been collected since the species was originally described in 1877, but the illustration of the male palp by L. Koch (1877, pl. 80, fig. 5a) agrees fairly well with the palpal organs of Western Australian males. A detailed comparison of the male palpal organs from New South Wales and Western Australia is required.

DISTRIBUTION

New South Wales, South Australia, and southwestern Western Australia.

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THE WOLF SPIDERS OF AUSTRALIA (ARANEAE: LYCOSIDAE): 10. A NEW SPECIES OF THE GENUS *FLANONA* SIMON

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Queensland Museum

ABSTRACT

The genus *Flanona,* previously known from one species *Flanona puellula* Simon 1898 from Ceylon, is reported from northwest Australia. A new species, *Flanona minuta,* is described.

The construction of the Main Dam, Ord River, in the East Kimberley area of Western Australia, was completed in 1971. The area now inundated by Lake Argyle was surveyed by the Western Australian Museum, prior to the 1971–72 wet season, to determine the species diversity and the habitats occupied by the vertebrate animals, molluscs and spiders. During the course of this survey a large collection of lycosid spiders was made by the author. An attempt was made to collect lycosid spiders from all habitats represented in the area, to fully document the lycosid fauna. One habitat investigated was the banks of small creeks that originate in mound springs or swamps at the spring-line of rocky cliffs and valley-like depressions within the ranges. At one site situated at the base of a small rock outcrop some 5 km southwest of Old Lissadel Homestead, the spring consisted of a large mound, some 3 to 4 metres high and about 20 metres in diameter, composed of decaying fern remains broken down to the consistency of peat-moss; live ferns *(Acrostichum speciosum* Willa) were scattered over the surface of the mound, adding their fronds to the accumulation of organic material. The rotting trunks of dead ferns were rapidly breaking down under the hot humid conditions to build up the mound of moist crumbly material (Pl. 1 A,B). A small *Artoria* species was abundant over the surface of the mound. On disturbing the damp rotted vegetation, I was astonished to see a minute lycosid spider with a total body length of about 2 mm dragging an even smaller egg cocoon attached to the spinnerets. This small lycosid spider was not collected on the creek banks and appears to be confined to 'mound springs'.

The smallest lycosid spider is *Flanona puellula* known only from Sri Lanka. This species is easily recognized by the arrangement of the eyes and was briefly described by Simon (1898) who states *'Flanona puellula* E. Sim. is the smallest lycosid known, it does not exceed the size of an erigonid and has the coloration of *Lycosa (Pirata) piratica* and *uliginosa,* I have found them on the beach at Pointe-de-Galle, dragging their little, round, white cocoon containing only 3–4 eggs.' The Australian specimens belong to the genus *Flanona* and are described below.

Genus **Flanona** Simon, 1898

Flanona Simon, 1898, pp. 338, 343, 349; type species by original designation *Flanona puellula* Simon, 1898.

DIAGNOSIS: Extremely small spiders; legs in order of decreasing length 4, 1, 2, 3; tibia of first leg with no more than 3 pairs of ventral spines (apical ventral spines present); first row of eyes straight, about as long as second row, and touching the inferior margin of the PM eyes; PM eyes about 1/5 of a diameter apart; retromarginal cheliceral teeth 2–3; fourth tibia with the proximal dorsal spine equal in size to the distal spine.

Two species. Sri Lanka and Australia.

Flanona minuta sp. nov.
(Fig. 1 A–D)

MATERIAL EXAMINED

HOLOTYPE: Western Australian Museum WAM 76–98, ♀M, C. L. 1·06 mm, Mound Spring, 5 km southwest of Old Lissadel Station Homestead, Ord River area, W.A., collected by R. J. McKay, October 13, 1971. In spirit.

PARATYPES: Mound Spring, data as above, 17 ♀M C. L. 0·9 mm–1·1 mm, 2 ♂P, 14J, QM W5810.

DESCRIPTION: Based on holotype.

Carapace pale brown with some very faint grey wedge-shaped markings radiating from the centre (Fig. 1A); paturon, sternum, coxae, and legs pale brown to light honey colour. Abdomen light grey above becoming dark grey posteriorly before spinnerets; sides pale grey; venter light brown. No distinct pattern on carapace or abdomen. Area between PM and PL eyes and behind PM eyes dark grey to dark brown.

Anterior row of eyes very slightly recurved, about equal in width to the second row which is situated immediately above the AM and AL eyes so that the bases are contiguous; AM eyes not on a raised mound; PM eyes with the lenses slightly less than half their diameter apart, the bases touching; PL eyes wide apart. Ratio of eyes in micrometer units (lenses only), AM:AL:PM:PL = 5:4:9:7; distance AM–AM 1·5, AM–AL 1, PM–PM 4, PL–PL 19. Length of first eye row 20; length of second eye row 19.

Chelicerae with 2 + 2 retromarginal teeth.

TABLE 1: MEASUREMENTS OF LEG SEGMENTS OF *F. MINUTA* IN MM

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1	0·81	0·24	0·59	0·56	0·42
2	0·73	0·20	0·63	0·56	0·41
3	0·71	0·28	0·52	0·59	0·38
4	0·96	0·28	0·88	0·98	0·35
Palp	0·35	0·17	0·22	—	0·38

VARIATION: Penultimate males have the same coloration as females. Five female paratypes had the paturon forced anteriorly to count the retromarginal cheliceral teeth, all had 2 + 2, remaining paratypes not examined. All paratype females had 2 + 2 ventral spines on the tibiae of the anterior pair of legs, no apical spines were present. All paratypes had 1 + 1 spines on the dorsal surface of the femora. The epigynum and internal genitalia of a paratype female is illustrated in Fig. 1C, D.

SIZE RANGE: Mature females C.L. 0·9 to 1·1 mm.

DIAGNOSIS: Differs from *Flanona puellula* Simon, the only other species in the genus in having 2 + 2 retromarginal teeth instead of 3 + 3, a simple epigynum in the shape of a lightly sclerotized flap (Fig. 1C) instead of an oval epigynum with a poorly defined median guide as figured for *F. puellula* by Roewer 1960, fig. 465.

LIFE HISTORY

Mature females carrying egg cocoons were collected in October. The egg cocoons (8 examined) contained from 3 to 5 eggs measuring 0·38 to 0·43 mm in diameter. Two penultimate males were collected, but no mature males were found. The females carry the egg cocoon firmly attached to the spinnerets.

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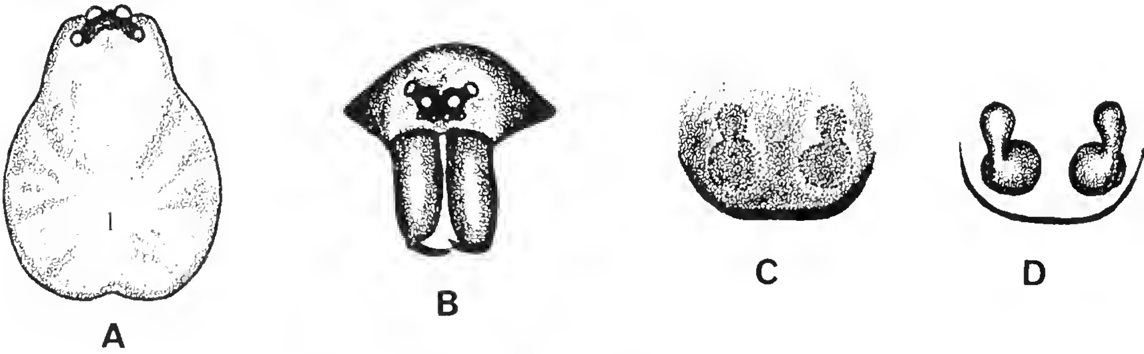
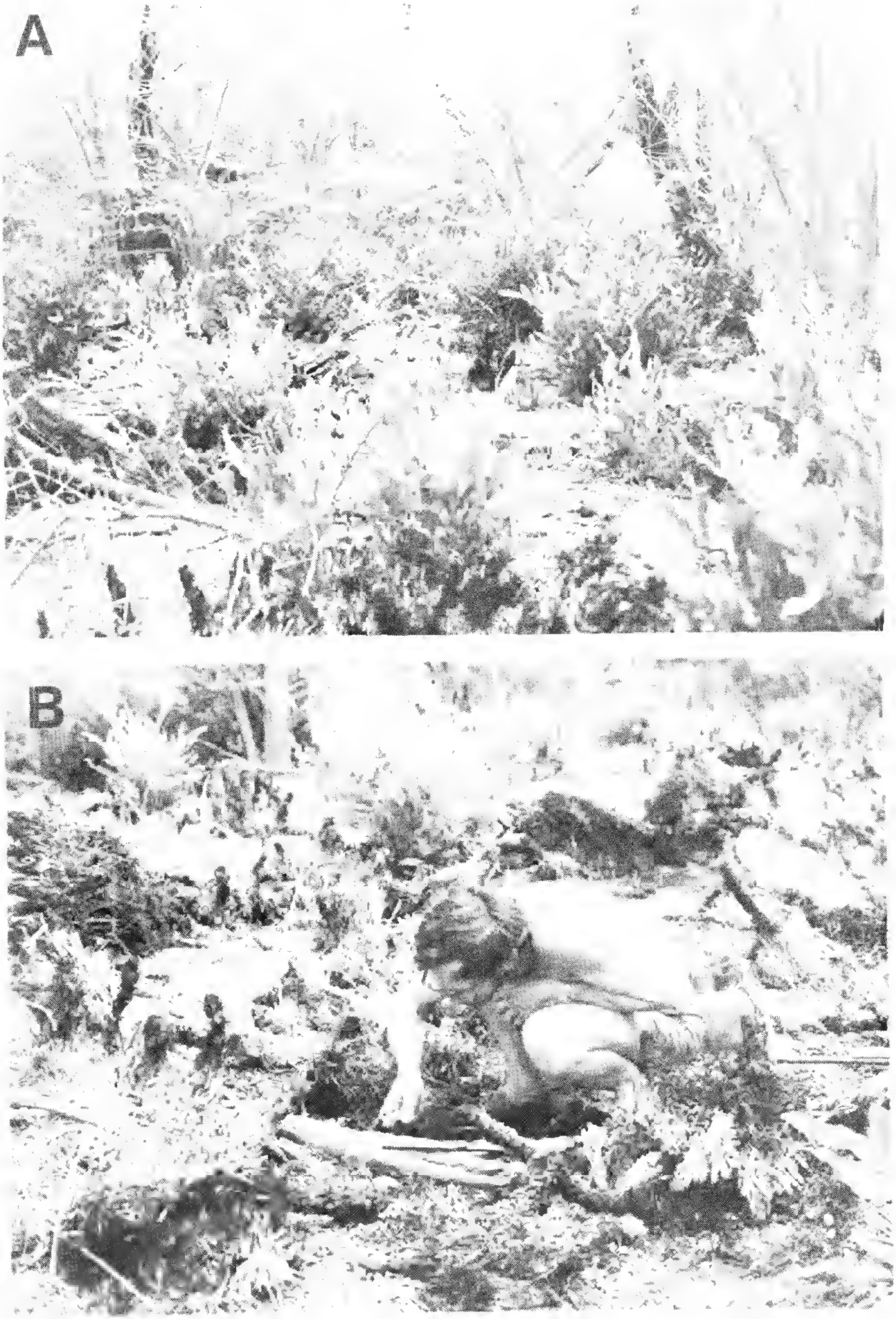


FIG. 1: *Flanona minuta*. A, carapace; B, face; C, epigynum; D, internal genitalia.

PLATE 1

FIG. A: Habitat of *Flanona minuta* showing *Acrostichum* fern in foreground.

FIG. B: Habitat of *Flanona minuta* showing peat-moss consistency of fern remains.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Mem. Qd Mus. **19**(3): 237–40. [1979]

THE WOLF SPIDERS OF AUSTRALIA (ARANEAE: LYCOSIDAE): 11

A NEW SPECIES FROM LORD HOWE ISLAND

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ABSTRACT

A new species, *Lycosa howensis,* is described from Lord Howe Island. A redescription of *Lycosa gloriosa* Rainbow 1920 is provided.

Lord Howe Island (31°32'S, 159°04'E), situated some 630 kilometres off the coast of northern New South Wales, consists of a narrow twelve kilometre strip of land dominated by the twin peaks of Mount Gower (866 m) and Mount Lidgbird (765 m) to the south. For a bibliography of Lord Howe Island see Recher (1974).

The first account of the spiders of Lord Howe Island was provided by Rainbow (1920) on the collections made by A. M. Lea. During January–February 1971 a comprehensive collection of the spiders of the island was made by Mr M. R. Gray of the Australian Museum (Gray 1974). Two *Lycosa* species were collected during the 1971 survey, *Lycosa gloriosa* Rainbow 1920, and a *Lycosa* recognised by Mr Gray as representing an undescribed species. Mr Gray generously forwarded this material for inclusion in my revisional studies on the Australian species of the family Lycosidae.

Lycosa howensis sp. nov.
(Fig. 1A–E)

MATERIAL EXAMINED

HOLOTYPE: Australian Museum KS60, mature female, C.L. 4·7 mm, Lord Howe Island, near beachfront, collected by M. R. Gray.

PARATYPES: Lord Howe Island; AM KS61, 4 juveniles; AM KS62, 2 mature males; AM KS63, 1 mature male.

DESCRIPTION (Based on the holotype).

Carapace pale brown with a lighter median longitudinal stripe that commences behind the PL eyes and narrows abruptly before the fovea and continues to the posterior margin where it merges with a similarly coloured marginal band; some slightly darker stripes radiate out from the centre of the carapace over the light brown sides; paturon dark brown, contrasting markedly with the colour of the carapace, fang dark red-brown; labium and maxillae brown; sternum light brown with a conspicuous dark brown to blackish V-shaped marking (Fig. 1B), coxae light brown. Abdomen light brown to yellowish-brown with a very faint slightly darker anterior dorsal stripe surrounded by a vague light longitudinal median stripe which continues to the spinnerets; ventral surface uniform light yellow-brown. Legs uniform yellow-brown becoming darker distally; spines dark brown.

Anterior row of eyes slightly procured, the AM larger than the AL. Ratio of eyes AM:AL:PM:PL = 16:12:31:25; distance AM–AM 7, AM–AL 4, AM–PM 8, AL–PM 9, PM–PM 17. Clypeus to AM 11. Length of first eye row 67; length of second eye row 72.

Chelicerae with three retromarginal teeth on each side. Labium as wide as long.

TABLE 1: MEASUREMENTS OF LEG SEGMENTS OF *LYCOSA HOWENSIS* IN MM

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1	3·1	1·8	2·4	2·4	1·6
2	3·1	1·7	2·2	2·1	1·8
3	2·8	1·5	2·0	2·5	1·6
4	4·0	1·8	3·0	4·1	2·2
Palp	1·7	0·6	0·9	—	1·1

VARIATION: Juveniles have a broad pale longitudinal median stripe and a broad pale median band, the sides of the carapace are slightly darker or pale brownish with black hairs, occasionally marked with vague radiating stripes of dark brown or black; the abdomen is pale yellow-brown, with the anterior slopes dark brown to black, and the dorsal surface blotched with dark brown in a vague pattern of paired spots or blotches extending posteriorly; venter of abdomen and sternum without markings; legs pale yellow.

Adult males vary in colour pattern; one male is very pale with faint stripes on the carapace and uniform abdomen and legs; two males are patterned with dark blotches on the dorsal and lateral surfaces of the abdomen, median and lateral pale bands are present, and the sternum has a dusky V-shaped marking similar to that of the holotype; one male has the femora banded (Fig. 1A).

The eye dimensions of the male are similar to those of the female. Ratio of eyes (measured from the lens of the eye) AM:AL:PM:PL = 10:7:20:22, the PM eyes measured across the base are 26 units in diameter; distance AM–AM 9, AM–AL 5, PM–PM between bases 14; length of first eye row 54; length of second eye row 61.

The promarginal cheliceral teeth are 3 + 3; the retromarginal teeth are 2 + 2 in the two males, 3 + 3 in the other; juveniles are 2 + 2.

The adult male has a conspicuous pointed tubercle on the outer curve of the fang; females and juveniles lack the tubercle.

The epigynum of the holotype is illustrated in Fig. 1C. The male palpal organ has a plate-like median apophysis with a pointed cusp on the inner proximal edge (Fig. 1D) and a curved, medially expanded plate-like embolic guide (Fig. 1E).

SIZE RANGE: Mature female C.L. 4·7 mm. Mature males C.L. 3·4 to 4·0 mm.

DIAGNOSIS: *Lycosa howensis* differs from *L. gloriosa* the other species recorded from Lord Howe Island in shape of epigynum, male palpal organ and the presence of a tubercle on the fang of mature males. The epigynum differs markedly from that of *Lycosa strenua* Rainbow, from Norfolk Island (Rainbow 1920, pl. 30, Fig. 93).

HABITAT

This new species was collected from disturbed rainforest near the beachfront. 'Scalybark' *(Cleistocalyx fullageri)* and the 'greybark' *(Drypetes australasica)* were the dominant trees with grasses below. *Lycosa gloriosa* was also present at this site (station 25).

DISCUSSION

Lycosa howensis belongs to the 'arenaris' group of species (McKay 1974) which includes such Australian species as *L. arenaris, L. pullastra, L. lapidosa, L. furcillata,* and *Venator fuscus* (type species of the genus *Venator).* An expanded diagnosis of the genus *Venator* to include the species above is premature without a survey of all the *Lycosa* species in which the male has a tubercle on the outer surface of the fang. *Trochosa ruricola* (de Geer), the type species of the genus *Trochosa,* has a tubercle on the fang of mature males, and the epigyna of the *Trochosa* species resembles those of the 'arenaris' group; the anterior row of eyes (AM + AL) is wider than the second row (PM) in *Trochosa* but smaller in most specimens belonging to the 'arenaris' group of species. Locket, Millidge and Merrett (1974, p.37) record that as result of the work of Engelhardt in Germany, eleven percent of *T. ruricola* males lacked the tubercle on the outside of the fang. All mature males examined (over 200) belonging to the 'arenaris' group of species possessed the tubercle on the outside of the fang.

Lycosa gloriosa Rainbow 1920
(Fig. 1F-K)

Lycosa gloriosa Rainbow, 1920, pp. 261–2, pl. 30, figs. 94, 95, Lord Howe Island; Roewer, 1954, p. 272; Bonnet, 1957, p. 2643; McKay, 1973, p. 379.

MATERIAL EXAMINED

HOLOTYPE: South Australian Museum, mature female labelled '*Lycosa gloriosa* Rainb. Lord Howe Is. TYPE'. The holotype is in good condition and agrees with the description by Rainbow (1920). The epigynum is illustrated (Fig. 1F).

OTHER MATERIAL: Lord Howe Island; AM KS52, 1 mature female, 1 mature male, 11 juveniles; AM KS53, 1 mature female; AM KS54, 1 mature female; AM KS55, 1 mature female; AM KS56, 1 mature female with young, 2 juveniles; AM KS57, 1 penultimate female, 2 juveniles; AM KS58, 1 mature female; AM KS59, 1 juvenile.

DESCRIPTION (after Rainbow 1920, pp. 261–262)

Carapace yellow with dark brown markings, marginal band yellow; paturon yellow; labium and maxillae yellow; sternum yellow with paler margins. Abdomen yellow above with dark brown markings and spots; sides yellow, spotted with dark brown; ventral surface spotted with dark brown and having two broad dark brown bars commencing at the epigastric furrow and converging towards the spinnerets. Legs yellow, banded with dark brown.

VARIATION: Anterior row of eyes slightly procurved, AM larger than AL, about a diameter apart; PM eyes slightly less or slightly more than

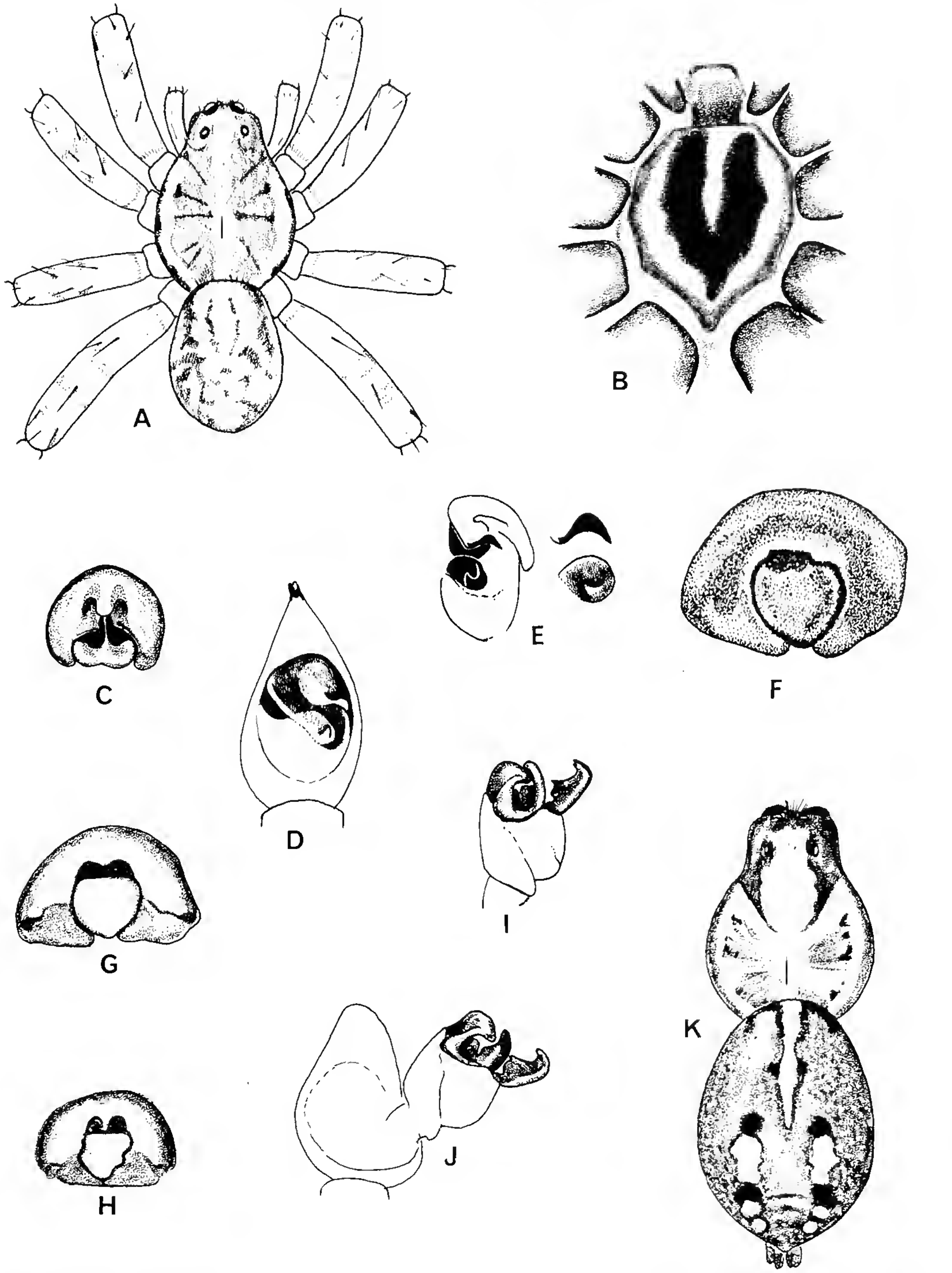

FIG. 1: *Lycosa howensis*. A–E; A, paratype male; B, sternum of holotype; C, epigynum of holotype; D, palpal organ of paratype male; E, embolic guide and median apophysis of paratype male palpal organ.
Lycosa gloriosa. F–K; F, epigynum of holotype female; G–H, epigyna of two females showing variation; I–J, palpal organ of mature male shown in an expanded condition from two positions, one lateral and one anterolateral; K, mature female.

their diameter apart. One female (KS55) had the ratio of eyes in micrometer units AM:AL:PM:PL = 9:7:21:20; distance AM–AM 9, AM–AL 7, PM–PM 24. Length of first eye row 52, length of second eye row 65.

Chelicerae with 3 promarginal teeth, the middle one largest; retromarginal teeth 3+3 (1♂ 2♀) or 4+4 (2♀ mature 1♀ penultimate). Mature males without tubercle on the outer surface of the fang.

Venter of abdomen with three brown converging bars fusing before base of spinnerets in one mature female, and the normal two converging brown bars that do not fuse together posteriorly in other mature females.

Epigynum of holotype illustrated in Fig. 1F, the epigyna of two additional females (KS53, KS55) in Fig. 1G, H. The male palpal organ is very complex and must await study under the scanning electron microscope; the palpal organ of the only mature male is illustrated from two positions in an expanded condition in Fig. 1I, J.

One mature female (KS56) is illustrated in Fig. 1K.

SIZE RANGE: Mature females C.L. 3·4 to 6·2 mm. Mature male C.L. 3·1 mm.

DIAGNOSIS: Differs from *Lycosa howensis* in the shape of epigynum and the complex palpal organ of the mature male. Mature males lack a tubercle on the outer curve of the fang.

HABITAT

Lycosa gloriosa was collected from the beachfront with a disturbed *Cleistocalyx–Drypetes* association and grasses (station 25), from lowland palm groves with *Pandanus–Howea* association (stations 4–5) or lowland mixed rainforest *Howea–Drypetes–Cleistocalyx* (stations 38, 42), to the summit of Mt Gower at 866 metres with a low mossy forest, ferns, mosses, lichens and small palms.

DISCUSSION

Nothing is known of the life history of *Lycosa gloriosa* and *Lycosa howensis*.

ACKNOWLEDGMENTS

Mr M. R. Gray, Australian Museum, Sydney, kindly forwarded the material of *Lycosa howensis* and *Lycosa gloriosa* for study. Mr D. C. Lee, South Australian Museum forwarded the holotype of *L. gloriosa* for examination. Mrs Janet Byrne typed the manuscript.

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THE WOLF SPIDERS OF AUSTRALIA (ARANEAE: LYCOSIDAE): 12. DESCRIPTIONS OF SOME WESTERN AUSTRALIAN SPECIES

R. J. McKay
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ABSTRACT

Redescriptions are provided for *Lycosa australicola* (Strand 1913), *L. clara* L. Koch 1877, *L. crispipes* L. Koch 1877, *L. marcentior* Simon 1909, *L. meracula* Simon 1909, and *L. tula* (Strand 1913). *Lycosa ariadnae, L. gibsoni, L. koyuga, L. maini, L. woonda,* and *L. yalkara* are described as new.

The lycosid fauna of Western Australia is, despite recent collecting, very poorly known. Large areas of the state, particularly the more arid and inaccessible regions, have not been surveyed for wolf spiders, and much collecting remains to be done before the fauna is documented. A large number of undescribed wolf spiders have been found, but in many cases these are represented by a few individuals of one sex only, or juveniles.

Because most species of wolf spiders show pronounced habitat specificity, many microhabitats need to be examined when collecting. These include:

Sand beaches: under shells and dead seaweeds.

Shingle beaches: under pebbles or stones; in coral shingle.

Coastal sand dunes: on dune slipfaces; in interdune areas; under shrubs and trees; on dune grasses.

Coastal plains: open sand areas; heathlands; below shrubs and trees in litter; grasslands; margins of swamps and lakes.

Rivers, lakes and ponds: wet sands at waters edge; under stones on creek beds; under gravel or pebbles; in decaying humus; on river banks under trees; in dry river sands; on grassy banks; at waters edge or on floating aquatic vegetation; in cracking clay soils.

Montaine habitats: on stony outcrops; under exfoliating boulders; under shrubs and trees; in grasslands; under snow; in litter or decaying humus.

Inland sandplains: on sand ridges; at base of dunes under vegetation; interdune clay soils; in *Triodia* grasslands; below trees.

Mulga *(Acacia* shrublands): open clay-loam soils; open sandy soils; below low shrubs; below trees in litter; in stony areas.

Rock ridges and gibber plains: on rock ridges (sheltering); on rocky soils (burrowing); on gibber plains; on sheetwashed pebble slopes.

Saltpans and claypans: burrowing in salt; burrowing in moist clays; in samphire clumps; in dry clay fissures.

Forest habitats: below stones; below logs; within leaf litter or humus; within fern humus (moundsprings); on heavy clay loams; on sandy soils; on previously burnt areas.

Disturbed habitats: pastured areas and crops; suburban lawns and gardens; margins of farm dams and tanks.

A number of quite distinct species may be found on saltpans or sandridges in different regions and these may have restricted distributions (McKay 1976), whereas other species may be found Australia-wide. The greatest diversity of wolf spiders is to be found in arid or semi-arid regions and are generally rare or cryptic in rainforest or wet sclerophyll forests (see Main 1976). For a list of Australian species see McKay (1973), and subsequent papers in this series.

Lycosa ariadnae sp. nov.

(Fig. 1A–L)

MATERIAL EXAMINED

HOLOTYPE: Western Australian Museum WAM 72–246, ♀M, C.L. 7·9 mm, 5 km west of Darkan, W.A., collected by Dr Barbara Y. Main, 26 October 1961. In spirit.

Paratypes: Western Australia; Arthur River 1·6 km south (121 mi. peg), 27.x.1961, BYM, WAM 72–244; Augusta, 21.ii.1969, RJM, R. W. George, WAM 71–468–71; Australind, 22.x.1969, RJM, R. W. George, WAM 71–368–73; Bakers Hill, 23.xi.1962, W. D. Lane, WAM 69–413–26; Bremer Bay, 29.iv.1972, P. G., A. J., G. W. Kendrick, QM.W4666; Brentwood (Perth), 23.iv.1969, RJM, WAM 69–767–70; Bruce Rock at Nangeen Hill, 21.iv.1971, N. McKenzie, A. A. Burbidge, WAM 71–1856; Brunswick Junction, 22.x.1969, RJM, R. W. George, WAM 71–330–41; Bunbury, 22.x.1969, RJM, R. W. George, WAM 71–357; Bunker Bay, Cape Naturaliste, 20.ii.1969, RJM, WAM 69–485–94, 22.x.1969, RJM, R. W. George, WAM 71–342–49, 25.v.1971, RJM, WAM 71–1406; Busselton 8 km north, 22.x.1969, RJM, R. W. George, WAM 71–303–7; Cape Freycinet, 25.i.1971, HB, WAM 71–716–30; Cape Naturaliste, 22.x.1969, RJM, R. W. George, WAM 71–308–29; Cockleshell Gully, 24.ii.1963, BYM, WAM 71–926–33; Cowaramup Bay, ix.1970, RH, WAM 71–666; Dandaragan, 4.iv.1953, BYM, WAM 71–662; Darkan 5 km west, 26.x.1961, BYM, WAM 72–245; Dempster Inlet, 5.i.1971, L. E. Koch, K. Youngson, WAM 71–962–3; Desperate Bay north of Snag Island, 27.ii.1971, RJM, B. Ryle, WAM 71–850, WAM 71–935–6; Dongara, 5.vii.1971, RJM, WAM 71–1858; Dryandra State Forest, 11–12.x.1969, P. G., G. W. Kendrick, WAM 70–43–7; Dunsborough at beach, 22.x.1969, RJM, R. W. George, WAM 71–466; Fitzgerald River Reserve, 7.i.1971, L. E. Koch, K. Youngson, WAM 71–203–6, 16.vii.1970, AB, WAM 71–400–3, 11.vii.1970, RJM, WAM 71–514–5, 6.i.1971, L. E. Koch, K. Youngson, WAM 71–957–61, 11.vii.1970, RJM, J. G., RH, WAM 71–1937–44, 15–18.vii.1970, AB, WAM 71–1945–55; Fremantle at Buckland Hill, 10.i.1969, RJM, WAM 69–54–63; Golden Bay, Mandurah, 21.i.1971, RJM, WAM 71–670–3, WAM 71–754–8, WAM 71–840–1; Green Head, 27.ii.1971, R. Johnstone, WAM 71–761, WAM 71–839, 22.iv.1972, R. Johnstone, WAM 72–723–33, WAM 72–734–41; Hill River, 18.ii.1971, RJM, WAM 71–851; Hyden, 9.iv.1971, B. Evans, WAM 71–1101–2, WAM 71–1857; Meelup, 22.x.1969, RJM, R. W. George, WAM 71–478; Mississippi Bay, 31.iv.1972, A. Chapman, WAM 72–332–4; Moora, 23.xi.1962, W. Lane, WAM 71–920–3; Moore River National Park, 5.ii.1971, N. McKenzie, WAM 71–745–7; Moorine Rock 13 km west, 8.i.1970, HB, QMW 4665 Murchison River, 24–25.i.1969, RJM, JG, P. Snowball, WAM 69–303–5; National Park west of Mundaring, 29.v.1968, RJM, JG, WAM 69–44, WAM 69–101; Perth at Kings Park, i.1969, RJM, WAM 69–45, 19.xi.1962, W. Lane, WAM 71–904–19; Pingelly, 8.xii.1962, W. Lane, WAM 69–412, 9.xii.1962, W. Lane, WAM 71–924; Pingrup 27 km east at Greenshields Soak, 31.iii.1971, J. Ingram, WAM 71–1089–1100; Point Peron, 14.iv.1968, RH, WAM 70–198, 29.xii.1962, BYM, WAM 71–479–88; Rossmoyne, Canning River, 1970–71, RJM, WAM 70–220–3, WAM 71–553, WAM 71–664–5, WAM 71–683–91, WAM 71–759–60, WAM 71–947; Rottnest Island, 8.xi.1962, W. Lane, WAM 69–411, WAM 71–925, 25.xi.1970, RJM, WAM 71–667–9, WAM 71–842–3, WAM 71–937–8, 18.i.1954, BYM, WAM 71–844–8, WAM 71–949–56, xii.1962, BYM, WAM 71–964–71, 20.i.1954, BYM, WAM 71–1409–20; Tarin Rock Reserve, 17.v.1971, WAM Survey, QM W4663; Thomsons Lake Reserve, 28.iv.1970, RJM, WAM 70–61)6; Two People Bay, 9–11.ii.1970, J. L. Bannister, WAM 71–378, WAM 71–934, 5.ii.1970, J. L. Bannister, A. Burbidge, WAM 71–1407–8; Walyamoning Rock, 31.iii.1972, AB. A. Chapman, QM W4664; Wanneroo, 12–13.iv.1969, RH, WAM 71–377, at Badgerup Swamp, 26.iv.1969, RH, WAM 71–396–7; Windy Harbour, 21.i.1971, G. W. Kendrick, WAM 71–849; Yanchep, Forestry Reserve, 17.iii.1971, RJM, T. Wood, WAM 71–852–5; Yorkrakine Rock, 12.vi.1971, RH, WAM 71–1405.

Description (Based on the holotype)

Carapace light brown with an indistinct pale lateral band and some vague dark brown marks radiating from the centre; a distinct pale longitudinal stripe commences within the ocular quadrangle, broadens behind the PL eyes and continues to before the fovea where it widens to form a short anteriorly directed arm on both sides, narrowing to the commencement of the fovea where it again broadens into a diamond shape and then narrows to the posterior margin; paturon brown with pale hairs on the anterior surface becoming dark brown to black towards the fang; labium and maxillae brown with dark brown hairs; sternum and ventral surface of the coxae dark brown. Abdomen light brown above, densely speckled with dark brown to form a vague pattern of three light tent-shaped chevrons surrounded by dark areas, and two large posterio-lateral pale blotches; the anterior dorsal surface has a large pale transverse broad lunate-shaped pale area; sides pale brown to buff with close-set dark brown spots and flecks, becoming paler on the lower slopes; venter pale brown with a triangular black field pointing posteriorly and not reaching the spinnerets. Legs and palpi pale brown with indistinct brown blotches and some longitudinal brown stripes on the retrolateral surface of the femora; the distal ends of the femora and the tibiae dark brown.

Anterior row of eyes slightly procurved and shorter than the second row, AM larger than AL. Ratio of eyes AM:AL:PM:PL = 10:6:26:21; distance AM–AM 4, AM–AL 3·5, AM–PM 4, AL–PM 4, PM–PM 12. Clypeus to AM 7. Length of first eye row 44; length of second eye row 59.

Chelicerae with three promarginal teeth, the middle one largest; three retromarginal teeth of equal size. Labium longer than broad.

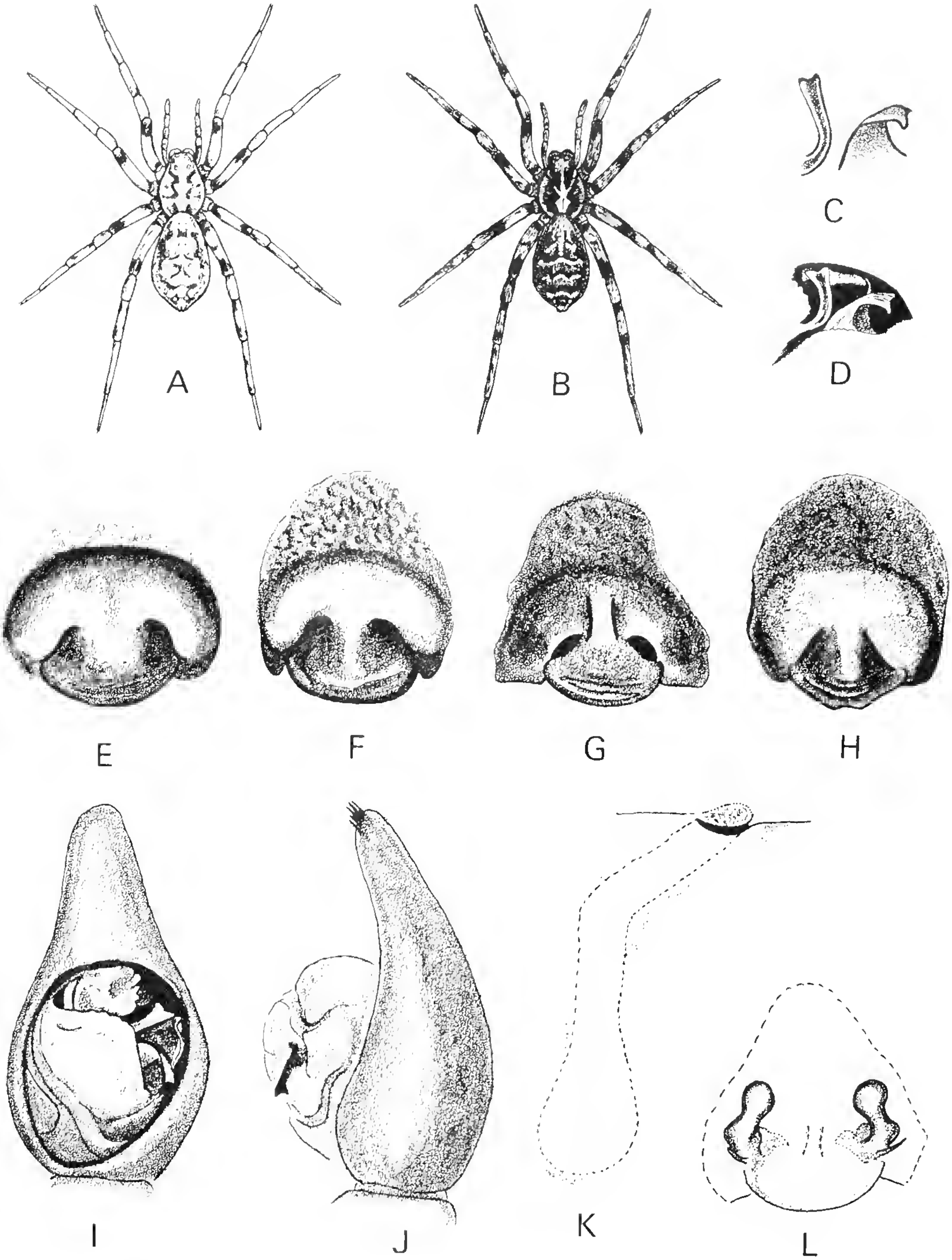

FIG. 1: *Lycosa ariadnae*. A, mature female WAM 71–664; B, mature female WAM 71–665; C, D, embolic guide and median apophysis of two mature males; E, epigynum of holotype; F, G, H, epigyna of WAM 71–949, WAM 70–338, WAM 72–245; I, male palpal organ of WAM 71–884; J, palpal organ of WAM 71–884 expanded; K, burrow; L, internal genitalia of a female from Fitzgerald River.

VARIATION: The colour pattern of *Lycosa ariadnae* is very variable. On the white dune sands the colour is frequently white, pale cream or light brown with dark brown flecks and streaks that outline the typical colour pattern described above. On dark soils or red earths the coloration may be quite striking with a distinct longitudinal stripe and lateral band on a dark brown to red-brown carapace, and a well marked abdomen with three to four pale chevrons surrounded by dark brown, the anterior dorsal surface frequently much lighter brown, cream, orange or pale pink, with the sides dark brown or very pale. On dark loams, near swamps or on burnt substrates this species may be almost black with a white or cream pattern as above. Two paratypes WAM 71–664 and WAM 71–665 are illustrated (Fig. 1 A, B).

The juveniles may have the adult coloration but frequently have the anterior dorsal surface of the abdomen bright orange, pink, or orange-red. The paturon may have the anterior surface brown, orange or reddish with the lateral condyle brown, orange or bright red.

The venter in juveniles below C.L. 4·0 mm is usually pale, the black area commences as a small posteriorly directed triangle or a pair of small triangles which fuse with subsequent moults to form one large triangle which may terminate before the spinnerets in mature specimens from the drier eastern localities or expand into a completely black venter with rounded margins touching or enclosing the spinnerets in adults from the coastal plain. The sternum is normally pale in small juveniles but becomes darker as the venter assumes the normal black field. The legs may be banded with dark brown or black, or may have the distal tips of the femora and all other joints dark brown or black. This species may show considerable variation in colour on the sandy soils of the Swan Coastal Plain, especially in areas dominated by *Banksia* and *Casuarina* scrub and subjected to periodic burning.

TABLE 1: MEASUREMENTS OF LEG SEGMENTS OF *L. ARIADNAE* IN MM

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1	5·3	2·9	3·9	4·0	2·0
2	5·0	2·8	3·6	3·9	2·0
3	4·9	2·5	3·5	4·5	2·0
4	6·3	2·7	4·9	6·1	1·8
Palp	2·5	1·4	1·4	—	2·0

Variation in the shape of the epigynum is shown for the holotype and three paratypes in Fig. 1E-H. The epigynum has a broad median guide surrounded anteriorly by a raised and well sclerotized boss; the internal genitalia of one paratype is shown in Fig. 1L. The male palpal organ is illustrated in Fig. 1C, D, I, J, and electron scanning micrographs of a male palp (regd. ANN 26–27, Uni. Qd.) at 45 and 110 magnifications provided in Plate 1. The median apophysis is curved proximally with the tip expanded and slightly bifurcate (Fig. 1C, D) somewhat similar in shape to the flattened embolic guide shown pointing distally in micrographs (see also McKay 1974, fig. 4). A study of the male palpal variation under a low power dissecting microscope showed that the shape of the median apophysis and embolic guide varied slightly. An analysis of this variation employing the electron scanning microscope may demonstrate that two races of *Lycosa ariadnae* may exist; one on the coastal plain, and one inland, although the mature males of the coastal plain respond to females from the inland population that is characterised by having a more uniform coloration and smaller black area on the venter.

Eye measurements of the holotype and six paratypes are given as a percent of the total width of the first eye row in Table 2.

SIZE RANGE: Mature females C.L. 5·2 to 7·9 mm. Mature males C.L. 5·0 to 5·7 mm.

DIAGNOSIS: *Lycosa ariadnae* has a distinctive epigynum and the male palp has a flattened

TABLE 2: EYE DIAMETERS AND INTERSPACES OF *L. ARIADNAE* CONVERTED TO PERCENT OF THE TOTAL WIDTH OF THE FIRST ROW OF EYES

Regd. No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM	AL:PM
HOLOTYPE	♀M	7·9	23	14	59	48	9	8	27	9	9
WAM 71–844	♀M	7·5	25	14	57	50	5	6	25	9	11
WAM 71–845	♀M	7·2	24	19	58	51	6	5	29	9	10
WAM 71–846	♀M	6·2	27	15	60	51	9	6	27	9	12
WAM 71–847	♀M	6·1	28	16	62	55	9	5	25	9	9
WAM 70–340	♀M	7·3	27	14	64	52	6	4	26	7	8
WAM 72–245	♀M	8·0	24	15	57	48	5	6	24	9	11

terminally expanded embolic guide with a slightly bifurcate to emerginate tip.

LIFE HISTORY

Mature males may be found throughout the year but are more numerous during the summer months. The mature males appear in November, are most abundant in January, and decline rapidly in number by late February. Courtship and mating is at a peak during January, especially at dusk on warm still nights with a temperature of between 22–28°C.

Courtship was observed in the laboratory and the male commences as soon as the female pheromone is sensed. The male rapidly drums or scratches the palps on the ground so vigorously that the noise is quite audible. A series of quick jerky movements accompanied by very rapid up and down bobbing of the abdomen continues while the male searches for the female, who responds by lowering the body and remaining motionless. The male mounts the female from above and whilst continuing the abdominal vibrations places the left palpal organ around the left side of the female and makes contact with the epigynum which is then pulled slightly around to the left with a twisting of the female abdomen. The haematodocha then expands, sperm transfer takes place through the embolus, the membrane deflates, and the palpal organ is removed, the entire process taking about 10–15 seconds. The palps are applied alternately, left palp to left side of the female, the right palp to the right side; up to 80 separate applications may take place and a successful mating can take up to 56 minutes to complete. The male then breaks free and retreats.

On 15 January 1971 a series of cross mating experiments were undertaken to assess the response of mature males to females. The results of these experiments are shown in Table 3. A vigorous response by the male consisting of vigorous palpal drumming and scraping, abdomen bobbing and searching movements is denoted by + + +, a palpal drumming and slow abdomen bobbing by + +, and a weak response by slow palpal scratching by +; a nil response is denoted by — and a successful mating by M Only four males were allowed to mate with the test females; the males were removed prior to mating to ensure that the female did not kill the male, and so that males could be tested with a number of females. On two occasions males mated with females before they could be removed from the test jar; these mated females were not used for further tests as they frequently attacked the males as soon as they were placed in the jar. Egg-cocoons were not produced by females employed in any of the tests. Males were found to respond to females after a successful mating but on some occasions showed a diminished response. By 2 February, 1971, many males that had shown a + + + response to females were reluctant to respond and when disturbed or placed into a test jar occupied by a female, frequently lost their co-ordination and with violent spasmodic twitching died very rapidly.

By the end of February almost all mature males have died and most females are gravid. The egg cocoons are constructed throughout March into mid April. The cocoon measures about 5·9 to 7·0 mm and 4 cocoons contained 102, 103, 140 and 151 eggs, 1·15 to 1·20 mm in diameter. The

TABLE 3: *Lycosa ariadnae* Courtship of Mature Males to Mature Females

	MALES									
FEMALES	Rossmoyne 1	Rossmoyne 2	Rossmoyne 3	Rossmoyne 4	Golden Bay 1	Golden Bay 2	Golden Bay 3	Rottnest 1	Rottnest 2	Dongara 1
Wickepin 1	—	+ +	+ + +	+ + +		—	+ + +			
Wickepin 2	+	+ +	+ +	+ +	+ +	—	+	+ + +	M	—
Cowaramup 1	+ +	+ + +	+ + +	+ + +		—	+ + +	+ + +	+ +	—
Rottnest 1	—	—	+ + +	+ +	+ +	+	M	+ + +	+ + +	—
Rottnest 2	+	+ +	+ + +	+ + +	+ + +	+	+ + +	+ + +	+ + +	+
Golden Bay 1			+ + +	M					+ + +	+
Rossmoyne 1		+ + +	M	+ + +	+ + +			+ + +	+ + +	+ +
Rossmoyne 2		+ +	+ +	+ +				+ + +		+
Rossmoyne 3	—	—	+	+	—	—	+	+ +		—
Rossmoyne 4		+ + +	+ + +	+ +	+ + +		+ + +	+ + +	+ + +	—

female remains in the burrow with the egg–cocoon until the spiderlings hatch, and only rarely are females observed with an egg cocoon in the field. The young remain on the female for about two weeks and disperse during April, May and early June. The young spiders are vagrant throughout the winter and construct burrows in early spring.

Growth is rapid during October and November until maturity is attained. Although all males appear to die during February, some females continue through the winter months until the following season; it is not known if these females are unmated or have produced an egg-cocoon.

Lycosa ariadnae will survive temperatures of up to 42·2°C under laboratory conditions for a period of 30 minutes. During the summer months ground temperatures may exceed this limit, and all adults are within the burrow during the day, only emerging at dusk to hunt. On still warm summer nights *L. ariadnae* may be exceedingly numerous in suitable habitats, frequently in association with *Lycosa immansueta (=V. spenceri?) L. pullastra, L. godeffroyi, L. leuckartii, P. serrata, T. impedita, L. propitia, T. phegeia, T. oraria, L. dimota* and *L. australicola.*

HABITAT

Lycosa ariadnae is most abundant on the sandy soils of the Swan Coastal Plain particularly in *Banksia* scrublands. A variety of other habitats are also occupied including coastal dune systems, coastal heathland, open cleared areas with sparse grass cover, open forests of Jarrah and Red Gum on lateritic soils and clay-loams, Tuart forests, *Casuarina* and Yate thickets. Unsuitable habitats are grasslands, thick swamp vegetation, and forest areas with a heavy leaf litter. Sandy tracks or gravel road verges in heavy coastal forest areas frequently have many *L. ariadnae* wandering in the open whereas this species is uncommon on the leaf littered habitat nearby.

At Rossmoyne near Perth a small area of *Banksia* forest with a thick cover of leaf litter and grass contained very few *L. ariandnae* and numerous *L. immansueta* although the former species was the dominant lycosid on the open sandy areas previously cleared or burnt three years previously. In 1969 the Banksia forest was burnt, thus removing the leaf litter; by 1971 this forest was dominated by *L. ariadnae.*

In March 1971 a controlled burn of a forestry reserve of Banksia and Tuart was made by the Forestry Department, W.A., at Yanchep. This area had been building up a ground cover of grass and leaf litter and the dominant species the previous month was *L. immansueta.* At 8.00 p.m., 9 hours after the burn another collecting survey was made whilst logs in the area were still burning. The ground was largely cleared of undergrowth and burnt black. The only species collected was *L. ariadnae,* specimens of which were found adjacent to the burrows or actively hunting nearby. Five burrows were excavated in the burnt area and the depth of the burrow varied between 5·0 and 5·5 cm. Unfortunately, time did not permit the burrows of *L. immansueta* and *L. ariadnae* to be marked before the fire and no survival data was obtained. It is possible that *L. immansueta* had also survived the burn but no specimens had emerged by 9.30 p.m. *L. immansueta* is quite constant in coloration and frequents leaf litter in forested areas below trees.

BURROW

A shallow burrow some 5 to 12 cm in depth with the upper part slanted and an abrupt bend, has a soft silk lid or flap covered with sand grains. The female enters the burrow head first and the soft lid falls back into place completely covering and concealing the burrow entrance (Fig. 1K).

DISTRIBUTION

Southwestern Western Australia within a line drawn from the Murchison River bridge at the North West Coastal Highway to Mullewa, 30 km east of Wubin, between Merredin and Southern Cross and Hopetown. *L. ariadnae* is absent from the Karri forest near Manjimup, Pemberton and Walpole, and in areas of heavy Jarrah forest.

DERIVATION

Named after Mrs Ariadna Neumann of the Western Australian Museum in appreciation for her painstaking translation of the numerous descriptions of Australian Wolf Spiders in L. Koch's 'Die Arachniden Australiens'.

Lycosa australicola (Strand, 1913)
(Fig. 2A-L)

Tarentula australicola Strand, 1913, pp. 619–20, Central Australia.
Allocosa australicola: Roewer, 1954, p. 205.
Lycosa australicola: McKay, 1973, p. 378.

MATERIAL EXAMINED

HOLOTYPE: Senckenberg Museum No. 2255, ♀M, C.L. 8·0 mm, collected V. Leonhardi, 1909, 'Central Australien'.

OTHER MATERIAL: Western Australia; Cadgi Hills, 14.x.1962, BYM, WAM 71–1360–1; Caren Caren Brook, near Jurien Bay, 28.ii.1971, RJM, WAM 71–866; Carnarvon 81 km north, 20.ii.1962, BYM, WAM 71–1323, WAM 71–1740–3; Cockleshell Gully, 26.ii.1963, BYM, WAM 71–1337; Coorow 14 km SSW, 22.xi.1970, AB, WAM 71–1315–8; Desperate Bay north of Snag Island, 27.ii.1971, RJM, B. Ryle, WAM 71–861–5; Dryandra State Forest, 11–12.x.1969, P. G. & G. W. Kendrick, WAM 71–473–4, 17–19.xi.1971, T. Evans, QM W4201; East Pingelly, 8.xii.1962, BYM, WAM 71–1339–42; 23.ix.1962, BYM, WAM 71–1346, 9.xii.1962, BYM, WAM 71–1353–4, WAM 71–1362–5, WAM 71–1375–6, Fields Find, 30.i.1968, L. E. Koch, QM W4202; Fitzgerald River Reserve, 7.i.1971, L. E. Koch, K. Youngson, WAM 71–207; Greenhead, 22–23.iv.1972, R. Johnstone, WAM 72–720–2; Greenshields Soak 27 km east Pingrup, 30.iii.1971, J. Ingram, T. Evans, WAM 71–1357–9; Houtman Abrolhos Islands, 1963, BYM, WAM 71–422, Gun Island, 6.vii.1971, RJM, WAM 71–1377–80, Island NW of Middle Island, 7.vii.1971, RJM, WAM 71–1381–6; Jiliman Rock, 28.iii.1954, BYM, WAM 69–1012; Kalbarri, Murcheson River 17 km south, 3–5.ii.1969, Kalbarri WAM Survey, WAM 69–666; Kings Park, 10.iii.1971, RJM, S. Stanley, WAM 71–858, 19.xi.1962, BYM, WAM 71–1324–7; Lake Austin, 9.i.1962, BYM, WAM 71–1338; Learmonth, 13.iv.1969, N. Cross, WAM 71–1345; Madura, 19 km south, WAM 71–1343–4; Moora, 23.xi.1962, BYM, WAM 71–1355; Moore River at Guilderton, 12.xii.1971, RJM, WAM 71–1996; Mt. Hampton, 10.xi.1970, N. McKenzie, WAM 71–859–60; Murchison River at highway, 12.ii.1962, BYM, WAM 69–471, 30.i.1969, RJM, WAM 71–1006, at Tutula Well, Paradise Flat, 22–3.i.1969, RJM, JG, WAM 71–1319–22, 12.v.1972, RJM, QM W4200; Point Walter, 15.ii.1963, BYM, WAM 71–1329–32; 27.xii.1962, BYM, WAM 71–1366–74; Rottnest Island, 10.iii.1960, BYM, WAM 71–892–3, 20.i.1954, BYM, WAM 71–1005, 9.xi.1962, BYM, WAM 71–1333–6, WAM 71–1347–52, 20.i.1954, BYM, WAM 71–1738–9; Tarin Rock Reserve, 16.v.1971, WAM 71–1356; Wiekenpin, 19.i.1971, A. Paterson, WAM 71–775, WAM 71–1328; Wiluna, WAM 37–2203; Wubin, 7.xii.1971, RJM, JG, P. Snowball, WAM 71–284.

DESCRIPTION (Based on WAM 71–1740)

Carapace dark brown with a sharply defined broad fawn longitudinal stripe that fills the ocular quadrangle, broadens slightly behind the PM eyes and tapers to the posterior margin; a fawn marginal band gradually merges with the dark brown hair of the lateral slopes; some faintly darker radiating stripes appear on the lateral slopes of the carapace after preservation but these are not present in life; paturon dark brown with an oblique orange stripe near the base; lateral condyles red-brown; fangs black; labium and maxillae brown; sternum and lower surface of coxae brown. Abdomen pale fawn above, the anterior side brown, defining the pale fawn upper surface, lateral surface speckled with fine dark brown specks; within the pale slightly pointed dorsal area is a triangular dark brown mark pointing anteriorly and followed by two much smaller triangular brown marks and indistinct very pale brown chevrons; undersurface with a somewhat triangular black field pointing posteriorly and scattered black-brown spots outlining a vague rounded pale brown field that reaches the spinnerets. Spinnerets pale brown. Legs and palpi uniform dark honey-brown.

Anterior row of eyes with the upper tangent slightly procurved, the lower tangent very slightly recurved, narrower than the second row, AM larger than AL. Ratio of eyes AM:AL: PM:PL = 10:8:24:20; distance AM–AM 4·5, AM–AL 3, AM–PM 6, AL–PM 6, PM–PM 10. Clypeus to AM 8. Width of first eye row 47; width of second eye row 56.

Chelicerae with three promarginal teeth, the middle one largest; three retromarginal teeth of about equal size. Labium slightly longer than broad.

TABLE 4: MEASUREMENTS OF LEG SEGMENTS OF *L. AUSTRALICOLA* IN MM

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1	5·8	3·1	4·3	4·3	2·3
2	5·5	3·0	3·8	4·0	2·2
3	4·9	2·7	3·3	4·5	2·1
4	6·0	2·2	4·7	6·6	2·9
Palp	3·1	1·4	1·3	—	2·1

Epigynum horseshoe-shaped with a narrow median guide and a broad almost rectangular transverse guide.

VARIATION: Juveniles are similarly patterned to adults although the colour may be brighter and the pattern more distinct; the venter of juveniles is at first uniform pale cream to fawn, then two small dark spots appear anteriorly, gradually elongate with growth and may form two (sometimes three) black-brown bars, the lateral ones longest; all bars may merge anteriorly and then posteriorly to form a rounded black field enclosing two pale fawn diverging or parallel stripes in some adults or the triangular field of others. Carpace may be dark brown to rust-red brown with cream, fawn, or tan longitudinal median and lateral bands; legs pale fawn-brown to light brown, red-brown or dark brown.

The epigyna of six mature females is illustrated in Fig. 2E, F, I, J, K, L. The male palpal organ has a curved cutlass-shaped or blade-like embolic

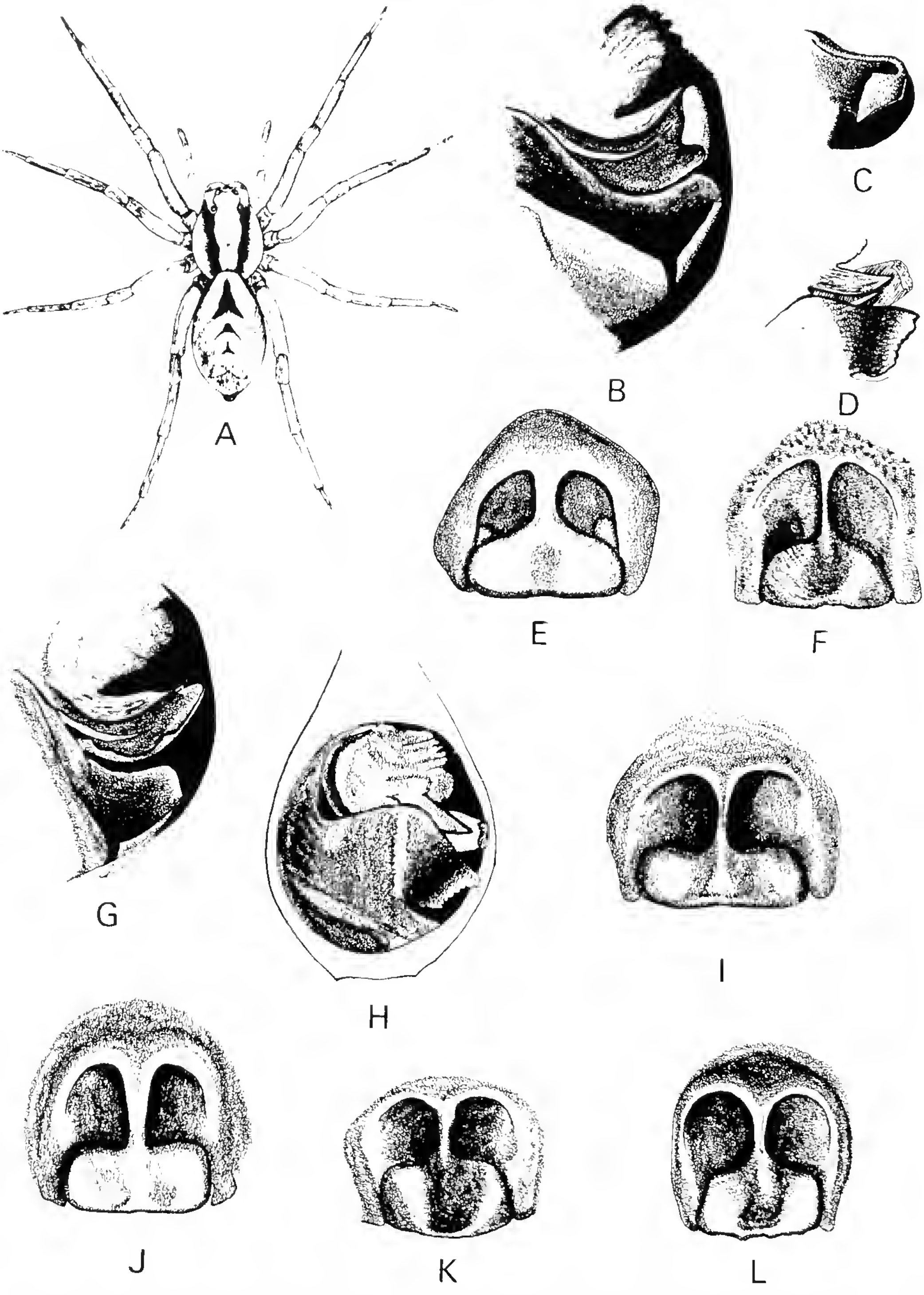

FIG. 2: *Lycosa australicola*. A, mature female WAM 69–779; B, male palpal organ of WAM 71–1738; C, D, median apophysis of male palpal organ WAM 71–1741; E, F, I, J, K, L, epigyna of females WAM 71–1740, WAM 71–1358, WAM 71–1743, WAM 71–1345, WAM 71–892, WAM 71–1356; G, H, male palpal organs of WAM 71–1329, WAM 71–1741.

guide; the median apophysis is a broad structure with the end bent, curved, cup-shaped or strongly recurved (Fig. 2B, C, D, G, H).

SIZE RANGE: Mature females C.L. 5·5 to 8·8 mm. Mature males C.L. 5·8 to 7·0 mm.

DIAGNOSIS: *Lycosa australicola* is distinct from all other Australian species in coloration, shape of the epigynum and in having a broad stout median apophysis with a bent or recurved tip.

LIFE HISTORY

Mature females are present throughout the year but are more abundant during the summer months. Males are present from late November to March and abundant in February. Courtship commences late November and continues through the summer months; the response to the female pheromone is quite rapid, the male drums the palpal cymbium on the ground and approaches with short quick movements and mounts the female in a dorsal head to tail position whilst curling the abdomen over the face of the female and bobbing it up and down, or vibrating it rapidly before the eyes of the stationary female. Palpal insertions were counted in one male from Desperate Bay mated with a female from Wickepin; after 18 alternate insertions the male cleaned the palp with the chelicerae, vibrated one foreleg and then continued mating for 2 more alternate insertions before suddenly breaking free and rapidly retreating from the female who instantly recovered, gave chase, and killed the male.

Two females carrying egg-cocoons were found in March, one with the cocoon measuring 7·2 mm in diameter and containing 141 young ready to emerge. Females with young were found during April and May, and in June and July very small juveniles were observed. Growth appears to be quite rapid in spring; penultimate males and females appear during November and are abundant in December.

HABITAT

A variety of soil types are inhabited, usually in open sclerophyll forest but coastal heathlands may have scattered individuals. Red earths with Salmon Gum *Eucalyptus salmonophloia* carry large populations of *L. australicola,* found wandering on open ground or more commonly near leaf litter below trees. Sandy soils including the vegetated sand dunes of the coastal heathland near Jurien Bay may have occasional specimens but the species becomes more numerous in the Jarrah forests on laterite and in light clay-soils with Wandoo or Brown Mallet *E. astringens*. On the red loam soils and hard red clay soils with Red Gum *E. camaldulensis* between Carnarvon and Murchison River this species is abundant, although not the dominant wolf spider. Small populations were found on littered sand areas under Swamp Yate *E. occidentalis* at the Fitzgerald River, but *L. australicola* was not found on the open sandplain areas nearby.

BURROW

Only two burrows were located, both were situated at the base of trees in well consolidated clay-sand (Kings Park) or heavy red clay-loam (south of Wubin). The burrows were open with a diameter of 10 and 12 mm and descended obliquely downwards adjacent to the tree roots for a distance of 11·5 cm and 5 cm where they enlarged slightly. On both occasions the female moved into the burrow head first and both burrows were difficult to excavate due to the presence of tree roots.

DISTRIBUTION

Western Australian and Northern Territory.

Lycosa clara L. Koch 1877
(Fig. 3A–L)

Lycosa clara L. Koch, 1877, pp. 912–14, pl. 79, figs. 1, 1a, 1b, Bowen, Queensland; Rainbow, 1911, p. 266; Rack, 1961, p. 37; McKay, 1973, p. 379.

Allocosa clara: Roewer, 1954, p. 206; Roewer, 1961, p. 2.

MATERIAL EXAMINED

SYNTYPES: British Museum (N.H.), BM 1919. 9.18.219. M, C.L. 8·1 mm, Bowen, Qd. Hamburg Zool. Mus. Inst. No. 14559, Ar. 449, M, Bowen, Qd.

OTHER MATERIAL. Western Australia; Canning Stock Route at Well 46, 13.xii.1971, N.S.E. Exp. IV, 1 M 1 P 9 M, WAM 1 M QM S 46; Maitland R., 23.ii.1962, BYM, 1 M, WAM; Munda, 25.ii.1962, BYM, 1 M 2 P, WAM, 1 M 1 P, WAM; Ord River at Old Lissadell Station, 13.x.1971, RJM, 1 M, WAM.

Northern Territory; near Darwin, 1.vii.1917, G. F. Hill, 2 M 1 P, NM; Harriet Creek 25 km North Pine Creek, 12.ix.1964, A. M. Douglas, 3 M 1 M 9 P 4 P, WAM.

Queensland; Cooloola, 3–7.ii.1976, R. Raven, V. E. Davies, 1 M, QM W5648; Cuddapan turnoff on Birdsville Road, 9.xi.1976, RJM, 1 M, QM W6407; Musgrave Station 10 km east (north of Laura), 3.vi.1973, RJM, 2 M, QM S 47; Peak Downs, 30.xi.1973, RJM, 2 M 7 M, QM W3916; Thargomindah, 27.xii.1974, G. Ingram, 2 M, QM W4670.

DESCRIPTION (After L. Koch, 1877)

Female. Carapace light yellow-brown with a deeply serrated longitudinal pale yellow marginal band. Lateral declivity yellow-brown with three oval white ring-spots. A white or yellow longitudinal median band, narrow at the posterior declivity, expanded at the median groove, and extending anteriorly after a short constriction at the cephalic part; immediately behind the eyes the median band narrows but fully covers the interspace between the eyes. Around the PL posteriorly is an orange-yellow half-ring. A white diagonal line at the lateral declivity of the cephalic part. Abdomen yellow-brown with white dots

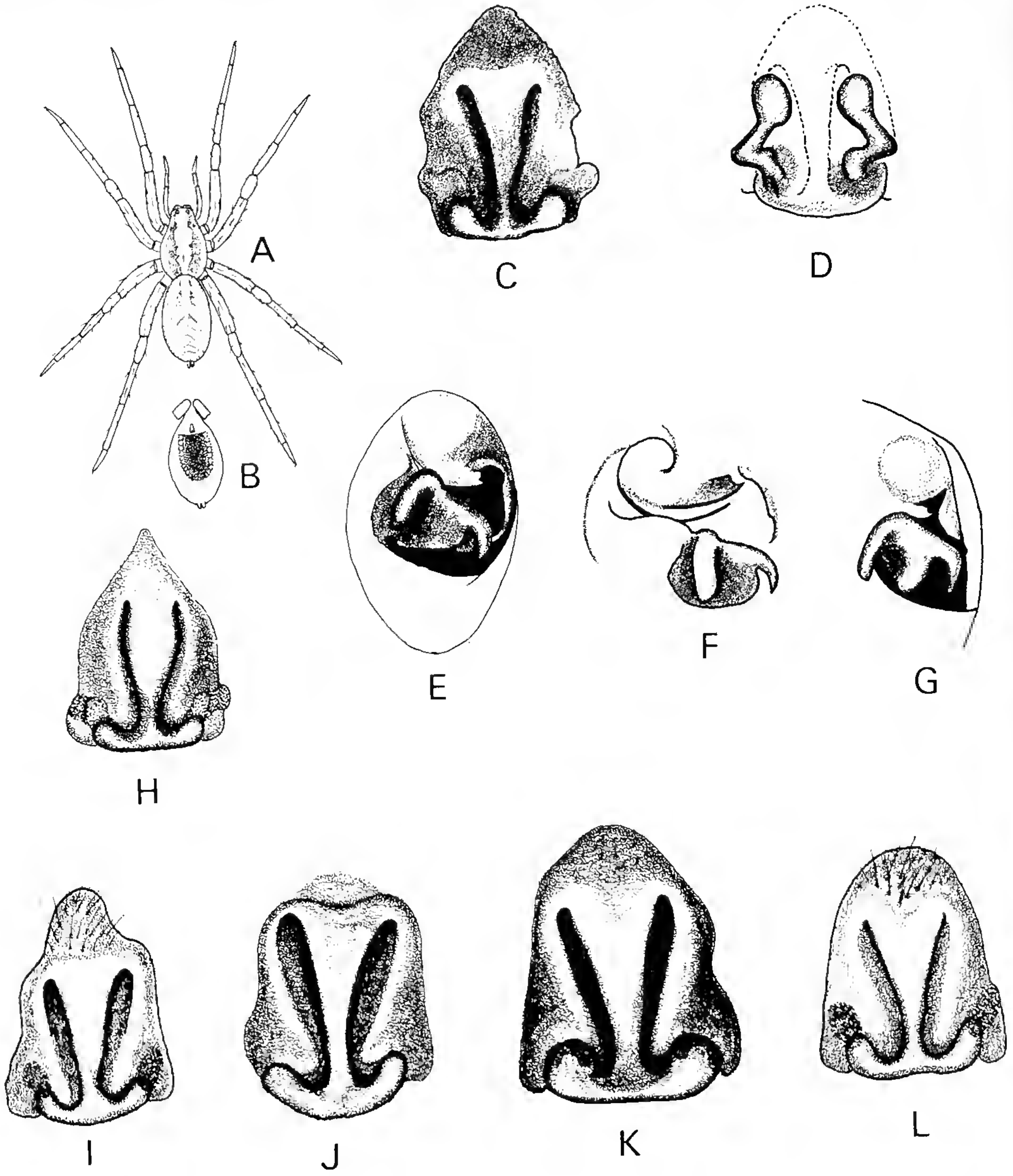

FIG. 3: *Lycosa clara*. A, mature female from Munda, W.A.; B, undersurface of abdomen; C, epigynum of female from Munda; D, internal genitalia of female from Maitland River; E - G, male palpal organs from Well 46, Canning Stock Route; H, epigynum of syntype from Hamburg Zool. Mus. Inst; I, epigynum of syntype from British Museum; J, K, L, epigyna of females from Peak Downs, near Darwin, and Ord River.

laterally; at the base is a moon-shaped yellow spot followed by a posteriorly notched and white tipped longitudinal yellow spot. More posteriorly is an arcuate white stripe with a series of transverse lines, black anteriorly, and white posteriorly. The sides and undersurface grey, with a black heart-shaped spot behind the epigaster ventrally.

Anterior row of eyes straight, narrower than the second row. AM considerably larger than AL and situated slightly further apart than from the almost adjoining AL. AM less than a radius from the PM. PM very large, less than a radius apart, and less than a diameter from the PL which are also large but considerably smaller than the PM. Legs with a scopula on the metatarsi and tarsi of both anterior pairs. A spine present on the anterior end of patellae 1 and 2, and both anteriorly and posteriorly on patellae III and IV. Two spines anteriorly on femur 1.

VARIATION: Specimens from the Northern Territory and the Ord River, Western Australia have two brown curved marks within the pale longitudinal stripe on the carapace behind the PL eyes. Specimens from Munda and Maitland River, W.A., have the carapace sandy-brown with a pale longitudinal stripe commencing between the PM eyes, filling the ocular quadrangle and constricting between the PL eyes to broaden into a somewhat quadrangular area constricting before the fovea where the lateral margin becomes scalloped and again narrows to the posterior margin; a rather vague pale lateral band is present; sides of carapace with vague radiating brown wedge-shaped markings that are darkest adjacent to the longitudinal stripe and fading laterally; paturon and fang brown; labium and maxillae mid-brown with paler margins; sternum brown with a paler marginal band; coxae light brown. Abdomen pale sandy-brown with an indistinct pattern of darker brown forming the outline of a pale longitudinal stripe on the dorsal midline followed by indistinct brown chevrons (Fig. 3A); undersurface pale sandy-brown with a dark brown to black shield-shaped spot containing paler spots on the lateral margin (Fig. 3B). Legs pale sandy-brown without markings.

Anterior row of eyes procurved, shorter than the second row; AM larger than AL. Ratio of eyes in micrometer units AM:AL:PM:PL = 16:9:35:28; distance AM–AM 5, AM–AL 4, PM–PM 15, AM–PM 4, AL–PM 6. Clypeus to AM 9. Width of first eye row 60; width of second eye row 80. Eye diameters and interspaces for a syntype and seven specimens are given in Table 6 as a percent of the total width of the first row of eyes. Chelicerae with three promarginal teeth, the outer one small and located near the base of the large median one; three retromarginal teeth of about equal size.

Epigynum elongate, the median guide broad anteriorly and tapering to the transverse guide which is narrow, horizontal and with expanded tips directed anteriorly (Fig. 3C, H, I–L).

TABLE 5: MEASUREMENTS OF LEG SEGMENTS OF *L. CLARA* IN MM

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1	5·2	3·1	4·3	4·3	2·6
2	5·1	3·0	4·2	4·4	2·5
3	5·0	2·8	3·9	4·7	2·9
4	6·0	3·1	5·4	6·4	3·3

Mature males from Well 46, Canning Stock Route, W.A., have the palpal organ identical to males from Peak Downs, Queensland. One mature male from Harriet Creek, N.T., has the terminal hook on the median apophysis less curved than the above males but is certainly conspecific. The palpal organ of a male from Well 46, Canning Stock Route is figured (Fig. 3E, F, G).

The epigyna of the syntypes from Bowen are illustrated in Fig. 3H, I, with the epigyna of mature females from Peak Downs, Darwin and Ord River (Fig. 3J, K, L).

TABLE 6: EYE DIAMETERS AND INTERSPACES OF *L. CLARA* CONVERTED TO PERCENT OF THE TOTAL WIDTH OF THE FIRST ROW OF EYES

Regd No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM	AL:PM
SYNTYPE	♀M	8·1	27	15	60	45	11	5	24	7	8
Munda	♀M	8·6	27	15	58	47	8	7	25	7	10
Munda	♀M	9·7	30	15	54	46	6	3	24	6	10
Maitland R.	♀M	9·5	29	14	56	45	6	3	23	6	9
Well 46	♀M	9·7	29	15	55	45	8	3	24	6	9
Well 46	♂M	7·7	31	15	61	48	4	4	24	6	7
Darwin	♀M	12·1	29	14	57	45	7	4	27	5	9
Peak Downs	♂M	8·2	30	16	56	41	6	4	24	6	7

SIZE RANGE: Mature females C.L. 8·1 to 12·1 mm. Mature males C.L. 6·7 to 8·2 mm.

DIAGNOSIS: A black shield-shaped spot on the ventral surface of the abdomen; epigynum with the median guide expanding anteriorly; male palpal organ with a broad median apophysis carrying a blunt curved dorso-basal hook and a sharp curved dorsolateral hook.

LIFE HISTORY

Unknown.

HABITAT

Banks of rivers and creeks in northern and inland Australia. Some specimens were collected from open woodlands near creeks at Peak Downs, and two were collected in open woodlands on sandy soil beneath logs near Musgrave Station, north Queensland. This species inhabits sand or sandy loams near permanent or temporary watercourses and swamps.

BURROW

Most specimens are found wandering at night and may be found below logs during the daytime. The burrow is unknown.

DISTRIBUTION

Queensland, Northern Territory and Western Australia.

DISCUSSION

The record of this species from Goolwa, South Australia by Hogg (1905, p. 590) is erroneous as this specimen is *Lycosa spenceri* (Hogg 1900). Specimens from Hermite Island, Montebello Islands, Western Australia, collected by P. D. Montegue, 11–23.viii.1912, (BM.1924.III.1.1018–27) and recorded as *L. clara* by Hogg (1914, p. 88) are *Lycosa meracula* Simon 1909.

Lycosa crispipes L. Koch, 1877
(Fig. 4A–M)

Lycosa crispipes L. Koch, 1877, pp. 923–25, pl. 79, figs. 8, 8a, pl. 80, figs. 1, 1a. Bowen and Rockhampton, Queensland; Karsch, 1878, p. 794, New South Wales; Hogg, 1896, p. 351, Palm Creek, Northern Territory; Rainbow, 1911, p. 266; Rack, 1961, p. 37.

Hygrolycosa crispipes: Roewer, 1954, p. 261; McKay, 1973, p. 380.

MATERIAL EXAMINED

SYNTYPES: Hamburg Zool. Mus. Inst. No. 14572, Ar. 450 ♀M, Bowen, Qd; British Museum (N.H.) BM 1919.9.18.222. ♀M. C.L. 5·0, Bowen, Qd.

OTHER MATERIAL: Western Australia; Argyle Downs homestead pool edge of Behn River, 9.x.1971, RJM, 1 ♀M, QM W 5058; Barradale at Yannarie River, 13.v.1972, RJM, JG, 1 ♀M 1J, QM W 5061; Behn River near Ord River, 24.x.1971, RJM, 1 ♀M 1 ♂P, QM W 5059; Monsmount at Ord River, 3.x.1971, RJM, 1 ♀M 2 ♂M 2 J, WAM 72–161–4; Murchison River at the Loop, 26.i.1969, RJM, JG, P. Snowball, 1 ♀M 10 J, WAM 69–318–28, 1 ♀M, WAM 69–441; Murchison River near Highway, 29.i.1969, RJM, JG, P. Snowball, 3 J, WAM 69–457–59; Ord River, 21.x.1971, RJM, 2 ♀M 2 ♂M 2 J, WAM 72–155–60; Port Hedland, 10.iv.1972, P. Sadlier, 1 ♀M, QM W 5062.

Northern Territory: Borroloola 14 km N.W., 3.xii.1974, W. Nash, 1 ♀M, QM W5105.

Queensland: Allingham Creek, Bluff Downs, N.W. of Charters Towers, 1.v.1974, M. Archer, A. Elliott, 1 ♀M, QM W 5052; Archer River at crossing, 23–27.v.1973, RJM, V. E. Davies, 4 ♀M 1 ♀P 1 ♂P, QM W 5049, 2 ♀M 1 ♂M, QM W 5063; Coen, 3.2 km north, 25.v.1973, RJM, 2 ♀M 3 ♂M 4 ♀P 2 ♂P 2 J, QM W 50478, Coen, 63 km south, 4.vi.1973, RJM, 1 ♀M 2 ♂M 2 J, QM W 5051; Laura River, 10.vi.1973, RJM, 1 ♀M 1 ♀P, QM W 5069; Morehead River, 18.v.1973, RJM, V. E. Davies, 3 ♀M 3 ♀P 2 ♂M 1 ♂P 9 J, QM W 5050; Musgrave Station, 9.vi.1973, RJM, V. E. Davies, 1 ♀M 5 ♀P 1 ♂P 2 J, QM W 5054; Peach Creek near Coen, 25.v.1973, RJM, 1 ♀M, QM W 5068; Rokeby Station, 30.v.1973, RJM, 1 ♀P, QM W 5067.

DESCRIPTION (After L. Koch, 1877)

Female: Carapace yellow-brown, darkening to black-brown between the eyes. From the posterior margin runs a light longitudinal median stripe covered with white hair at the declivity and with yellow hair above; the stripe continues as far as the PM; lateral margin white; indistinct radiating white stripes on the lateral slope of the thoracic part, and white spots on the lateral convexity of the cephalic part. A transverse white stripe on either side of the AL. Abdomen above and up to half of the lateral convexity olive-brown; a yellow-brown spot gradually broadening posteriorly and forming on either side a sharply projecting denticle runs from the base dorsally and narrows steeply to a truncate margin at its posterior end; on each side of the denticle is a white spot with a white transverse line behind. Posterior part of abdomen with a series of bow-shaped white transverse lines terminating in a white spot. Sides with white dots. Undersurface and lower sides pale yellow. Spinnerets pale yellow with a white spot at upper pair. Palpi yellow-brown, with a white spot at the end of the femur patella and tibia. Legs yellow-brown with white half rings on the dorsal aspect of the femora; white spots and present on the dorsal end of the femora, tibiae, and tarsi. The patellae of legs I and II with white spots on either side and on the end; the patellae of the posterior legs with two white spots dorsally.

Anterior row of eyes, because of the deep position of the AL, slightly curved; the eyes very close to each other and equidistant. AM considerably smaller than the PL. PM not quite a diameter apart, and about the same distance from the PL.

Legs with a single long hair on the tibiae and metatarsi. Two spines on the anterior end of femur I.

Male: Carapace light yellow-brown with white hair on the thoracic part and yellow-brown hair on the cephalic part. A median narrow brown-yellow longitudinal stripe commencing at the posterior margin and reaching the PL: at the posterior

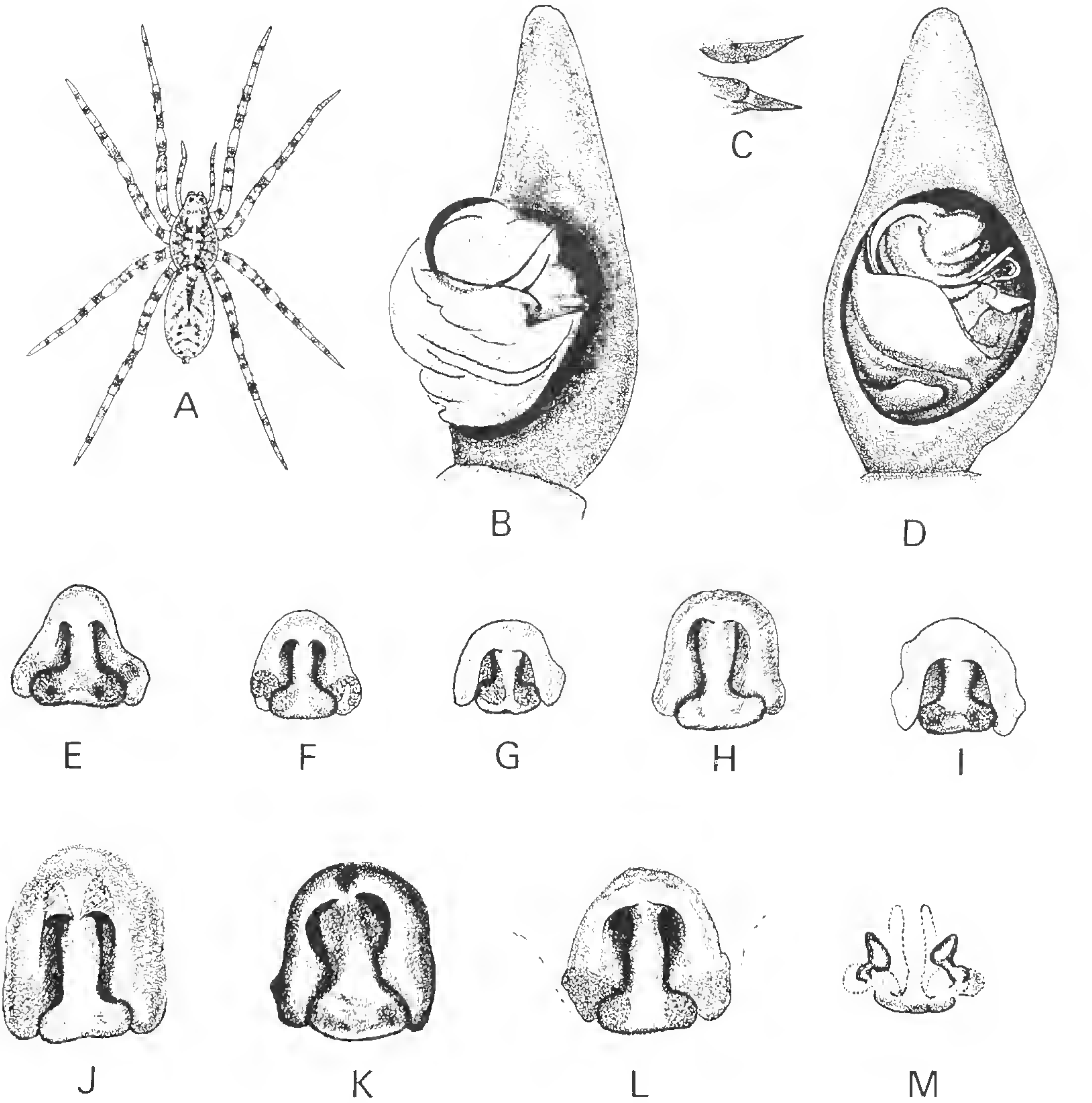

Fig. 4: *Lycosa crispipes*. A, mature female from Laura River, Qd; B, palpal organ of WAM 72–155 expanded; C, embolic guide and median apophysis of a male from Coen; D, palpal organ of WAM 72–155; E, epigynum of syntype from British Museum; F, epigynum of syntype from Hamburg; G, I, L, epigyna of females from Ord River; H, J, epigyna of females from Archer River; K, epigynum of female from Murchison River; M, internal genitalia of female from Behn River.

declivity the stripe is white, and more yellowish anteriorly. Abdomen black above, with a yellowish-brown longitudinal stripe which originates at the base but does not quite reach the middle; a white spot is present on each side of this stripe. At the end of the stripe is a series of transverse bars with a pair of brownish spots in the interspaces. Undersurface and sides yellow-white. Palpi yellowish-brown with the cymbium darker. Legs yellowish-brown ringed with black, the interstices of the rings white.

Anterior row of eyes straight, as wide as the second; AM considerably larger than AL, their distance apart not quite equal to their radius, and closer to the AL than each other; AM more than their radius from the PM. PM about a radius apart and their diameter from the PL.

Legs without scopula; a spine on the anterior end of femur 1; 1 + 1 spines on the tibiae of both posterior pairs; spines on the patellae of all legs.

VARIATION: *Lycosa crispipes* is very variable in coloration and some examples are described.

Coen River: Carapace light brown with an indistinct pale longitudinal stripe and indistinct brown wedge-shaped stripes. Dorsal stripe on abdomen indistinct, some darker diffuse blotches and pale spots on the dorsal surface; sides of abdomen with dark blotches, some of which contain light brown spots. Ventral surface of abdomen with a broad gently tapering longitudinal median brown bar terminating abruptly before the spinnerets; remainder of venter with scattered brown blotches vaguely arranged in a longitudinal line on each side of the median bar. Legs pale brown; femora with two ring-like dark blotches, the distal one widest dorsally, extending obliquely towards the base and then angled sharply forwards and downwards to continue on the ventral surface, the proximal dark band is narrow to absent on the dorsal surface, but expands on the sides, particularly on the retrolateral surface to form a somewhat longitudinal dark streak before continuing to the ventral surface where it completes or almost completes a ring, the base may have an indistinct darker ring present; patellae with the proximal half darker; tibiae with two dark rings, one almost at the middle, the other at the distal end; metatarsi with two faint dark rings; palpal patella with a diffuse dark ring.

Laura River: Carapace with a distinct longitudinal median pale stripe that commences behind the PL eyes and constricts abruptly to form a lobe on each side before continuing as a narrow band to the foveal region where it again expands to form a trilobate pattern and then tapers to the posterior margin (Fig. 4A). Abdomen with a dark lanceolate median longitudinal stripe anteriorly; some vague dark chevron-like spots posteriorly. Ventral surface of abdomen with a dark longitudinal bar tapering towards the spinnerets; on each side of this bar is a narrow dark brown line from the epigastric furrow to the base of the spinnerets. Legs conspicuously banded (Fig. 4A). Sternum with two brown lines converging posteriorly.

Musgrave Station: Abdomen with the anterior slope dark brown; a horseshoe-shaped pale area with the posterior tips pointed and almost surrounding a somewhat square dark brown spot anteriorly; a pair of brown spots on each side at the middle of the abdomen followed by a pair of brown blotches; sides spotted with brown flecks.

Ord River: A serrated pale marginal band on the carapace commencing before the coxae of the third legs and broadening posteriorly but not meeting at the posterior midline due to an extension of the dark brown carapace. Ventral surface of abdomen a uniform pale sandy-yellow.

Behn River: A longitudinal pale median stripe on the carapace. Legs conspicuously banded.

Murchison River: Carapace with a serrated pale marginal band that continues around the posterior margin. Legs conspicuously banded on the dorsal surface and upper sides only.

Chelicerae with three promarginal teeth, the middle one largest and sometimes joined to the base of the outer tooth; three retromarginal teeth of about equal size. Labium slightly longer than broad.

TABLE 7: Measurements of Leg Segments of QM W5047, ♀M, C.L. 7·5 mm, in mm

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1	5·9	2·7	4·6	4·2	2·7
2	5·7	2·6	4·3	4·2	2·7
3	5·3	2·3	4·1	4·6	2·4
4	6·7	2·5	5·3	7·0	2·9

Female epigynum with a short broad median guide and a broad transverse guide. Variation in the shape of the epigyna is shown in Fig. 4E-L.

The male palpal organ with a triangular plough-like median apophysis directed laterally with a dorsal pointed spur at the base; embolic guide blade-like and gently tapering to a fine point (Fig. 4B, C, D).

Anterior row of eyes with the upper tangent procurved, narrower than the second row, AM larger than AL. Ratio of eyes in micrometer units (QM W5047, M, C.L. 7·5 mm) AM:AL:PM:PL = 12:8:23:17; distance AM–AM 4, AM–AL 2, AM–PM 5, AL–PM 6, PM–PM 13. Clypeus to AM 12. Width of first eye row 47; width of second eye row 57. Eye diameters and interspaces for a syntype and eight specimens are given in Table 8 as a percent of the total width of the first row of eyes.

SIZE RANGE: Mature females C.L. 4·5 to 9·2 mm. Mature males C.L. 6·1 to 7·3 mm.

DIAGNOSIS: Legs conspicuously banded; epigynum with a short broad median and transverse guide; male palpal organ with a triangular pointed median apophysis bearing an upright spur-like point at the base, and a thin tapered embolic guide. Habitat is dry to moist river sands.

LIFE HISTORY

Mature females may be collected throughout the year. Mature males have been collected during October in Western Australia and May in Northern Queensland.

Mature females with egg cocoons and carrying young have been taken in May in Queensland, and females carrying young were collected during October in Western Australia. A female from Allingham Creek collected 1 May, 1974, C.L. 6·2 mm had an egg cocoon measuring 6·7 × 7·5 mm containing 221 eggs of 1·0 mm diameter.

HABITAT

This species is most abundant on dry sands on the bed of rivers and creeks. Coarse sand to fine gravel may be occupied, and on occasions damp or wet sand, clay-sands, gravel or small pebble shingle may support small populations. The banks of creeks and lagoons with heavy clay soil are infrequently inhabited by *L. crispipes*. Where large areas of river washed sand is deposited during the dry season the adults may be found well away from pools of water, but juveniles rarely move far from moist sand. The species is difficult to detect on speckled sand during the daytime, and if disturbed, run rapidly.

BURROW

A simple open vertical burrow may be excavated in most sand.

DISTRIBUTION

Queensland, Northern Territory and northern Western Australia.

Lycosa gibsoni sp. nov.

(Fig. 5A-F)

MATERIAL EXAMINED

HOLOTYPE: Western Australian Museum WAM 70–1 ♂M, C.L. 7·7 mm, Millstream Station, Fortesque River, Western Australia, collected by R. J. McKay and R. Dear, 24 September, 1969. In spirit.

PARATYPES: Western Australia; Bamboo Creek, 22.v.1971, A. M. Douglas, 3 ♀P 1 J, WAM 71–1712–15, WAM 71–1846; Dales Gorge, 29.ix.1969, RJM, R. Dear, 1 ♀P, WAM 71-532; Hammersley Gorge, 28.ix.1969, RJM, R. Dear, A. Burbidge, 1 J, WAM 69–1050, 1 ♀P, WAM 70–239; Nullagine, 23.v.1971, A. M. Douglas, 1 ♀P, WAM 71–1855; Pyramid Pool, 5.vi.1970, collector unknown, 1 ♀P, WAM 71–1710; Walgun, east of Ethel Creek, 23.v.1971, A. M. Douglas, 1 J, WAM 71–1711.

DESCRIPTION (Based on holotype)

Carapace brown to chocolate brown with some flecks of lighter brown on the margin; a longitudinal median stripe of bright buff hair extends from within the ocular quadrangle, narrows behind the PL eyes and then expands

TABLE 8: EYE DIAMETERS AND INTERSPACES OF *L. CRISPIPES* CONVERTED TO PERCENT OF THE TOTAL WIDTH OF THE FIRST ROW OF EYES

Regd. No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM	AL:PM
BM 1919.9.18.222	♀M	5·0	23	16	43	36	9	6	26	13	14
QM W5047	♀M	7·5	25	17	49	36	9	4	28	11	13
QM W5048	♀M	6·0	25	15	47	40	6	5	30	15	15
QM W5048	♀M	6·0	25	15	47	40	8	5	30	13	15
QM W5048	♂M	5·7	28	17	50	39	6	6	30	14	17
QM W5054	♀M	5·9	23	15	50	40	7	5	30	13	15
QM W5060	♀M	6·2	25	17	50	42	7	5	26	11	12
QM W5062	♀M	7·4	24	15	52	43	9	5	27	8	10
QM W5105	♀M	6·6	24	19	53	43	8	4	26	10	12

towards the centre of the carapace to continue to the posterior margin as a somewhat serrated band; a faint paler marginal band is present but not obvious, near the posterior extremity of this band is a dark brown to blackish spot; some very faint dark brown stripes radiate out from the centre of the carapace; on the posterior slope of the carapace near the posterior margin on each side of the longitudinal stripe is a dark brown to black area; face dark brown with a dark stripe between the PM eyes. Paturon dark brown with the anterior surface bright orange basally; labium, maxillae, sternum and ventral surface of anterior coxae jet black; third coxae brown below; fourth coxae orange below. Abdomen orange-brown above with a vague longitudinal lanceolate stripe anteriorly, on each side of which is a buff spot; some rather diffuse dark chevrons posteriorly;

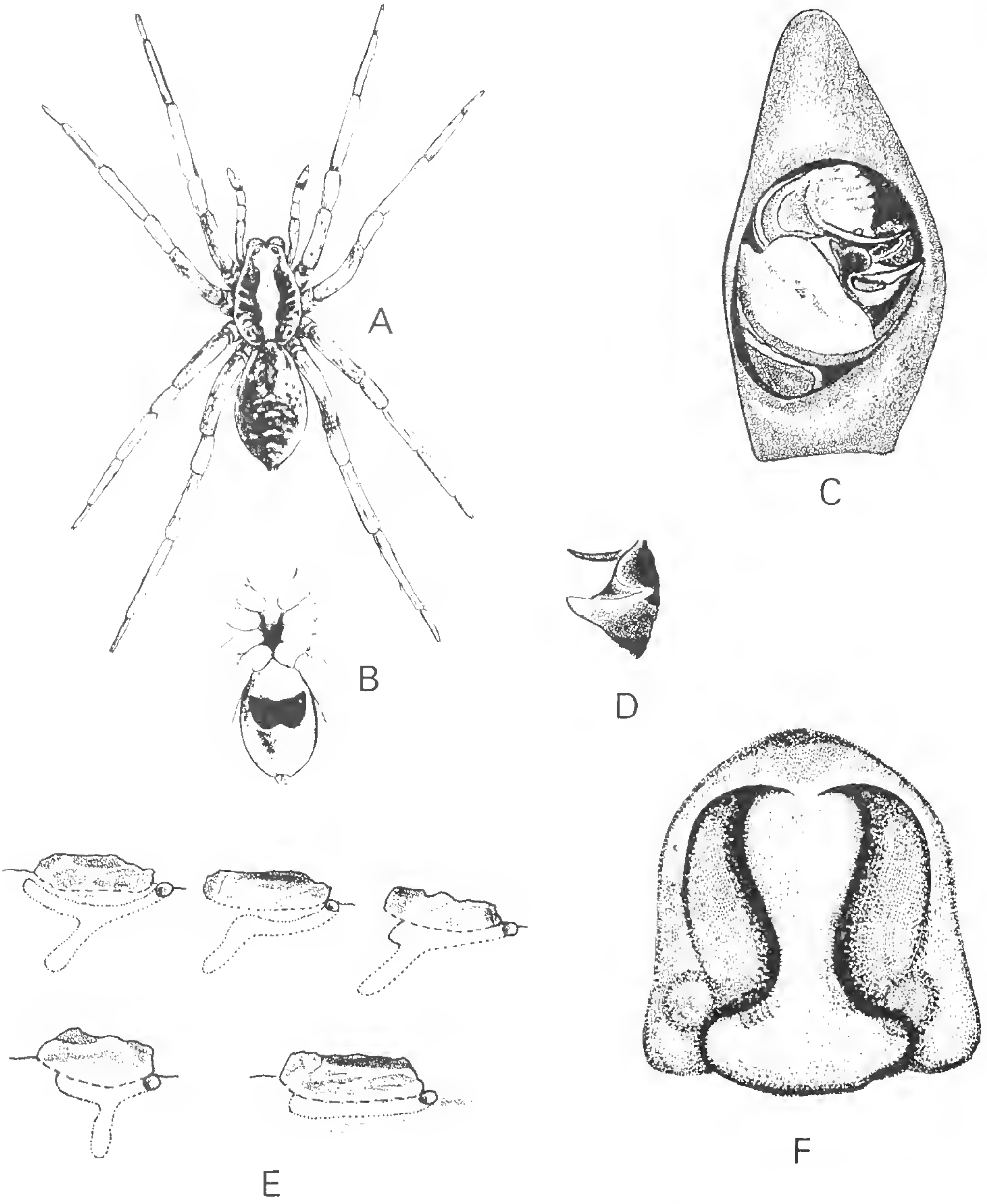

FIG. 5: *Lycosa gibsoni*. A, holotype; B, undersurface of abdomen; C, left palpal organ of holotype; D, embolic guide and median apophysis of right palpal organ of holotype; E, burrows of *L. gibsoni;* F, epigynum of female.

sides brown with flecks of bright orange; ventral surface bright orange with a black lobate transverse shield-shaped spot commencing at the epigastric furrow and reaching almost half-way to the spinnerets. Legs dark brown to black below, femora dark brown tinged with orange above; patellae, tibiae, metatarsi and tarsi ash-grey above.

Anterior row of eyes procurved, shorter than the second row; AM larger than AL. Ratio of eyes in micrometer units AM:AL:PM:PL = 10:8:31:22; distance AM–AM 5, AM–AL 5, PM–PM 13, AM–PM 5, AL–PM 6. Clypeus to AM 5. Width of first eye row 50; width of second eye row 72.

Chelicerae with three promarginal teeth on the right side, the outer two joined at the base, two promarginal teeth on the left side, the outer one largest; three retromarginal teeth on each side, the middle one largest.

Male palpal organ with a somewhat triangular median apophysis, the upper crest recurved to the rear of the laterally directed blade; embolic guide slender and pointed (Fig. 5C, D).

TABLE 9: MEASUREMENTS OF LEG SEGMENTS OF *L. GIBSONI* IN MM

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1	6·1	3·2	5·2	5·0	2·5
2	5·6	3·1	4·5	4·5	2·3
3	5·2	2·5	3·7	4·3	2·0
4	6·7	2·9	5·2	6·6	2·6

VARIATION: Juveniles below C.L. 2·8 mm have the ventral surface of the abdomen orange, at C.L. 3·1 to 3·4 mm a thin black transverse bar appears, and at C.L. 4·5 mm this bar is widening until at C.L. 5·5 mm the black field is fully developed in females. The longitudinal stripe on the carapace may be cream to bright buff in colour, straight, with parallel sides or scalloped around the fovea. The margin of the carapace may have scattered dark brown spots or blotches and some radiating dark brown and cream lines may cross the lateral slopes. The fourth tibiae is black-brown below, sometimes with an ash-grey spot in the middle.

Chelicerae with three promarginal teeth in females, the middle one largest.

Epigynum horseshoe-shaped with the median guide widest anteriorly and a robust transverse guide (Fig. 5F).

The eye diameters and interspaces of the holotype and two paratypes are given as a percent of the total width of the first row of eyes in Table 10.

SIZE RANGE: Mature females C.L. 8·3 to over 12·3 mm. Mature male C.L. 7·7 mm.

DIAGNOSIS: Ventral surface of abdomen bright orange with a jet black shield-shaped spot behind the epigastric furrow. Male palpal organ with the dorsal crest recurved to the rear of the laterally directed blade; embolic guide slender and pointed.

LIFE HISTORY

Mature males and females were not collected. A penultimate female and penultimate male collected during September were maintained in the laboratory until mature.

HABITAT

At Millstream this species was found below trees with burrows adjacent to tree roots in softer soils or below stones. Hammersley Gorge specimens were captured from open rock and spinifex. The spiders are very agile among rocks and crouch next to rocks or move head first into crevasses between broken angular rocks. They are abundant in areas of shattered ironstone rock. At Bamboo Creek the habitat was shattered rock piles.

BURROW

A rather shallow burrow is constructed adjacent to tree roots in soft soils, but in stony areas a shallow burrow is constructed below large slabs of stones or small pieces of stone surrounded by very compact soil (Fig. 5E). On rock piles this species may shelter well within the stone fragments and be exceedingly difficult to capture.

TABLE 10: EYE DIAMETERS AND INTERSPACES OF *L. GIBSONI* CONVERTED TO PERCENT OF THE TOTAL WIDTH OF THE FIRST ROW OF EYES

Regd. No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM	AL:PM
HOLOTYPE	♂M	7·2	20	16	62	44	10	10	26	10	12
WAM 70–239	♀M	8·3	22	15	61	49	5	7	20	7	9
WAM 71–1846	♀P	12·2	23	16	59	51	9	7	29	13	18

DERIVATION

Named after Alfred Gibson the member of Ernest Giles' expedition who disappeared in 1874 in the desert that now bears his name.

Lycosa koyuga sp. nov.
(Fig. 6A–H)

MATERIAL EXAMINED

HOLOTYPE: Western Australian Museum WAM 71–1968, ♀ M, C.L. 11·2 mm, Guilderton, Moore River, W.A., collected by R. J. McKay, 12.xii.1971. In spirit.

PARATYPES: Fitzgerald River, W.A., 16.vii.1970, AB, 3 ♀ M WAM 70–183–5, 4 ♀ M, WAM 71–48–51; Guilderton, Moore River, W.A., 12.xii.1971, RJM, 8 ♀ M, 4 ♀ P, 1 ♂ M WAM 71–1957–67, WAM 71–1969–75; Moore River National Park, 5.ii.1971, N. McKenzie, 2 ♀ M, WAM 71–743–4; Minganooka, 14 km SSW Coorow, W.A., 22.xi.1970, AB, 1 ♀ M, WAM 71–189; Pingrup, 27 km east at Greenshields Soak, W.A., 30.iii.1971, J. Ingram, T. Evans, 3 ♀ M, WAM 71–1748–50; Queen Victoria Springs, W.A., 2.x.1956, A. R. Main, 1 ♀ M, WAM 69–809; 29 km W of Southern Cross, W.A., 26.i.1968, L. Smith, N. Allen, 1 ♀ M WAM 69–806; Yanchep Beach, W.A., 2.i.1970, P. G. and G. W. Kendrick, 1 ♀ M, WAM 71–1751.

DESCRIPTION (Based on the holotype)

Carapace mid-brown with a light grey-fawn longitudinal stripe commencing behind the PM eyes, filling the ocular quadrangle and broadening behind the PL eyes to constrict before the fovea to form a diamond shape surrounding the fovea and narrowing to the posterior margin; within the broad longitudinal stripe before the foveal constriction are two dark marks laterally; a greyish marginal band merges into a bright buff premarginal band that has the upper edge sharply defined from the brown sides of the carapace and sharply serrated or scalloped; radiating fine dark brown marks are visible on the lateral slopes after preservation and some similar pale yellow marks are present in life; paturon black with the base buff or pale fawn; lateral condyles small and dark brown; labium, maxillae, sternum and undersurface of coxae jet black. Abdomen pale brown above with a conspicuous dark brown anterior longitudinal stripe with oblique brown stripes extending out from the middle and the posterior corners; four pale yellow chevrons outlined by brown spots and a fine brown dusting extend transversely and are arranged posteriorly, sides of abdomen finely spotted and speckled with brown; undersurface buff with a broad jet black field having a rounded posterior margin that commences at the epigastric furrow and extends posteriorly to before the spinnerets. Legs and palpi yellowish, the tips of the femora and patellae black-brown, tips of the tibiae dark brown, remainder of leg black-brown below; palpal femur with 2 brown rings.

Anterior row of eyes procurved, AM larger than AL. Ratio of eyes AM:AL:PM:PL = 20:12:46:42; distance of AM–AM 8, AM–AL 6, AM–PM 9, AL–PM 11, PM–PM 24. Clypeus to AM 15. Length of first eye row 80, length of second eye row 110.

Chelicerae with three promarginal teeth, the middle one largest; three retromarginal teeth of about equal size. Labium longer than wide.

Epigynum with a flattened and ill-defined median guide; the transverse guide raised and horseshoe-shaped with recurved ends (Fig. 6D).

TABLE 11: MEASUREMENTS OF LEG SEGMENTS OF *L. KOYUGA* IN MM

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1	8·3	4·0	6·2	6·2	3·3
2	8·0	3·7	6·1	6·3	3·4
3	7·8	3·5	5·5	6·7	3·4
4	9·7	3·7	7·4	9·6	4·2
Palp	3·8	1·9	2·1	—	3·2

VARIATION: The carapace may have a vague Union Jack-like pattern of dark brown elongate radiating wedges preceded by narrow white or cream stripes on each side of the longitudinal median stripe; the black field on the venter of the abdomen may almost touch the base of the spinnerets in some adults and fall far short of the spinnerets in others.

The eye diameters and interspaces of the holotype and nine paratypes are given as a percent of the total width of the first row of eyes in Table 12. The first row of eyes is always shorter than the second row. In one mature female WAM 71–1970 the left side AM eye is larger than the right AM in the ratio of 20:18 and the right PM eye is larger than the left PM in the ratio 43:46, in all other specimens the diameters of the AM and PM eyes are normal.

Variation in the shape of the epigynum may be quite marked and two paratype females are illustrated (Fig. 6C, G), the internal genitalia of one paratype female is illustrated (Fig. 6H). The male palpal organ is shown in Fig. 6E, F. The median apophysis is a flat rounded plate with a small projecting spine on the anterior inner edge and the lower corner is doubled over somewhat like the cover of a book; the membranous

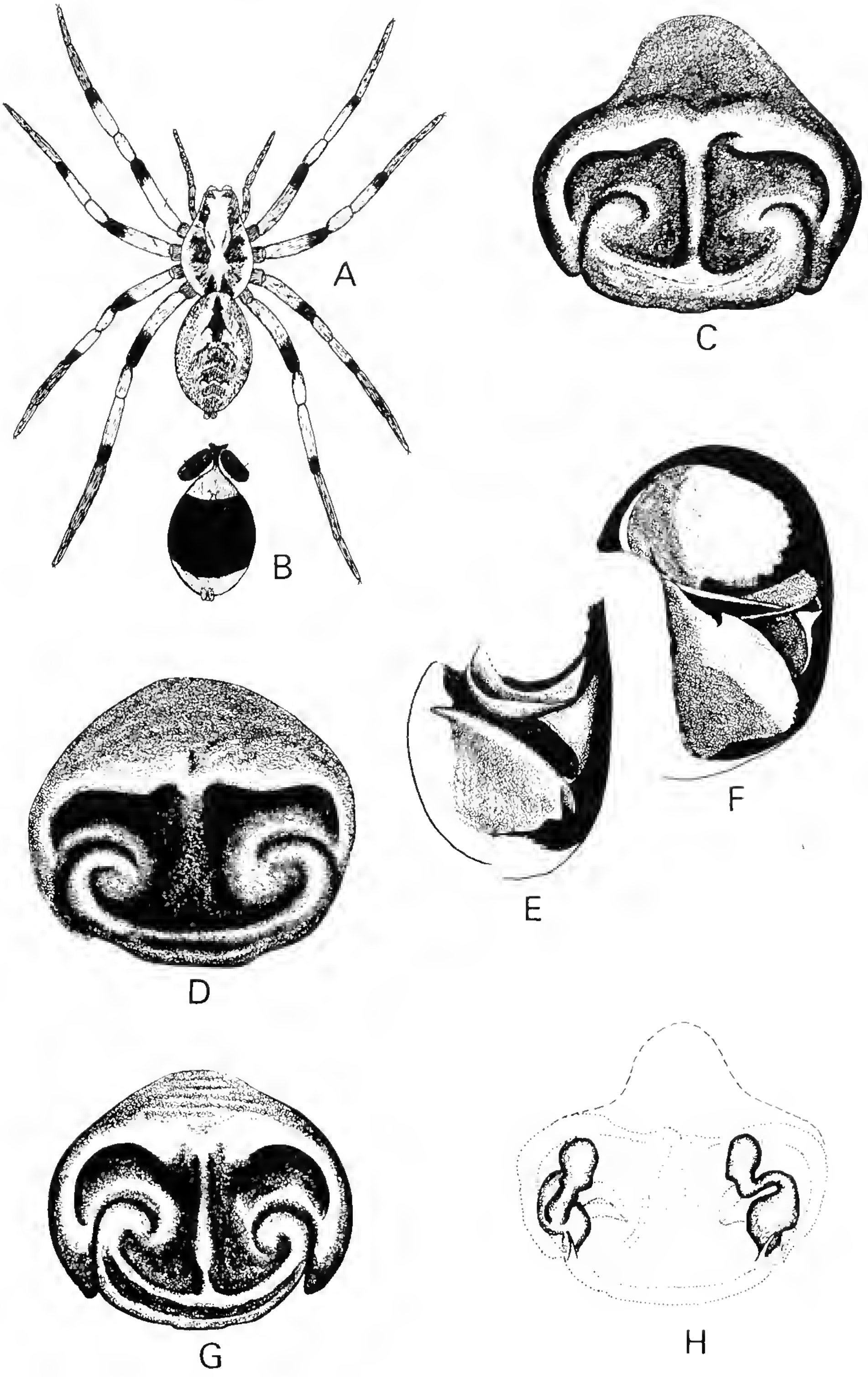

FIG. 6: *Lycosa koyuga*. A, holotype; B, undersurface of abdomen; C, epigynum of WAM 69–806; D, epigynum of holotype; E-F, male palpal organ; G, epigynum of WAM 71–48; H, internal genitalia of WAM 71–743.

secondary conductor is pointed and curled inwards, and the embolic guide, lying above the embolus, is a deep scoop-shaped structure with a flattened and slightly recurved tip. The median apophysis appears to be quite distinctive in shape and facilitates identification of the male of this species.

SIZE RANGE: Mature females C.L. 8·5 to 11·2 mm. Mature male C.L. 9·3 mm.

DIAGNOSIS: *Lycosa koÿuga* has a characteristic epigynum and coloration. The jet black area on the undersurface of the abdomen and the dark brown to black tips on the femora and tibiae provide easy identification in the field.

LIFE HISTORY

Largely unknown; mature females are present during the summer months and mature males are found on coastal sand dunes during December.

HABITAT

All specimens were taken on sandplain areas inland and on or near coastal sand dunes. Yellow sandy soils with spinifex, Mallee *Eucalyptus pyriformis*, *Hakea*, *Casuarina*, and various *Acacia* species in the inland areas, and on coastal sandplain the habitat is largely *Eucalyptus tetragona*, *Banksia* or heathlands; the species is frequently abundant when these areas have been recently burnt.

BURROW

Unknown. All specimens were found wandering on open sandplain or sheltering below coastal dune bushes at night.

DERIVATION

From the aboriginal "koyuga" meaning plain surrounded by forest.

Lycosa maini sp. nov.

(Fig. 7A-E)

MATERIAL EXAMINED

HOLOTYPE: Western Australian Museum WAM 69–115, ♀M, C.L. 7·7 mm, 88 km north of Murchison River, W.A. on red soil with Mulga *Acacia* sp., collected by R. J. McKay, 30 January 1969. In spirit.

PARATYPES: Billabong Roadhouse near Shark Bay turnoff, 3 km south, 12.v.1972, RJM, 1 ♀J, QM W 4668; Menzies, 6 km north, 1.ix.1954, BYM, 1 J, WAM 68–821; Mt. Magnet area, 7–8.xii.1968, RJM, JG, J. Ayres, 1 ♀P, WAM 69–1031, 1 ♀P, WAM 69–1036; Murchison River, 19 km north, 20.ii.1962, A. R. Main, 1 J, WAM 68–820; Norseman, 76 km north, 26.xii.1968, W. H. Butler, WAM 69–105–6; Paynes Find, 61 km west, 8.xii.1968, RJM, JG, P. Snowball, 1 J, WAM 68–819; Tarin Rock Reserve, 22.v.1971, AB, 1 J, WAM 71–1859; Wubin, 32 km northeast, 14.vii.1968, RJM, JG, J. Ayres, 1 ♀P 1 ♀P, WAM 68–817–8.

DESCRIPTION (Based on the holotype)

Carapace uniform black with a green-brown to bronze-green sheen; paturon and fangs black; lateral condyle dark brown; labium and maxillae black; sternum and coxae black with a dull bronze-green sheen. Abdomen black with a bronze-green sheen above, black-brown below; on the dorsal surface is an anterior wide fawn arcuate transverse bar with ill-defined margin; a pair of fawn spots towards the centre of the abdomen closely followed by a fawn chevron and about three paler fawn chevrons more posteriorly. Legs black-brown.

Anterior row of eyes with the upper tangent procurved, shorter than second row, AM larger than AL. Ratio of eyes AM:AL:PM:PL = 19:15:44:31; distance AM–AM 9, AM–AL 5,

TABLE 12: EYE DIAMETERS AND INTERSPACES OF *LYCOSA KOYUGA* CONVERTED TO PERCENT OF THE TOTAL WIDTH OF THE FIRST ROW OF EYES

Regd. No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM	AL:PM
HOLOTYPE	♀M	11·2	25	15	58	53	10	8	30	11	14
WAM 71–1957	♀M	10·0	24	15	58	51	11	7	27	11	12
WAM 71–1964	♀M	10·5	24	15	57	50	11	7	30	15	16
WAM 71–1965	♀M	10·4	24	15	55	48	11	7	29	11	15
WAM 71–1966	♂M	9·3	24	16	60	49	11	6	32	13	14
WAM 71–1970	♀M	10·2	24	16	58	54	8	5	35	13	12
WAM 71–1971	♀M	10·5	24	16	58	55	9	7	30	11	14
WAM 71–1972	♀M	10·2	25	16	60	48	9	7	29	11	13
WAM 71–1973	♀M	10·6	24	16	59	50	11	8	28	11	13
WAM 71–1974	♀M	10·3	25	15	60	51	10	6	27	11	15

AM–PM 8, AL–PM 12, PM–PM 14. Clypeus to AM 12. Length of first eye row 88, length of second eye row 98.

Chelicerae with three promarginal teeth, the middle one largest; three retromarginal teeth of equal size. Labium slightly longer than broad.

TABLE 13: MEASUREMENTS OF LEG SEGMENTS OF *L. MAINI* IN MM

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1	5·4	2·7	4·1	4·1	2·1
2	5·0	2·2	3·7	3·7	2·0
3	4·3	2·2	2·9	3·9	1·9
4	5·8	2·6	5·1	6·9	2·5
Palp	2·7	1·5	1·9	—	2·4

Epigynum with a short reduced median guide and a broad curved transverse guide (Fig. 7C).

VARIATION: Juveniles are similar to adults in coloration but may have the fawn to yellow chevrons on the abdomen much brighter and more distinct. Adults vary slightly in colour pattern, some specimens may have a yellow or orange-bronze longitudinal median stripe on the carapace and a dull orange to yellow indistinct lateral band; black lines or broad wedges may radiate out from the centre of the carapace after preservation, but are not obvious in life; some specimens have a collar-like ring of black hairs extending from the anterior ventral corners of the carapace around behind the PL eyes. The abdomen may have a distinct or quite diffuse pale fawn to yellow-gold bar across the anterior part of the dorsal surface followed by a pair of yellow to orange spots about one third the length of the abdomen and more posteriorly 5 to 6 yellow-orange chevrons decreasing in size; occasional specimens have a faint short longitudinal stripe on the anterior dorsal surface. Legs may be uniform bronze-green to blackish with or without black rings on the extremities of the femora, occasionally on the patella and on the remaining leg segments. Penultimate males are similar to females in coloration.

The male palpal organ and the internal genitalia of the female is at present unknown; the holotype female was not dissected.

Variation in the eye diameters and interspaces is given in Table 14 as a percent of the total width of the first eye row.

SIZE RANGE: Mature females may not exceed C.L. 8·0 mm.

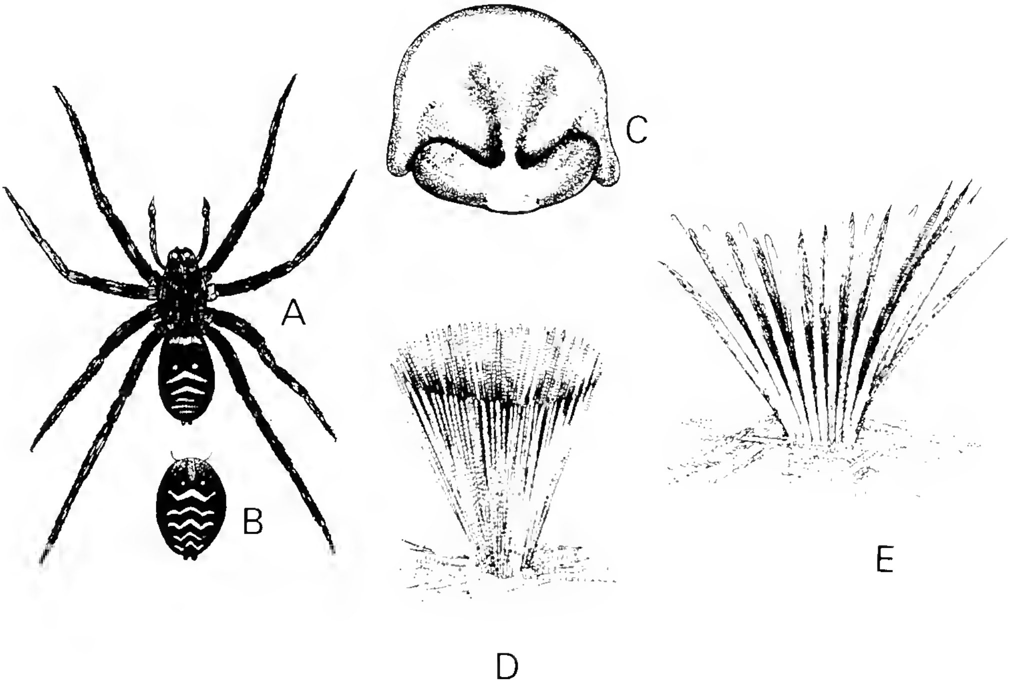

FIG. 7: *Lycosa maini*. A, penultimate male from N.E. of Wubin; B, abdomen of WAM 69–1036; C, epigynum of holotype; D, E, palisade burrows.

DIAGNOSIS: A small species inhabiting burrows with a high palisade of narrow leaves. Dark brown to jet black with a bronze-green sheen and yellow, orange or gold chevrons on the abdomen. Epigynum with a very reduced median guide.

LIFE HISTORY

Females probably mature in the summer months. Mature males have not been collected.

HABITAT

The holotype was collected in red clay-loam soil below Mulga trees. At Wubin red sandy-loam soils with a shallow hardpan layer below Mulga trees had some occupied and many vacant burrows. At Mt Magnet *L. maini* was common in red soils below Mulga, and again at Paynes Find and northeast of Wubin, but half-way between Wubin and Paynes Find a large area of similar habitat was searched without success, although in Mallee or Jam thickets with loose yellow-buff fine sandy soils this species was common.

BURROW

The burrow of *Lycosa maini* is very distinctive (Fig. 7D, E). A large number of elongate narrow Mulga leaves or phyllodes, the 'linear litter' of Main (1957), are webbed to the top of the burrow entrance with the base of the leaf within the burrow, and the remainder almost vertical to form a high palisade somewhat resembling a shuttlecock in shape. The palisade is securely webbed into a strong structure that projects high above the thick mat of thin leaves that builds up under Mulga *Acacia aneura* or dry adapted Acacias in the region of Western Australia receiving between 100 and 300 mm annual rainfall. On occasions the broader leaves of Jam trees may be used to form the palisade which is frequently lower than the linear litter structures. The opening of the burrow at the base of the palisade varies from 8 to 20 mm; normally 12 mm; the burrow then enlarges to form a chamber over twice the diameter of the entrance, measuring between 20 and 40 mm, before constricting to the diameter of the entrance and continuing vertically downwards to a depth of 15 to 23 cm.

All burrows were constructed in heavy leaf litter below shrubs and trees and appeared to favour the side of the tree where the afternoon shade fell. One wall of the palisade is frequently more vertical than the opposite side and adjacent burrows may have the vertical side facing the same direction, although insufficient burrows were examined to substantiate the few isolated observations made at Wubin and Mt. Magnet.

Two specimens, a penultimate male and a penultimate female from Wubin, were maintained in the laboratory and supplied with well compacted red soils and scattered piles of Mulga leaves. During the night both specimens built a typical high palisade around the burrow entrance. The male appeared to have a more vertical palisade than the female who built one wall almost vertical and the opposite half of the palisade leaning out a little more to form an angled platform area where she normally remained in wait for prey. When the leaves of the palisade were gently disturbed by introduced mealworms, the female would vacate the palisade and capture the prey, consuming it outside. In the laboratory both specimens would leave the palisade to hunt nearby, but when disturbed, would retreat within the palisade very rapidly, and would not re-emerge for hours. Both palisades were destroyed 2 months after their construction in the laboratory in an attempt to witness their reconstruction; the palisades were rebuilt but were not as symmetrical nor as elaborate as those in the field and first constructed in the laboratory two days after the spiders were collected. Both laboratory specimens died three months after capture, before attaining maturity.

DISCUSSION

This species is the 'shuttlecock spider' of Main (1976, pp. 142–3, fig. 37G).

TABLE 14: EYE DIAMETERS AND INTERSPACES OF *LYCOSA MAINI* CONVERTED TO PERCENT OF THE TOTAL WIDTH OF THE FIRST ROW OF EYES

Regd No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM	AL:PM
HOLOTYPE	♀M	7·7	22	17	50	35	10	6	16	9	14
WAM 69–1036	♀P	6·5	20	12	47	39	10	10	25	10	14
WAM 69–1031	♀P	6·4	24	16	48	41	8	7	24	11	11
WAM 68–817	♀P	7·3	23	15	55	37	10	9	16	8	16
WAM 68–818	♂P	6·0	23	19	55	39	9	6	17	13	16

Derivation

Named after Dr Barbara York Main in recognition of her studies on Australian spiders and her large collection of lycosid spiders donated to the Western Australian Museum to form the basis of the present revision of the Australian Wolf Spiders.

Lycosa marcentior Simon, 1909
(Fig. 8A–D)

Lycosa marcentior Simon, 1909, p. 185, fig. 3, Dongarra (= Dongara) and Boyanup, Western Australia; Rack, 1961, p. 38; McKay, 1973, p. 379.
Lycosa mercentior (misspelt): Rainbow, 1911, p. 270.
Hogna marcentior: Roewer, 1954, p. 253.

Material Examined

Syntype: Hamburg Zool. Mus. Inst. No. 466, Juvenile, 'Dongarra, Hamb. S.W. Austral. Exp. 1905, 84, Dunenbusch, 17.vii.1905'.

Other Material

Desperate Bay, south of Dongara, W.A., 27.ii.1971, RJM, B. Ryle, 4 ♀M, WAM 71–1262–65, 1 ♀M 1 ♀J, QM S50; Dongara, 5.vii.1971, RJM, 1 J, WAM 71–1998.

Description (Based on WAM 71–1262–65)

Carapace sandy-brown to dark brown with a pale longitudinal median stripe commencing within the ocular quadrangle as a diamond-shaped area narrowing between the PL eyes and abruptly expanding into a quadrangular or oval-shaped area before becoming scalloped laterally and narrowing to the posterior margin; the longitudinal stripe has a thin brown line commencing between the PM eyes and continuing down the middle of the pale longitudinal stripe to well posterior of the PL eyes to almost reach the centre of the carapace; on each side of this narrow brown line within the rectangular or oval-shaped area behind the PL eyes is a lunate shaped longitudinal spot that may continue faintly forwards to join the brown line forming an elongate somewhat diamond-shaped mark open posteriorly; a lateral pale marginal band, somewhat serrated on the upper margin, has some scattered dark brown spots around the middle of the band or along its entire length; some dark brown wedge-shaped marks radiate out from the foveal region across the brown lateral slopes; paturon dark brown to black; labium and maxillae dark brown with pale anterior margins; sternum dark brown to black; ventral surface of coxae brown. Abdomen light brown with an indistinct dark brown longitudinal stripe broken up into dark chevrons posteriorly and surrounded by a lighter area anteriorly and laterally; upper sides flecked with dark brown, lower sides pale brown to sandy-yellow; ventral surface sandy-yellow with a distinct jet black or indistinct dusky somewhat quadrangular or shield-shaped spot commencing at the epigastric furrow and reaching about half-way to the spinnerets. Legs sandy-brown with or without dark brown, dusty-brown or greyish rings.

Anterior row of eyes procurved, narrower than the second row; AM larger than AL. Ratio of eyes of WAM 71–1264 in micrometer units AM:AL:PM:PL=13:7:30:25; distance AM–AM 7, AM–AL 3·5, AM–PM 4, AL–PM 4, PM–PM 18. Clypeus to AM 7. Width of first eye row 53; width of second eye row 74.

Chelicerae with 3 promarginal teeth, the middle one largest; three retromarginal teeth of about equal size.

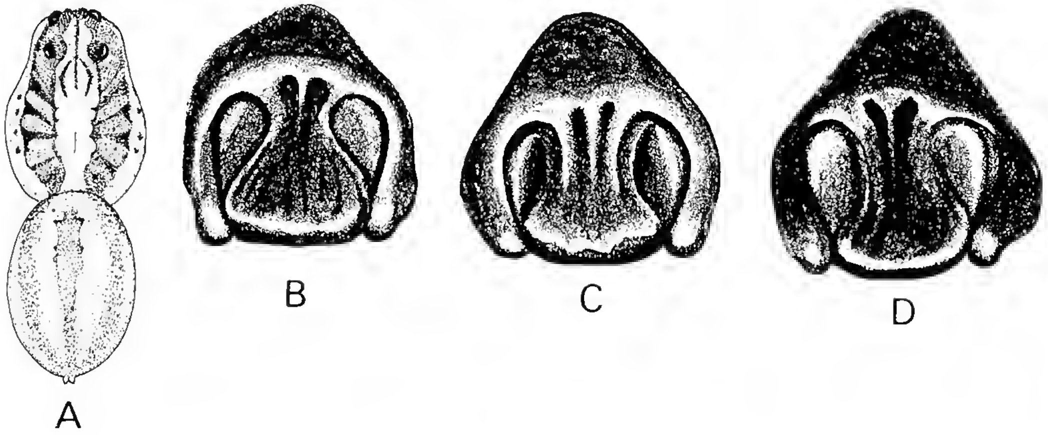

Fig. 8: *Lycosa marcentior*. A, mature female WAM 71–1265; B, C, D, epigyna of females WAM 71–1262, WAM 71–1263, WAM 71–1265.

TABLE 15: MEASUREMENTS OF LEG SEGMENTS OF *L. MARCENTIOR* (WAM 71–1264) IN MM

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1	4·5	2·5	3·4	3·4	2·0
2	4·3	2·5	3·2	3·3	2·0
3	4·1	2·2	2·9	3·5	1·9
4	5·3	2·5	4·1	5·7	2·4

VARIATION: The syntype from Dongara is quite pale and has traces of the longitudinal median stripe on the carapace. The abdomen is darker with a longitudinal dorsal stripe outlined in dark brown anteriorly, faint posteriorly. A faint series of brown wedge-shaped stripes are present on the carapace. The retromarginal teeth in this juvenile are 2+2; promarginal teeth 3+3 close together, the median largest. No mature female syntype was available for study, but the female genitalia of specimens from Deception Bay (Fig. 8B–D) agree quite well with Simon's description but have the anterior epigynal furrows much less divergent than in Simon (1909, fig. 3).

Eye diameters and interspaces of four mature females are given in Table 16 as a percent of the total width of the first eye row.

SIZE RANGE: Mature females C.L. 6·8 to 7·1 mm.

DIAGNOSIS

Mature females with a black spot on the ventral surface of the abdomen and a characteristic epigynum.

LIFE HISTORY

Mature females captured on 27 January, laid egg-cocoons during March and April in the laboratory (Table 17). Ova measured 1·0 – 1·2 mm in diameter.

Mature males were not collected despite a careful search. This species was not abundant at Desperate Bay or Dongara, and may be an uncommon species on the Swan coastal plain. Adult females may have been sheltering within burrows during January to April.

TABLE 17: NUMBER OF EGGS IN THE COCOONS OF *LYCOSA MARCENTIOR*

Date	♀C.L.	Egg Cocoon	Number of eggs
21.iii.1971	7·0	7·3 × 5·8 mm	168
21.iii.1971	7·1	8·2 × 6·5 mm	196
29.iii.1971	7·1	5·6 × 5·5 mm	120
5.iv.1971	6·8	6·5 × 7·5 mm	171

HABITAT

Near the beach on white sands near dune plants, litter, grassed areas or below dune bushes in dry leaf litter. This species can be found well behind the coastal dunes on sandy soils or clay-sand soil below trees. Juveniles were observed in grassed areas and the majority were found off the ground on grass stems, grass clumps, and on low bushes as if to escape predation.

BURROW

Adults were found wandering or sheltering below leaf litter. No burrows were observed in the field although adult females were disturbed and followed for some distance in the hope that they would seek the burrow to escape harassment. In the laboratory gravid females constructed a burrow with a very low mound some 8·5 cm deep in the moist sand, and webbed litter and sand grains over the entrance; once completed, the burrow was impossible to locate without disturbing the surface.

Lycosa meracula Simon, 1909
(Fig. 9A–K)

Lycosa meracula Simon, 1909, pp. 190–1, Denham and 'Albany'. Western Australia; Rainbow, 1911, p. 270; Bonnet, 1957, p. 2652; Rack, 1961, p. 38.
[Not] *Lycosa clara:* Hogg, 1914, p. 88.
Tetralycosa meracula: Roewer, 1954, p. 296; Roewer, 1960, p. 949.
Lycorma meracula: McKay, 1973, p. 380.

TABLE 16: EYE DIAMETERS AND INTERSPACES OF *L. MARCENTIOR* CONVERTED TO PERCENT OF THE TOTAL WIDTH OF THE FIRST ROW OF EYES

Regd No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM	AL:PM
WAM 71–1264	♀M	7·1	25	13	57	47	13	7	34	8	8
WAM 71–1262	♀M	7·1	25	14	63	53	12	5	29	6	8
WAM 71–1263	♀M	6·8	24	14	60	52	14	6	30	7	7
WAM 71–1265	♀M	7·0	24	14	59	51	14	6	33	8	9

MATERIAL EXAMINED

PARATYPES: One immature female, C.L. 3·5 mm, Hamburg Zool. Mus. Inst., No. 467, labelled 'Hambg. S.W. Austral. Exp. 1905, 65 Denham, 9–11.vi, *Lycosa meracula* ES'. One immature specimen C.L. 2·7 mm, Western Australian Museum, previously dried and pinned, labelled 'Hambg. S.W. Austral. Exp. 1905, 5 Shark Bay Denham, Ebbestrand, 20.vi'.

OTHER MATERIAL: Western Australia; Barrow Island, 23.v.1968, HB, WAM 69–366–7, 31.iii.1971, HB, WAM 71–1812–19, WAM 71–1807–11, 21–25.viii.1973, L. A. Smith, WAM: Bernier Island, 16.iv.1969, J. Bannister, WAM 70–173–7; Carrarang Station, False Entrance, Shark Bay, AB, QM S49; Dorre Island, 20.iv.1969, J. Bannister WAM 70–178–9; Maud Landing, 20.v.1968, JG, WAM 70–64–76, WAM 69–96, 7–12.vii.1971, B. & D. Parker, WAM 71–1820–40; Onslow, 28.ix.1971, RJM, J. Dell, WAM 71–1860–4, QM S48; Rosemary Island, Dampier Archipelago, 27–28.x.1971, RJM WAM 72–120–152, WAM 72-198-219; Warroora Station, 23–24.viii.1970, RJM, WAM 70–365–420, WAM 70–232, WAM 70–238, WAM 70–221, 13.vii.1971, B. and D. Parker, WAM 71–1841–5; Warroora Station, 14 mi. north, viii.1968, JG, WAM 69–95.

DESCRIPTION (After Simon 1909)

Male: Carapace pale tawny-red; area around eye black; cephalic part with two very small dark marks posteriorly; thoracic part marked by a fine marginal line and by very thin, short, dark lines radiating out; carapace covered with white hair becoming light-yellow, and is decorated by a wide white marginal band and a narrower white line in the middle; chelicerae tawny-red; sternum golden-olive covered with white hairs.

Abdomen tawny to brick-coloured, covered above with white to ash-grey hair tinged gold towards the anterior part; a fine line on the dorsal surface anteriorly, not extending past the middle, and with rows of snow-white spots on both sides. Undersurface completely covered with white hair.

Legs pale golden, reddish-tinged towards the extremities, and with some white hairs and a few fine long bristles.

Anterior row of eyes almost equidistant in an almost straight line, about the same width as the second row (smaller than second row); AM almost twice as large as AL; AL closer to the edge of the clypeus than to the PM; PM separated by a space narrower than a quarter of an eye diameter.

Female: Differs from the male in having the first row of eyes a little narrower than the second row, and the PM larger. The abdomen is pale, brick-coloured, white haired, with a light net-like reticulated pattern and dark variegations. Legs are shorter. Palpi golden-orange with the tips black.

VARIATION: Simon (1909) records 4 retromarginal cheliceral teeth in the description of this species. and Roewer (1954) made *Lycosa meracula* the type species of *Tetralycosa*.

Both paratypes have 3 + 3 retromarginal cheliceral teeth and of 82 specimens listed above. 81 had 3 + 3 and one (WAM 70–420, an immature female, C.L. 5·4 mm) had 4 teeth on the right side and 3 on the left.

Eye measurements were recorded for 5 specimens; each measurement is given below in Table 18 as a percent of the total width of the first eye row.

Variation in the shape of the epigynum is illustrated in Fig. 9E, I, J, and the internal genitalia of QM S48 is shown in Fig. 9H. The male palpal organ is illustrated in Fig. 9F, G, K.

SIZE RANGE: Mature females C.L. 6·3 to 12·0 mm.

DIAGNOSIS: *Lycosa meracula* is similar to *Lycosa clara* but the lateral furrows of the epigynum converge anteriorly in *L. meracula* and diverge markedly in *L. clara*.

LIFE HISTORY

Mature females are present from April to October but are more numerous during August to late October. Mature males have been collected in August.

TABLE 18: EYE DIAMETERS AND INTERSPACES OF *L. MERACULA* CONVERTED TO PERCENT OF THE TOTAL WIDTH OF THE FIRST ROW OF EYES

Regd No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM	AL:PM
WAM 72–198	♀M	12·0	26	16	57	49	10	9	30	9	9
WAM 70–211	♀M	10·1	28	13	60	51	10	6	30	9	10
WAM 71–1807	♀M	6·3	28	15	64	53	8	5	33	6	9
QM S48	♀M	11·2	28	14	56	50	6	4	29	9	11
QM S49	♀M	7·8	26	13	62	51	8	6	27	6	8

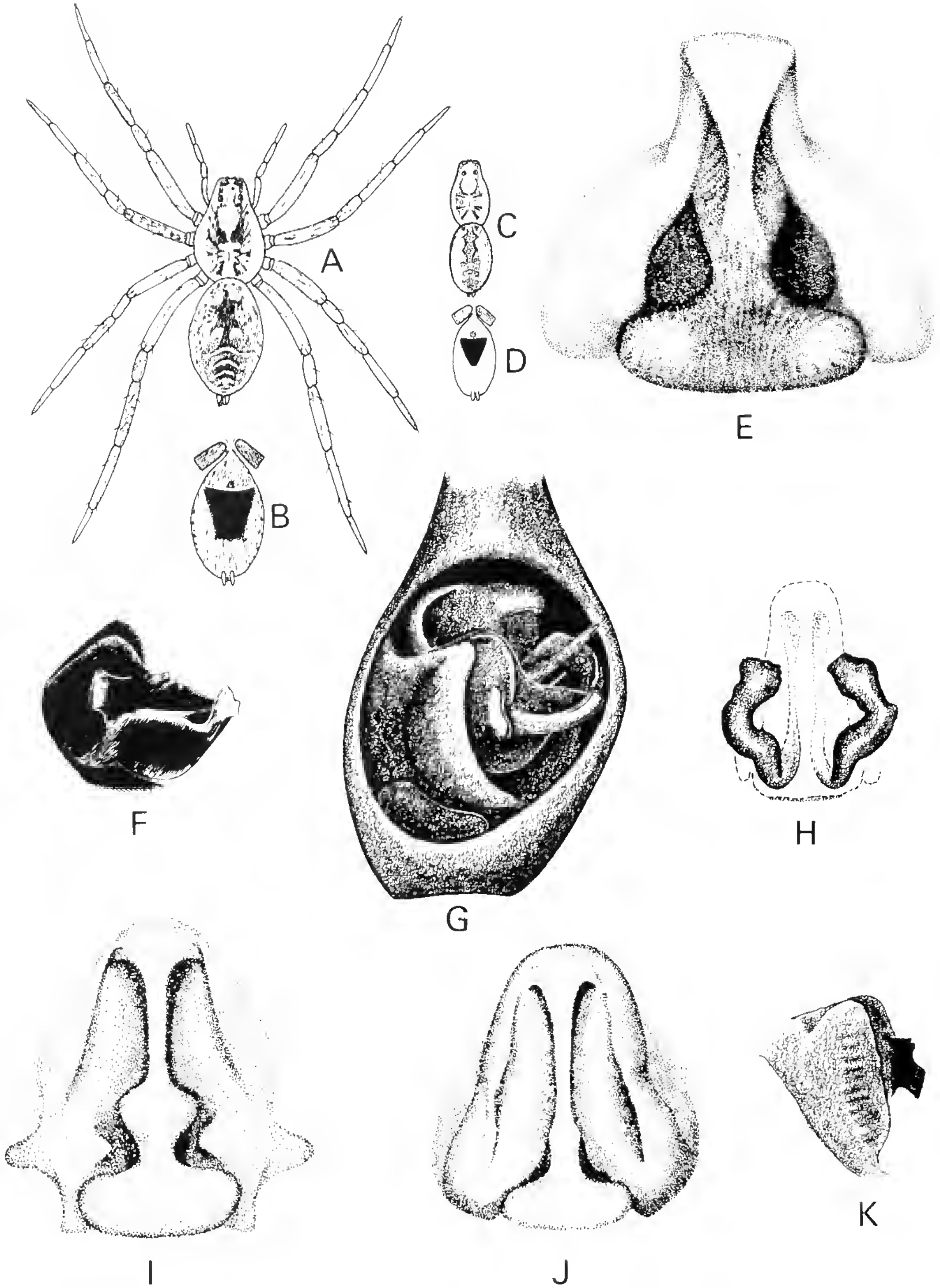

FIG. 9. *Lycosa meracula*. A, mature female WAM 72–198; B, undersurface of abdomen; C, mature female WAM 71–1807; D, undersurface of abdomen; E, epigynum of WAM 70–211; F, median apophysis of male palpal organ from Barrow Island; G, male palpal organ, Barrow Island; H, internal genitalia of female QM S48; I, J, epigyna of females WAM 69–64, WAM 69–65; K, basal part of median apophysis FM from side.

HABITAT

Coastal sandy soils. Open areas and on wind protected slopes of coastal sand dunes down to the wet sand of the beach. Adult females are found largely in the sand dune areas where they shelter below clumps of dune grass.

BURROW

An open burrow well lined with silk throughout its length is constructed on the slopes of sand dunes near the base of dune plants, and descends to a depth of between 65 and 130 mm. The entrance frequently collapses after the spider enters the burrow, and if the complete silk tube is excavated from the loose sand, the spider remains motionless within. Adult females may be found wandering well away from the burrow.

DISCUSSION

Roewer (1960, p. 949) has designated *Lycosa meracula* as the type species of the genus *Tetralycosa* characterised by the possession of four retromarginal cheliceral teeth, in having the upper tangent of the first row of eyes straight, the first eye row as wide as the second row, the distance AM–AL equal to AM–AM, the diameter of the AM larger than the AL, and the distance PM–PM shorter than the diameter of a PM. An examination of a series of specimens shows that the upper tangent of the first row of eyes is procurved, the first row of eyes is narrower than the second row, the distance AM–AL is shorter than AM–AM.

Tetralycosa is therefore a synonym of *Lycosa.*

The record of this species from Albany, Western Australia (Simon, 1909) is erroneous, as the southern limit of the species appears to be just north of the Murchison River. Station 5 of the Hamburg southwest Australia Expedition of 1905 is Denham, 8, 9, 20 June, 19-20 September. Station 65 'Albany' refers to station 65 Denham, 9, 11, 20 June, 4, 22 September, bushes at the coast, and not station 165 Albany.

Lycosa tula (Strand, 1913)
(Fig. 10A, B, F–L)

Tarentula tula Strand, 1913, pp. 622–23, Central Australia.
Allocosa tula: Roewer, 1954, p. 207.
Lycosa tuba (misspelt): Bonnet, 1957, p. 2667.
Lycosa tula: McKay, 1973, p. 380.

MATERIAL EXAMINED

SYNTYPES: Senckenberg Museum No. 2769, 1 ♂M 1 ♀M, collected V. Leonhardi, 1909, 'Central Australien'. A lectotype is here designated from this series. Strand (1913) records 4 ♀M 1 ♀P, 1 ♂M in the original description.

LECTOTYPE: Senckenberg Museum No. 2769, ♂M, C.L. ca. 6·5 mm with left palp missing.

OTHER MATERIAL: Western Australia; Albion Downs, Wiluna area, 10.i.1962, BYM, 2 ♀1 ♂M, QM S31; 15.i.1962, BYM, 2 ♀M, QM S33; Albion Downs-Wiluna at Palm Spring Flats, 13.i.1962, BYM, 1 ♀M, QM S32; Buntine Reserve, 3·5 km east of Buntine Railway Station, 2.ix.1972, AB, 10 ♀M, WAM 72–660–69.

DESCRIPTION (After Strand 1913)

Female: Carapace dark brown with radiating black stripes, a distinct marginal band of white hair and a longitudinal pale median stripe which at the fovea is about 0·7 mm wide, and gradually broadens anteriorly and posteriorly; at the ocular quadrangle this stripe abruptly narrows to continue anteriorly between the PM and AM eyes to the clypeus; paturon and fang black; labium and maxillae black with a lighter margin; sternum and coxae black. Abdomen brown with lighter and darker spots; a median longitudinal stripe of dirty-yellow hair which has, anteriorly, a black longitudinal band about 1·5 mm wide which continues to the middle of the abdomen where it becomes less distinct and continues to the spinnerets; on each side of this band before the middle is a small denticle; sides and belly yellow-grey with usually a deep black spot which stretches from the fissure to the beginning of the posterior third of the belly where the margin is more or less rounded; epigaster light coloured. Legs yellow-brown; the femora are lighter on the ventral surface; indications of darker spots on the sides and dorsal surface; scopula black; terminal segment of palpi mainly black.

Chelicerae with three promarginal and three retromarginal teeth.

Male similar to female but with a more distinct median stripe on the dorsal surface of the abdomen.

VARIATION: The median longitudinal stripe on the dorsal surface of the abdomen may be indistinct in preserved specimens; sides of abdomen, spotted with brown or black; the black field on the ventral surface of the abdomen may occupy half the length of the abdomen to almost the complete length of the venter, but not reaching the spinnerets. Legs ringed with dark brown in some adults.

Anterior row of eyes procurved, shorter than second row. Ratio of eyes (lectotype) in micrometer units AM:AL:PM:PL = 12:7:28:25;

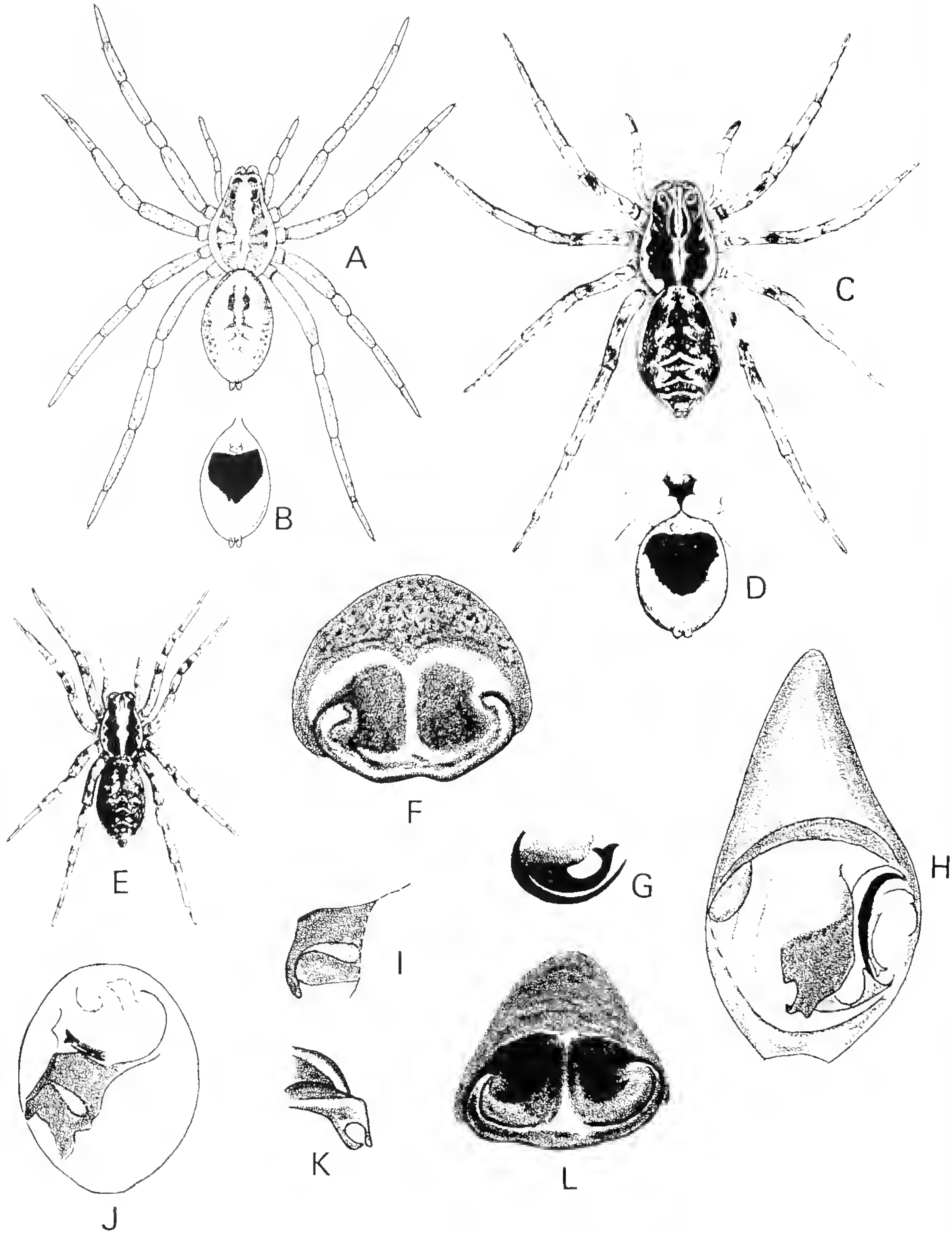

FIG. 10. *Lycosa tula*. A, mature female from Albion Downs, B, undersurface of abdomen; F, epigynum of paralectotype; G, embolic guide and embolus of male from Albion Downs; H, male palpal organ from Albion Downs; I, median apophysis of lectotype; J, embolic guide and median apophysis of lectotype; K, median apophysis of male from Albion Downs; L, epigynum of female from Albion Downs.

Lycosa woonda. C, female from Kalgoorlie; D, undersurface of abdomen; E, female from Kalgoorlie.

distance AM–AM 6, AM–AL 4, AM–PM 3, AL–PM 3, PM–PM 15. Clypeus to AM 4. Width of first eye row 49; width of second eye row 66. The eye measurements for the lectotype, paralectotype, and two Western Australian specimens are expressed as a percent of the total width of the first eye row in Table 19.

Epigynum of the paralectotype illustrated in Fig. 10F; a specimen from Albion Downs in Fig. 10L. The median apophysis of the lectotype male palpal organ is shown in Fig. 10I, J; the male palpal organ and the median apophysis of a specimen from Albion Downs shown in Fig. 10G, H, K.

DIAGNOSIS: *Lycosa tula* has a distinct black shield on the ventral surface of the abdomen; the male palpal organ is of characteristic shape with a distinct median apophysis that lacks a spine on the upper margin, and the tip of the embolic guide is bifurcate.

LIFE HISTORY

Unknown.

HABITAT

Red earths with sparse vegetation in arid regions of Western Australia and 'Central Australia'. At Buntine Reserve the substrate was deep yellow sand with sandplain vegetation of wattles and *Grevillea* species.

DISCUSSION

Lycosa tula is one of several arid zone wolf spiders of very similar appearance. A black shield-like marking is quite common on the ventral surface of the abdomen of these species and the female genitalia may be similar in shape. The shape of the median apophysis and the embolic guide of mature male palpal organs allows a separation of the various species and therefore mature males should be collected to provide positive identification. A number of undescribed species are present in inland Australia; these await the collection of conspecific males before description is justified.

Lycosa woonda sp. nov.

(Figs. 10C, D, E, 11A–E, 12I)

MATERIAL EXAMINED

HOLOTYPE Queensland Museum QM S34, ♂M, C.L. 7·2 mm, Albion Downs via Wiluna, Western Australia, collected by Dr B. Y. Main, 15 January, 1962. In spirit.

PARATYPES Albion Downs via Wiluna, W.A., 15.i.1962, BYM, 2 ♂M, QM S35; 10.i.1962, BYM, 2 ♀M, QM S36; Albion Downs, Wiluna, W.A., at Palm Spring Flats, 13.i.1962, BYM, 1 ♂M, QM S37; Moorine Rock, W.A., 29.viii.1954, BYM, 1 ♂M, QM S38; Kalgoorlie, W.A., ix.1968, A. McKay, 1 ♂M 2 ♀P 1 ♂P, QM S39.

DESCRIPTION (Based on the holotype)

Carapace brown with a pale longitudinal stripe commencing behind the PM eyes and broadening behind the PL eyes to taper towards the anterior end of the fovea where it expands in a somewhat diamond-shape and then again tapers to the posterior margin; within this longitudinal stripe are two curved brown stripes (Fig. 10C); a serrated cream marginal band containing scattered dark spots; margin of carapace with an irregular brown band-like pattern outlined by a thin creamy-white band on the lateral edge; irregular dark-brown, somewhat wedge-shaped markings radiate out from the foveal area; long pale cream hairs project anteriorly from the ocular quadrangle; paturon brown with a dense covering of pale cream hair, fang dark brown; labium and maxillae brown with the anterior margin lighter brown; sternum dark brown, almost black; coxae light brown with the anterior surface of the first pair dark brown. Abdomen light brown to fawn above with a bell-shaped dark brown mark that continues posteriorly to terminate in an inverted V-shaped chevron; more posteriorly are vague dark chevrons, the last has the ends expanded into a more or less distinct tent-shaped spot; sides of abdomen cream with scattered dark spots and blotches; ventral surface light brown to cream with a jet black transverse shield-shaped spot commencing behind the epigastric furrow and terminating half-way to the spinnerets. Legs brown with indistinct darker rings on segments;

TABLE 19: EYE DIAMETERS AND INTERSPACES OF *L. TULA* CONVERTED TO PERCENT OF THE TOTAL WIDTH OF THE FIRST ROW OF EYES

Regd No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM	AL:PM
LECTOTYPE	♂M	6·5	24	14	57	51	12	8	31	6	6
PARALECTOTYPE	♀M	8·5	23	15	54	49	12	8	26	9	9
WAM 72–660	♀M	6·3	25	15	61	53	9	5	30	6	9
QM S31	♂M	6·0	27	14	64	54	8	5	30	8	9

femora with indistinct dark elongate blotches on the prolateral and retrolateral surfaces.

Anterior row of eyes procurved, shorter than the second row; AM larger than AL. Ratio of eyes in micrometer units AM:AL:PM:PL = 12:7:30:25; distance AM–AM 4, AM–AL 6, PM–PM 15, AM–PM 2, AL–PM 3. Clypeus to AM 6. Width of first eye row 51; width of second eye row 73.

Chelicerae with three promarginal teeth on the right side, 2 on the left side; three retromarginal teeth of about equal size.

Male palpal organ with a broad somewhat spoon-shaped median apophysis with a terminal hook and an anteriorly directed sharp basal spine; embolic guide a flat half circle (Fig. 11A–C).

VARIATION: Two females from Kalgoorlie are illustrated (Fig. 10C, D, E). The longitudinal stripe on the carapace may lack the two curved brown marks behind the PL eyes in some examples, and the brown spots on the lateral band may be very pronounced or quite faint.

The eye diameters and interspaces of the holotype and three paratypes are given in Table 21 as a percent of the total width of the first eye row. The epigyna of two females from Albion Downs are illustrated in Fig. 11D, E. The internal genitalia of female QM S37 is illustrated in Fig. 12I. The median apophysis of the holotype is shown in Fig. 11B, and rotated slightly forwards in Fig. 11C.

DIAGNOSIS: The male palpal organ is characteristic. Females may be confused with *L. tula* but normally have the ends of the transverse guide of the epigynum very broad and raised.

TABLE 20: MEASUREMENTS OF LEG SEGMENTS OF HOLOTYPE OF *L. WOONDA* IN MM

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1	5·7	2·7	4·7	5·2	2·5
2	5·7	2·7	4·6	5·2	2·5
3	5·4	2·4	3·8	5·3	2·6
4	6·6	2·5	5·5	7·5	2·8

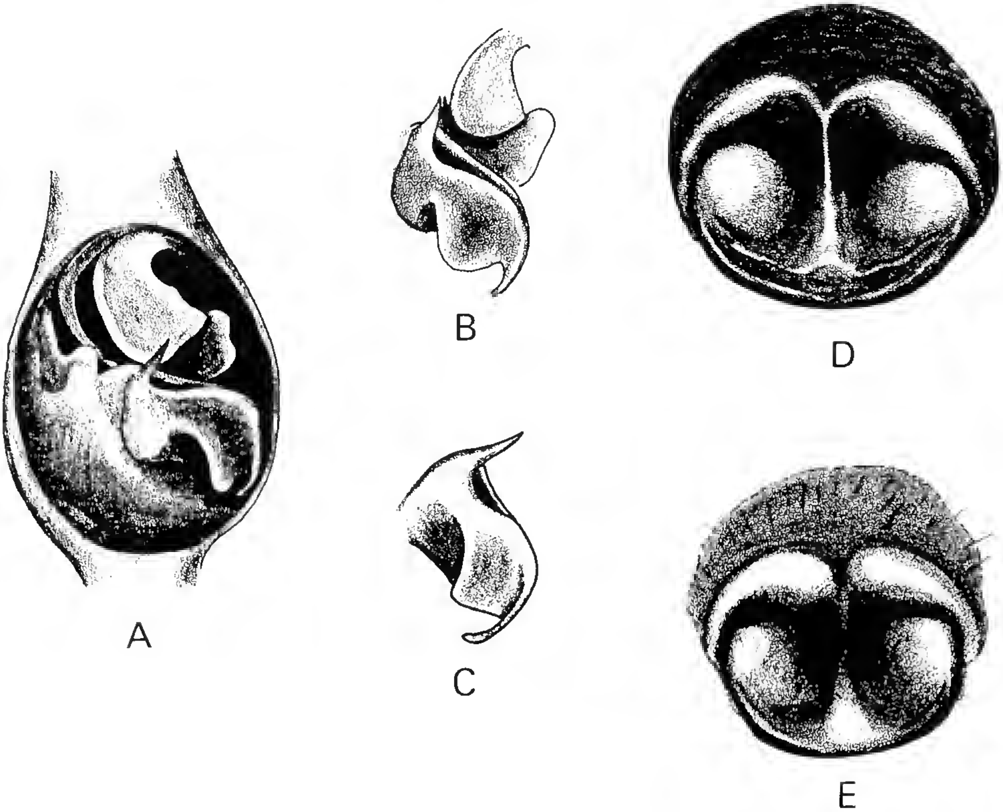

FIG. 11: *Lycosa woonda*. A, male palpal organ of holotype; B, embolic guide, conductor and median apophysis of holotype; C, median apophysis of holotype rotated slightly forwards to show comparative length of basal spine and terminal hook; D, E, epigyna of mature females from Albion Downs.

TABLE 21: EYE DIAMETERS AND INTERSPACES OF *L. WOONDA* CONVERTED TO PERCENT OF THE TOTAL WIDTH OF THE FIRST ROW OF EYES

Regd No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM	AL:PM
HOLOTYPE	♂M	7·2	23	14	59	49	8	12	30	4	6
QM S37	♀M	9·1	26	14	62	53	9	8	30	5	6
QM S38	♀M	8·5	25	15	59	51	10	5	33	7	7
QM S39	♀M	6·3	26	14	60	50	10	8	28	4	6

LIFE HISTORY

Unknown.

HABITAT

Red desert loam soils with scattered Mulga *Acacia aneura*.

BURROW

Unknown.

DISCUSSION

See *Lycosa tula*.

DERIVATION

From the aboriginal 'woonda' meaning shield, in reference to the shield-shaped black spot on the ventral surface of the abdomen.

Lycosa yalkara sp. nov.

(Fig. 12A–H, J, K)

MATERIAL EXAMINED

HOLOTYPE: Queensland Museum QM S40, ♂M, C.L. 7·8 mm, 40 km south of Mount Magnet, Western Australia, collected by R. J. McKay and J. Gilbert, 7 December, 1968. In spirit.

PARATYPES: Western Australia; Cue 2 km south, 2.ii.1970, JG, 1 ♂M, QM S43; Marloo Station, west of Yalgoo, 31.i.1968, A. Douglas, L. Koch, 1 ♂M, WAM; Mount Gibson, 27.ii.1962, BYM, 1 ♀M, QM S44, 28.ii.1962, BYM, 1 ♂M 1 ♀M, QM S42; Paynes Find, 28.ii.1970, RJM, 1 ♀M 1 ♂M, QM S41.

DESCRIPTION (Based on the holotype)

Carapace brown with a pale longitudinal stripe commencing behind the PM eyes and broadening behind the PL eyes to form a lateral round protuberance enclosing a conspicuous dark brown spot on each side before tapering to the fovea where the stripe broadens once again before tapering to the lateral margin; a pale marginal band that is irregularly serrated on the upper margin and does not meet on the posterior mid-line contains five to six dark brown blotches located on the lateral margin of the carapace; elongate wedge shaped dark brown markings radiate out from the centre of the carapace between the pale longitudinal stripe and lateral band to terminate in dark brown V or wedge-shaped expansions projecting into the lateral band; these radiating dark brown markings are immediately preceded by a faint pale line or stripe; pale hairs project anteriorly from the ocular quadrangle; paturon dark brown covered with pale hairs; fang dark brown; labium and maxillae brown, lighter anteriorly; sternum and coxae dark brown to black. Abdomen light brown with a dark brown rather diffuse bell-shaped marking followed by a series of poorly defined dark brown chevrons; the dorsal surface spotted with dark brown, sides streaked with brown, and the anterior slope dark brown on either side of the median pale stripe; just before the spinnerets on either side is a pale fawn spot edged with dark brown anteriorly; ventral surface pale fawn with a jet black shield-shaped spot commencing at the epigastric furrow and terminating before the spinnerets. Legs brown, with irregular dark brown blotches.

Anterior row of eyes procurved, shorter than the second row; AM larger than AL. Ratio of eyes in micrometer units AM:AL:PM:PL = 14:9:35:29; distance AM–AM 6, AM–AL 4, PM–PM 15, AM–PM 3, AL–PM 3. Clypeus to AM 8. Width of first eye row 58; width of second eye row 80.

Chelicerae with three promarginal teeth, the middle one largest; three retromarginal teeth, the middle one slightly larger than the laterals.

Male palpal organ with a robust median apophysis terminating in a flat recurved hook; embolic guide with a bifurcate tip.

TABLE 22: MEASUREMENTS OF LEG SEGMENTS OF *L. YALKARA* IN MM

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1	6·5	3·2	5·5	6·0	2·8
2	6·1	3·0	5·1	5·8	2·7
3	6·0	2·5	4·5	6·1	2·6
4	7·1	2·7	5·9	8·5	3·4

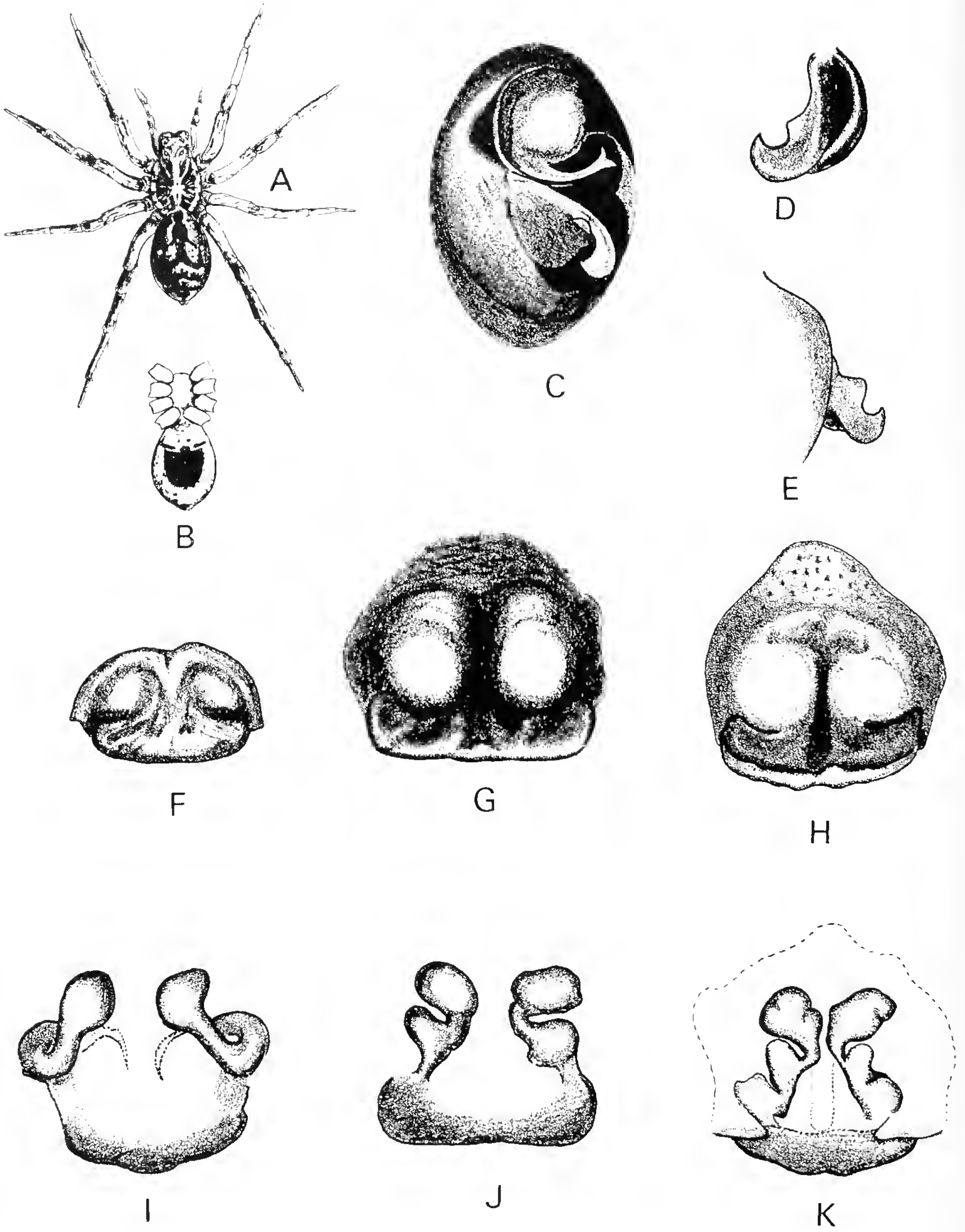

FIG. 12: *Lycosa yalkara*. A, mature female from Marloo Station; B, undersurface of abdomen; C, male palpal organ of QM S41; D, outer view of median apophysis of QM S41; E, inner view of median apophysis of QM S41 from side; F, G, H, epigyna of females QM S42, QM S44, QM S41; J, K, internal genitalia of females QM S44, QM S41.

Lycosa woonda. I, internal genitalia of QM S37.

TABLE 23: EYE DIAMETERS AND INTERSPACES OF *L. YALKARA* CONVERTED TO PERCENT OF THE TOTAL WIDTH OF THE FIRST ROW OF EYES

Regd No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM	AL:PM
HOLOTYPE	M	7·8	24	16	60	50	10	7	26	5	5
QM S43	M	8·7	24	14	59	52	10	7	28	7	7
WAM	M	8·8	25	17	58	55	8	7	27	7	8
QM S44	M	9·7	25	16	58	51	8	7	28	6	7

VARIATION: Three female epigyna are illustrated in Fig. 12F, G, H, and the internal genitalia of two females (Fig. 12J, K) are compared with the internal genitalia of *L. woonda* (Fig. 12I). The eye diameters and interspaces of the holotype and three paratypes are given in Table 23 as a percent of the total width of the first eye row.

DIAGNOSIS: Mature males with a bifurcate tip to the embolic guide and a robust median apophysis terminating in a flat hook. Female epigynum with a broad transverse guide and no median guide.

LIFE HISTORY

Unknown.

HABITAT

Red desert loam soils with scattered Mulga *Acacia aneura*.

BURROW

Unknown.

DISCUSSION

See *Lycosa tula*.

DERIVATION

From the aboriginal 'yalkara' meaning drought spirit.

ACKNOWLEDGMENTS

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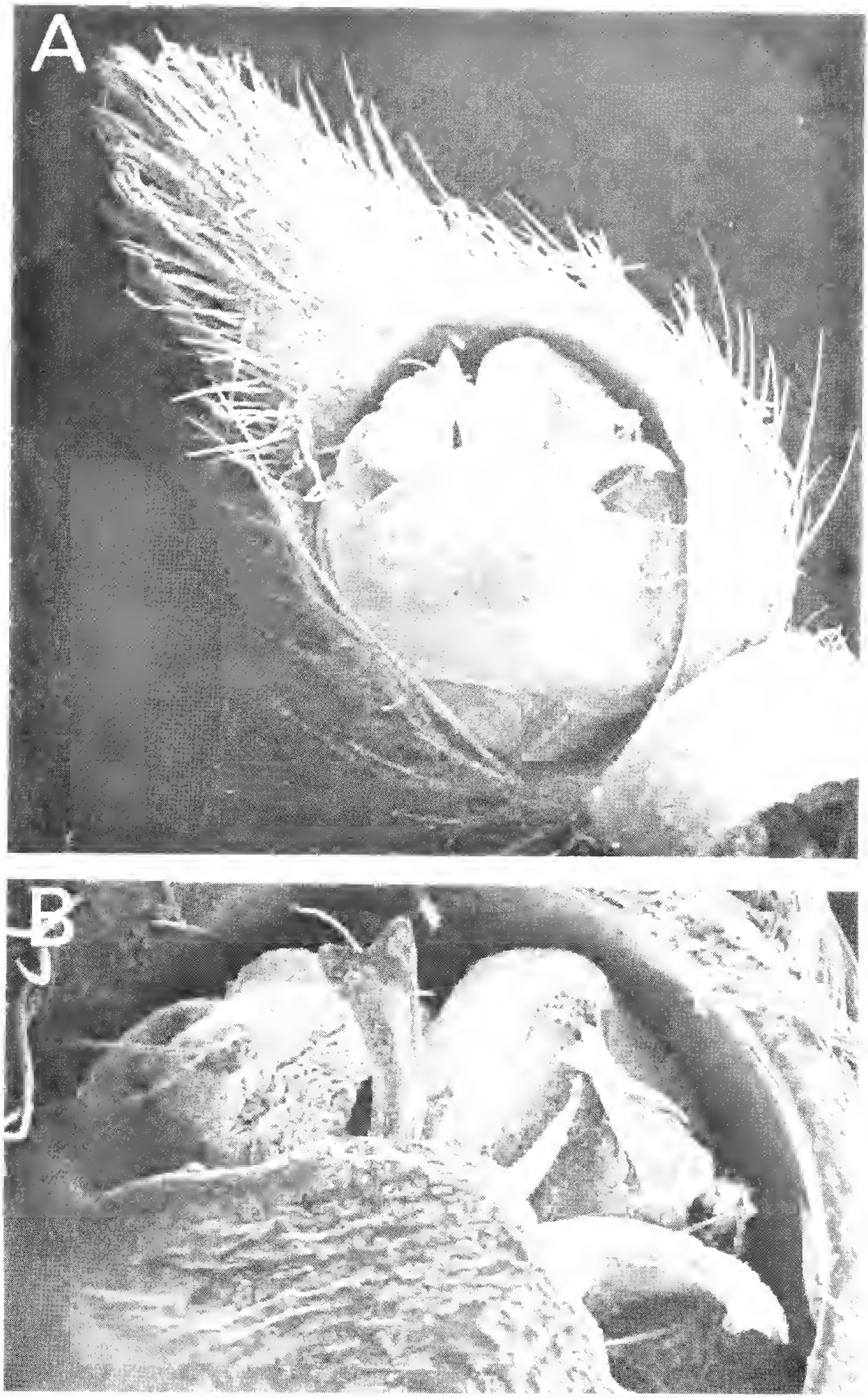
PLATE 1

A-B: *Lycosa ariadnae*, male palpal organ.


A
B

Mem. Qd Mus. **19**(3): 277–98. [1979]

THE WOLF SPIDERS OF AUSTRALIA (ARANEAE: LYCOSIDAE): 13. THE GENUS *TROCHOSA*

R. J. McKay
Queensland Museum

ABSTRACT

The Australian species of the genus *Trochosa* — *T. oraria, T. tristicula tristicula, T. tristicula phegeia, T. expolita expolita, T. expolita impedita, T. martensii, T. exculta, T. candicans, T. alboguttulata* and *T. properipes* — are redescribed. Two new species *T. glarea* and *T. wundurra* are described.

The subfamily Lycosinae has been subdivided into many genera (Roewer 1961), not all of which have been accepted by modern arachnologists. The genus *Trochosa* is one that is generally accepted and although variously defined, appears to be a natural grouping of species. The Australian species described below fall into *Trochosa* when using most of the available keys to the genera of the family Lycosidae.

Collectors names have been abbreviated where a large amount of material has been donated (see McKay 1973 for additional abbreviations): Mr G. B. and Mrs S. R. Monteith = GBSRM; Mr R. Raven = RR; Dr Valerie Davies = VED.

Genus **Trochosa** C. L. Koch 1848

Trochosa C. L. Koch, 1848, pp. 95–6; type species by original designation *Aranea ruricola* de Geer 1778.

Trochosina (subgen.) Simon, 1885, p. 10; type species *Trochosa terricola* Thorell 1856.

Allotrochosina Roewer, 1954, p. 213; type species *Lycosa maunganuiensis* Berland 1925 (misspelt *mananganuiensis* by Roewer).

Diahogna Roewer, 1954, p. 239; type species *Lycosa martensii* Karsch 1878.

Trochosomma Roewer, 1954, p. 304; type species *Trochosa annulipes* L. Koch 1875.

Diagnosis: Small to moderate sized spiders; legs in order of decreasing length 4, 1, 2, 3; tibia of first leg with no more than 3 pairs of ventral spines (apical ventral spines usually present); carapace frequently with a pale median longitudinal stripe including a long dark mark on each side in front of the fovea; first row of eyes gently procurved, as long as or longer than the second row (rarely shorter); AM eyes larger than AL eyes; retromarginal cheliceral teeth usually 3 on each side (occasionally 2 or 4); fourth tibia with the proximal dorsal spine thinner and more drawn out than the distal spine, frequently reduced to a fine bristle, or in some Australian species the proximal dorsal spine may be absent; first tarsus with or without a long dorsobasal bristle.

Discussion: The genus *Trochosa* was proposed by C. L. Koch in 1848. Simon (1876) considered *Trochosa* and *Arctosa* C. L. Koch 1848 to be synonyms of *Lycosa* Latreille 1804, but in 1885 Simon erected *Trochosina* as a group of *Lycosa* that had *Trochosa* characteristics but only 2 retromarginal cheliceral teeth. In 1937 Simon abandoned *Trochosina* but retained *Trochosa* as a group or subgenus. Dahl (1908) employed *Trochosa* as a full genus but many authors continued to follow Simon. Bonnet (1951) recognised 15 genera including *Trochosa* but excluded *Trochosina*. Roewer (1954) subdivided the subfamily Lycosinae into 88 genera, half of which were listed as new, and later (1959, 1960) provided a diagnosis for his genera and described an additional 10 genera to make a total of 93 genera recognised in his generic revision of the subfamily. Guy (1966) reduced 91 of the genera used by Roewer to 37 genera and 23 subgenera; the genus *Trochosa* was listed with two subgenera (*Allohogna* Roewer 1954, and *Mimohogna* Roewer 1954) whilst four genera were relegated to the synonomy of *Trochosa* (*Trochosina* Simon, *Allotrochosina* Roewer, *Diahogna* Roewer, *Trochosula* Roewer). Fuhn and Niculescu-Burlacu (1971) recognised *Trochosa* but placed

Allohogna and *Mimohogna* into the synonomy of *Lycosa*. From published descriptions of the type species of *Allohogna* and *Mimohogna* it seems clear that these genera are synonyms of *Lycosa*. *Allotrochosina* is regarded by me to be a synonym of *Trochosa* as the type species *Lycosa maunganuiensis* was originally assigned to 'the group *Lycosa terricola* (subgenus *Trochosina* of Simon)' by Berland (1925). *Trochosula* is based on *Lycosa conspersa* L. Koch 1882, a species placed in the genus *Alopecosa* by Bonnet (1955, p. 241); there is also *Trochosa conspersa* (Thorell 1877) listed by Bonnet (1959, p. 4710). I have followed Bonnet in referring *Trochosula* to the synonomy of *Alopecosa*. The genus *Diahogna* Roewer 1954, is here regarded as a synonym of *Trochosa* following the examination of the holotype of the type species *Lycosa martensii* Karsch 1878. *Arctosomma* Roewer 1954, is possibly another generic synonym of *Trochosa* as are the genera *Mustelicosa* Roewer 1954, and *Piratosa* Roewer 1954, but their type species have not yet been examined by me. *Varacosa* Chamberlain and Ivie 1942, was proposed as a subgenus 'for those species of *Trochosa* wherein the cross-piece of the epigynum has the ends curved far forward'; the type species *Trochosa avara* Keyserling 1876, is now regarded as a *Lycosa* by Bonnet (1959, p. 4699) and most American authors. *Dolocosa* Roewer 1960, is possibly a valid genus as the type species *Lycosa (Trochosa) dolosa* Cambridge 1873, has 5 pairs of ventral spines on the tibia of the first leg and numerous spines on other leg segments (Roewer 1960, pp. 935–6, figs. 519, a, c). Bonnet (1959, p. 4702) regards *L. dolosa* as a *Trochosa*, and Guy (1966) considers *Dolocosa* to be a synonym of *Leaena* Simon 1885. *Lycosa furcillata* L. Koch 1867, is not a *Trochosa* as listed by Bonnet (1959), as the first row of eyes is narrower than the second (McKay 1974, pp. 15–18), and the fourth tibia has a well developed dorsobasal spine.

KEY TO AUSTRALIAN SPECIES OF *TROCHOSA*

1. First row of eyes narrower than second row; dorsal surface of abdomen with a dark brown to black diamond-shaped mark bisected by a longitudinal pale stripe (Fig. 3B, C) 2

First row of eyes as broad as or broader than second row; dorsal surface of abdomen without a diamond-shaped mark bisected by a longitudinal pale stripe 3

2(1). Median apophysis of male palpal organ distinctly hook-shaped .... *Trochosa expolita impedita*

Median apophysis of male palpal organ straight, gently curved, or bent, but not hook-shaped .... *Trochosa expolita expolita*

3(1). Epigynum with a well developed chitinous hook on each antero-lateral surface (Fig. 4H) ....*Trochosa glarea* sp. nov.

Epigynum without chitonous hooks on antero-lateral surfaces 4

4(3). Two curved longitudinal white lines commence at the posterior margin of the carapace and extend forwards to join or almost join between the PL eyes where a short white line extends posteriorly from the inner margin (Fig. 4A) 5

No curved white lines on carpace 6

5(4). White spots on the dorsal surface of the abdomen converge towards spinnerets; no median guide to epigynum (Fig. 4B, C) ....*Trochosa martensii*

White spots on the dorsal surface of abdomen diverge posteriorly; a distinct median guide to epigynum (Fig. 4D) ....*Trochosa exculta*

6(4). First pair of legs longer than fourth pair ....(?) *Trochosa properipes*

First pair of legs shorter than fourth pair 7

7(6). Tibiae of first pair of legs with a pair of apical spines, but no median or basal spines on ventral surface; median guide of epigynum expanded into a plate-like structure (Fig. 4I) .... *Trochosa wundurra* sp. nov.

Tibiae of first pair of legs with one or two apical and median and basal pairs of spines normally present on ventral surface; median guide, if present, not expanded into a plate-like structure 8

8(7). Ventral surface of abdomen white or very pale brown 9

Ventral surface of abdomen dark brown with darker markings normally present 10

9(8). Femur of first leg with one anterior spine; anterior part of the first two tibiae with 1 + 1 spines; patellae of first and second legs without spines; coastal beaches of southwestern Western Australia (and South Australia?) .... *Trochosa oraria*

Femur of first leg with two anterior spines; anterior part of the first two tibiae with 1+1+1 spines; patellae of first and second legs with an anterior spine; Shelleys Flats near Goulburn, and coastal beaches, New South Wales . ... *Trochosa candicans*

10(8). Epigynum with lateral arms expanded, generally without a well developed median guide except between the lateral posterior extremities (Fig. 2A–B, D, J) 11

Epigynum without expanded lateral arms, and with a well developed median guide (Fig. 2I, 4F) .....*Trochosa alboguttulata*

11(10). Anterior inner margin of epigynum without well developed cusps; apical spermathecae of female with a curved fertilization tube on the ventral surface (Fig. 2Q); median apophysis of male palpal organ with a spine on the concave side (Fig. 2C, F–G); southwestern Western Australia .... *Trochosa tristicula phegeia*

Anterior inner margin of epigynum with two well developed cusps; apical spermathecae with a short fertilization tube on the ventral surface (Fig. 2N–P); median apophysis of male palpal organ without a spine on the concave side (Fig. 2K–L); Queensland and New South Wales .... *Trochosa tristicula tristicula*

Trochosa oraria (L. Koch 1876)
(Fig. 1A–H)

Lycosa oraria L. Koch, 1876, pp. 883–6, pl. 76, figs. 2, 2a, 3, 3a, King George Sound, Western Australia; Simon, 1909, p. 188, Obelisk Hill, Fremantle, Western Australia; Rainbow, 1911, p. 270; Bonnet, 1957, p. 2656.

Lycosa sibyllina Simon, 1909, pp. 188–9, fig. 7, Albany Western Australia; Rainbow, 1911, p. 272; Bonnet, 1957, p. 2664; McKay, 1973, p. 379.

Crocodilosa oraria: Roewer, 1954, p. 238.

Hogna sibyllina: Roewer, 1954, p. 253.

Trochosomma oraria: Roewer, 1960, p. 847.

Ocyale oraria: McKay, 1973, p. 380.

MATERIAL EXAMINED

Western Australia: Abrolhos, Gun Island, 6.viii.1971, RJM, WAM 71–1676–7; Post Office Island, 8.vii.1971, RJM, E. Little, WAM 71–1678–9, North Island, 13.vii.1971. RJM, WAM 71–1680–4; WAM 71–1802–6, WAM 71–1991–2, WAM 71–1994; Australind on estuary foreshore, 22.x.1969, RJM, R. W. George, WAM 71–360–2; Dongara, 5.vii.1971, RJM, WAM 71–1666–75; WAM 71–1697–709, WAM 71–1801; Fitzgerald River Inlet, 15.vii.1970, RJM, R. Prince, WAM 70–3800–14, WAM 71–642; Fremantle at North Mole, 12.ix.1970, RJM, JG, WAM 70–217; Garden Island, viii.1966, D. S. Adair, WAM 69–844; Geraldton, 5.vii.1971, RJM, WAM 71–1690–6; Guilderton near Moore River mouth, 12.xii.1971, RJM, WAM 71–1993; Lancelin Island, 6.vii.1966, Aquinas College, WAM 71–771–3; Rockingham, 19.v.1971, RJM, WAM 71–1685; Windy Harbour, 21.i.1971, G. W. Kendrick, WAM 72–251.

DESCRIPTION (After L. Koch 1876)

Female C.L. 5·0 mm: Carapace light yellow-brown with yellow hair; a broad white lateral band serrated on its inner margin; a triangular white spot on the fovae, with a straight white line running to the PM; an oblique white stripe on the border between the head and the thorax; the sides of the head tinged white. Mandibles red-brown with yellowish-white hair; maxillae yellow-brown, honey-yellow anteriorly; labium dark red-brown. Abdomen dirty yellow-brown with yellowish-white hair; a lance-shaped spot, anteriorly white, posteriorly yellow, and with a black border, runs from the anterior of the dorsal surface to the middle of the abdomen; on each side of this spot are three white spots in a longitudinal row; the posterior half of the dorsal surface has an area with a deeply serrated brown to black border which reaches to the middle of the lance-shaped spot, in the middle of this area is an indistinct, light, transverse band behind which are two pairs of white spots. Palpi and legs yellow-brown with wide dark rings at the basal half of the patellae, the tip of the tibiae, and the middle and tip of the metatarsi; remainder of legs with white hair.

Anterior row of eyes straight, and wider than the second row; AM larger than the AL, a radius apart, the same distance from the PM, but closer to the AL; PM about a radius apart, and over a diameter from the PL which are only slightly smaller.

Chelicerae with three promarginal and three retromarginal teeth.

Male C.L. 4·0 mm: Carapace dark brown with brown hair and with a grey-white marginal band deeply serrated on its inner margin; a yellowish longitudinal median stripe runs from the posterior slope to the posterior part of the head; sides of head grey-white with the ocular quadrangle yellowish-grey; mandibles light yellow-brown with yellow-white hair; maxillae and labium brownish-yellow, black to brown on the basal half; sternum yellowish-white. Abdomen grey-white above and below; a brown median field above, which is indented on the sides, and spreads from the base to the commencement of the posterior slope where it tapers, has the posterior margin deeply cut, and the angles so formed are connected to a brown spot by an oblique brown line; in the middle of this field is a grey-white longitudinal stripe of the same colour followed by a white spot on either side; spinnerets yellow-brown. Legs and palpi similar to those of the female.

TABLE 1: EYE DIAMETERS AND INTERSPACES OF SPECIES OF THE GENUS *TROCHOSA* CONVERTED TO PERCENT OF THE TOTAL WIDTH OF THE FIRST ROW OF EYES

Species	Regd No.	Sex	C.L.	AM	AL	PM	PL	AM–AM	AM–AL	PM–PM	AM–PM	AL–PM
T. oraria	WAM 71–1991	♀M	4·8	22	17	36	34	9	6	24	7	9
	WAM 71–1992	♀M	4·4	24	16	37	33	10	6	22	6	8
	WAM 71–1993	♀M	6·0	22	17	37	34	10	6	23	9	10
	WAM 69–884	♀M	6·2	20	16	37	31	9	8	24	9	12
	WAM 71–1802	♀M	5·2	24	17	38	31	11	7	22	8	11
T. tristicula phegeia	WAM 71–1571	♀M	5·5	24	18	36	27	12	5	17	11	14
	WAM 71–1572	♀M	5·8	26	22	32	26	10	4	19	8	9
	WAM 71–164	♀M	4·5	22	16	32	27	5	6	18	11	14
	WAM 71–165	♂M	3·2	25	17	35	33	6	5	14	10	14
	WAM 71–166	♀M	5·3	24	15	35	25	6	7	15	11	12
T. tristicula tristicula	W5786	♀M	4·5	19	16	35	30	9	12	21	7	10
	W5786	♀M	4·1	19	18	39	33	6	11	22	9	12
	W5786	♀M	3·8	18	15	36	31	9	14	22	6	11
	W5786	♀M	4·3	19	18	35	30	9	13	22	8	11
	W5786	♂M	4·0	18	18	37	32	8	10	19	6	10
	W5786	♂M	4·0	20	19	36	33	10	12	21	9	12
	W5786	♂M	3·4	21	20	42	38	10	13	18	7	11
	W5786	♂M	4·0	17	15	37	29	10	12	21	6	9
T. expolita expolita	SYNTYPE	♂M	4·0	20	18	43	39	12	5	34	10	12
	W5732	♂M	3·4	19	16	48	40	13	6	37	13	13
	S22	♀M	2·4	17	15	50	41	13	7	37	15	15
T. expolita impedita	WAM 71–423	♀M	3·8	19	22	46	38	11	4	36	13	11
	WAM 71–424	♀M	4·0	18	21	40	36	13	3	36	12	9
	WAM 71–548	♀M	4·5	18	18	42	34	15	3	35	13	10
	WAM 71–425	♂M	4·7	19	21	43	36	14	5	36	17	15
	WAM 71–426	♂M	4·0	19	22	47	39	11	5	38	14	14
	WAM 71–427	♂M	3·9	19	19	43	32	14	3	35	14	14
	WAM 71–428	♂M	4·5	17	21	41	37	12	3	37	16	12
	WAM 71–429	♂M	4·3	18	18	45	37	11	5	37	17	14
T. martensii	N.M.	♀M	6·3	20	17	29	26	10	6	29	20	19
	N.M.	♀M	5·5	20	17	31	26	13	7	27	18	25
	N.M.	♀M	5·6	20	16	30	26	13	6	32	16	24
T. exculta	LECTOTYPE	♀M	7·2	22	17	30	26	12	6	30	18	20
T. alboguttulata	HOLOTYPE	♀M	4·7	23	15	38	33	9	8	23	9	9
	S24	♀M	3·5	25	16	33	31	11	9	22	11	6
	S24	♀M	3·4	25	18	35	30	8	4	21	9	8
	S23	♀M	4·4	25	20	40	35	6	4	17	8	7
T. glarea	HOLOTYPE	♀M	3·5	24	17	36	32	10	5	19	7	6
T. wundurra	HOLOTYPE	♀M	4·5	21	16	32	30	9	7	25	5	7

Anterior row of eyes barely wider than the second; the eyes and their interspaces otherwise similar to those of the female.

VARIATION: *Trochosa oraria* is quite variable in colour. Specimens taken on the white beach sands away from piles of dead seaweed may have the colour pattern as described by Koch, or may have the abdomen very pale cream with two inverted V-shaped dark marks anteriorly on the dorsal surface followed or separated by a light longitudinal stripe to about the middle of the abdomen where it is bordered on each side by a white spot preceded by a dark brown irregular mark; two or three short forwardly pointing oblique brown bars may follow or be broken into spots or blotches. Some specimens taken from banks of dry brown seaweed (mainly *Posidonia)* may be a very dark red-brown colour matching that of the seaweed, with a pale marginal band on the carapace and the abdomen marked above by a pale anterior longitudinal stripe reaching the middle of the abdomen with rows of white dots on either side, frequently followed more posteriorly by two large pale to white oval spots; the sides of the abdomen may be brown or pale-brown with scattered black-brown spots. Extreme examples of each colour form appear quite distinct but numerous intermediate colour patterns may be found where the beach is littered with separate heaps of rotting seaweed.

Eye measurements were recorded for 5 specimens; each measurement is given below in Table 1 as a percent of the total width of the first eye row.

Variation in the ventral spines of the tibia of the first legs was as follows: 2+2+2 both legs in 3 females, 5 males, 2+2+0 both legs in 2 females, 2+2+2 (LHS) 2+1+2 (RHS) in 1 male, 1+2+0 (LHS) 2+2+0 (RHS) in 1 female. Tibia 4 with the dorsobasal bristle absent in all specimens.

Variation in the shape of the epigynum is illustrated in Figure 1B, D, F and the internal genitalia of WAM 71–1991 and WAM 71–1993 is shown in Figure 1C, E. The male palpal organ is illustrated in unexpanded and partly expanded conditions in Figure 1G, H.

SIZE RANGE: Mature females C.L. 4·2 to 6·8 mm. Mature males C.L. 3·5 to 4·5 mm.

DIAGNOSIS: *Trochosa oraria* is characterised by the shape of the epigynum, the anterior row of eyes wider than the second row, and restricted habitat. *Lycosa sibyllina* was described from the brown form of *Trochosa oraria* and is a junior synonym.

LIFE HISTORY

Mature females have been collected from May to January and are most common in July. Mature males have been found in July and October. Courting males were found at Dongara, Geraldton and the Abrolhos Islands during July. One female carrying young was collected at Guilderton in December.

The courtship behaviour of the male consists of palpal drumming, and a slow walk with the fore-legs held horizontally forwards, lifted in a slow alternate fashion, and vibrated fairly rapidly. Males from Dongara responded to the pheromone of females from North Island, Abrolhos, and a very dark brown male responded to the pheromone of a pale sand inhabiting female. One mature male from Green Head, north of Jurien Bay responded to a mature female from North Island, Abrolhos, and copulated with the female on 10 September 1971; this female was maintained in the laboratory until it died in late October.

HABITAT

Three specimens were collected on the damp sands of the estuary at Australind, all other specimens were taken from white beach sands or piles of rotting seaweed on the beach. *Trochosa oraria* shelters under seaweed or detritus on the beach or may shelter under the broad leaves of *Arctotheca nivea* on coastal sand dunes. Occasional specimens may be collected from limestone rubble on the beach.

BURROW

Simple retreats are built among strands of seaweed, or open burrows 4 mm in diameter and descending some 40 to 50 mm into the slope of coastal dunes may be constructed. This species wanders at night and may be located some distance from the burrow. When approached *Trochosa oraria* will withdraw the legs under the body and crouch low on the sand, or may retreat head first into the interspaces of the seaweed banks.

DISCUSSION

Roewer (1954) placed *T. oraria* into the genus *Crocodilosa* but after examining the type placed it in *Trochosomma.* Guy (1966) considers *Trochosomma* a synonym of *Crocodilosa* a subgenus of *Ocyale.* McKay (1973) placed *T. oraria* provisionally into *Ocyale.*

Ocyale and *Crocodilosa* have the length of the legs in decreasing order 4, 3, 1, 2, and are therefore quite distinct from *Trochosa* with the legs in order of decreasing length 4, 1, 2, 3. Bonnet (1959, p. 4701) retains *annulipes* in the genus *Trochosa* and from the description of this species given by Roewer (1960, pp. 852–3) I have no hesitation in relegating *Trochosomma* Roewer 1954 to the synonomy of *Trochosa*. Roewer erected *Trochosomma* on the basis that the distance AM–AL is less than the distance AM–AM whereas in *Trochosa* AM–AL = AM–AM. In *Trochosa oraria* AM–AL is less than AM–AM but in *T. tristicula phegeia* the distance AM–AM may be more or less than the distance AM–AL, and this character is therefore not regarded as consistent within all species of *Trochosa*.

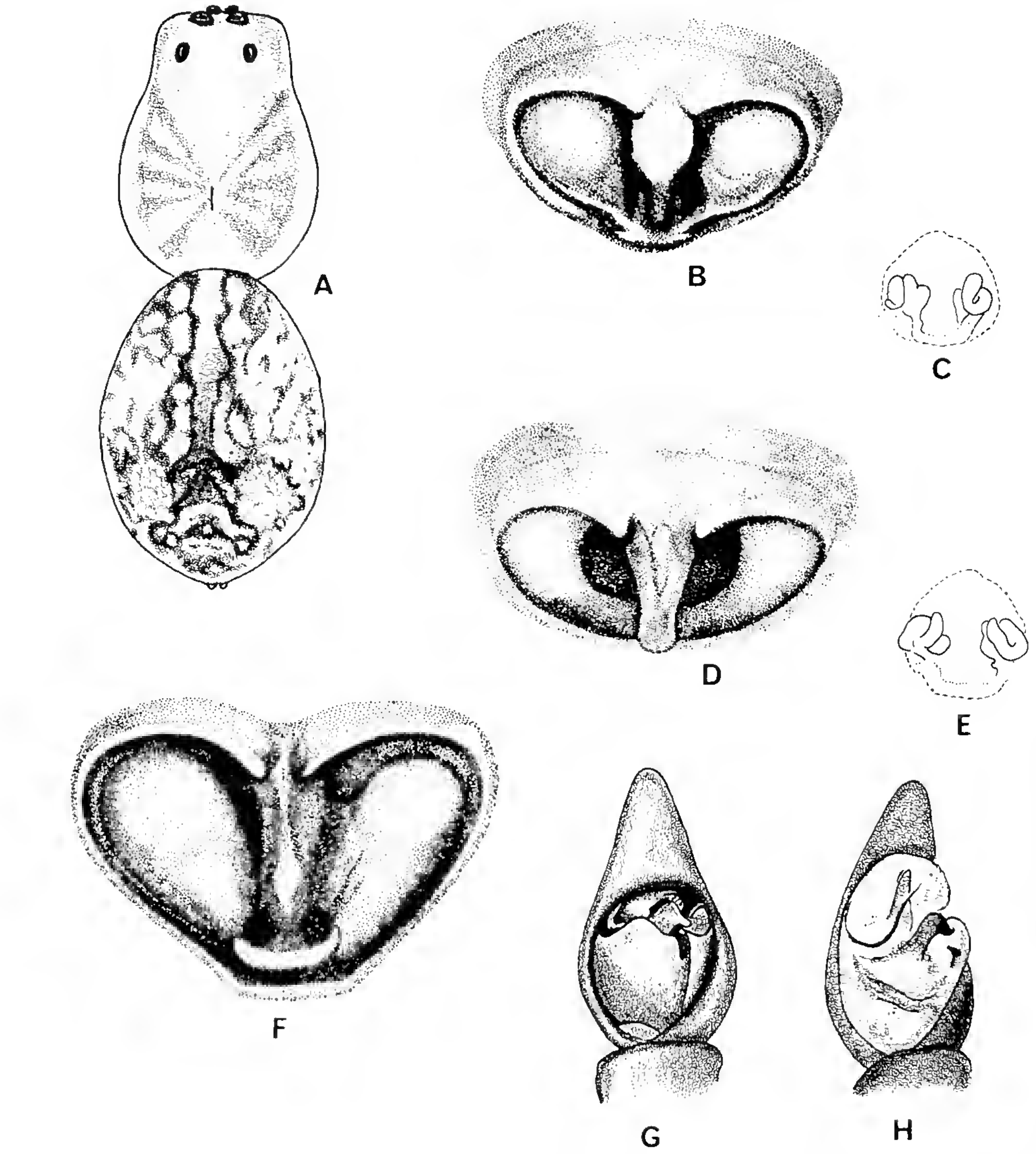


FIG. 1: *Trochosa oraria*. A, mature female; B, epigynum of WAM 70–217; C, internal genitalia of WAM 71–1991; D, epigynum of WAM 69–844; E, internal genitalia of WAM 71–1993; F, epigynum of WAM 72–251; G, male palpal organ of WAM 71–1922; H, male palpal organ of WAM 71–1922 expanded.

Trochosa tristicula phegeia (Simon 1909)
(Fig. 2A–H, Q)

Lycosa phegeia Simon, 1909, pp.189–90, fig. 8, Cannington, Western Australia; Rainbow, 1911, p. 271; Bonnet, 1957, p. 2658; Rack, 1961, p. 38.
Triccosta phegeia: Roewer, 1954, p. 298; 1960, p. 867.
Tricca phegeia: McKay, 1973, p. 381.

MATERIAL EXAMINED

SYNTYPE. Western Australian Museum labelled 'Hambg. S.W. Austral. Exp. 1905. 123 Cannington. 28.ci' dried and pinned, now in spirit.

OTHER MATERIAL: Western Australia: Australind on estuary foreshore, 22.x.1969, RJM, R. W. George, WAM 71–375–6; Bibra Lake, 4.xi.1960, BYM, WAM 71–1572; Brentwood Swamp, 6.xii.1970, RJM, WAM 71–164–9; Chinocup Reserve, 6 km east of Pingrup, 11–17.ii.1972, HB, WAM 72–331; Churchman's Brook, 23.x.1952, BYM, WAM 71–1571; Deepdene, 15.xi.1969, M. and E. Archer, WAM 71–510, WAM 71–1570; Pemberton at Beedelup Falls, 20.ii.1969, RJM, WAM 71–443; Walpole, near Point Nuyts, 17.ii.1969, RJM, WAM 69–876.

DESCRIPTION (After Simon 1909)

Male. Carapace tawny-red with sparse ash-grey to white hair, with a narrow white marginal band; space between eyes black; mouth parts dark chestnut; sternum tawny-red. Abdomen dark, ash-grey in middle, with the sides covered by white hair, and anteriorly marked by a short brick-coloured longitudinal band with three or four rows of very small white dots laterally. Undersurface deep ash-grey to yellow with the middle a little darker and irregularly banded with white hair. Legs tawny-red, a little darker and more rust-coloured towards the extremities.

Anterior row of eyes slightly recurved, slightly wider than the second row; eyes almost equidistant, the AM at least a third larger than the AL; AL further from the edge of the clypeus than from the PM; PM about a radius apart.

Female. Larger in size. Anterior row of eyes almost straight. Epigynum as long as wide, bluntly rectangular with a dark yellow egg shaped depression.

VARIATION: Some specimens may have the carapace dark brown to almost black without a marginal band. The abdomen has a lighter longitudinal stripe on the anterior dorsal surface in all specimens; the venter is usually brownish with about three or four longitudinal darker stripes. Legs uniform brown in all specimens. Anterior row of eyes straight or slightly recurved, and wider than the second row. Chelicerae with three to four promarginal teeth, the middle one largest; three retromarginal teeth about equal in size.

The eye measurements for WAM 71–1571, M, expressed in units are AM:AL:PM:PL = 13·5:10:20:15; distance AM–AM 7, AM–AL 3, AM–PM 6; AL–PM 8, PM–PM 9·3. Clypeus to AM 10. Width of the first eye row 56, width of second eye row 47. Eye diameters and interspaces given in Table 1, the first eye row wider than the second in ratio 72:60, 78:64, 63:51, 48:43.

Variation in the shape of the epigynum is illustrated (Fig. 2A, B, D). The internal genitalia is illustrated in Figure 2H. The shape of the median apophysis and embolic guide of the mature male is given in Figure 2C, E, F, G. The shape of the apical spermatheca from the side is given in Fig. 2Q.

SIZE RANGE: Mature females C.L. 2·7 and 5·8 mm. Mature males C.L. 2·5 to 3·2 mm.

DIAGNOSIS: First row of eyes wider than the second row; epigynum with expanded lateral arms, and the male palpal organ with a curved median apophysis bearing a spine on the concave side (Fig. 2C, F, G). Spermathecae of female with a curved fertilization tube situated on ventral surface.

LIFE HISTORY

Mature females have been collected during October to February, and mature males are common in December. Females with egg cocoons were captured at Bibra Lake in November, and at Walpole in February. This species is commonly associated with *Lycosa pullastra, Trochosa expolita impedita,* and occasionally *Trochosa oraria.*

HABITAT

Trochosa tristicula phegeia inhabits the damp or wet margins of swamps, lakes, streams and estuaries. One specimen was found at a freshwater seepage area on the beach at Walpole.

BURROW

A shallow burrow or retreat is excavated below stones or rotting vegetation. Most specimens are found wandering near grass or rushes.

DISCUSSION

Trochosa tristicula phegeia and *T. tristicula tristicula* are regarded as subspecies due to the similarity in coloration, eye pattern, epigynum and male palpal organ. Both subspecies inhabit damp situations and are at present known from geographically isolated populations.

Both subspecies evidence variation in the shape of the epigynum and the male palpal organ, and some specimens of both populations lack the converging dark bars on the ventral surface of the abdomen. The male of the eastern Australian subspecies differs from Western Australian specimens in lacking a small spine on the concave side of the median apophysis. Females of both subspecies have the epigynum variable in shape. The western subspecies lacks a median guide in some females, and has a well developed curved fertilization tube on the ventral surface of the apical spermathecae.

Additional material is required, and a series of male palpal organs from both subspecies should be scanned by electron microscope. Cross-mating both subspecies may indicate the closeness of the relationship and determine whether behavioural or genetic isolating mechanisms have evolved.

Trochosa tristicula tristicula (L. Koch 1877)
(Fig. 2J–P, 3A)

Lycosa tristicula L. Koch, 1877, pp. 892–93, pl. 77, figs. 2, 2a, Sydney, New South Wales; Rainbow,, 1911, p. 273.

Trochosula tristicula: Roewer, 1954, p. 304; 1960, p. 859; 1961, p. 4.

Trochosa tristicula: McKay, 1973, p. 381.

MATERIAL EXAMINED

HOLOTYPE: Not examined; location unknown.

OTHER MATERIAL: Queensland: Amamoor Creek via Amamoor, 29.xi.1974, GBSRM, 5 ♂M 1 ♀M, QM W6890; Bunya Mountains, 1.vi.1975, GBSRM 1 ♂M, QM W5790, 30.iii.1975, GBSRM, 1 ♀M, QM W5792, 12.i.1975, GBSRM, 1 ♀M, QM W5802, 30.iii.1975, GBSRM, 1 ♀M 1 ♂M, QM W5807; Bunya Mountains at Saddletree Creek, 29.iii.1975, GBSRM, 1 ♀M, QM W5805; Bunya Mountains National Park near Daranbayan picnic grounds, 4.ix.1974, R. Raven, B. Jamieson, 4 ♀M 4 ♂M, QM W5786; Casy Creek via Imbil, 9.xi.1974, GBSRM, 5 ♂M, QM W5900, 31.xii.1974, GBSRM, 1 ♀M 4 ♂M, QM W5901, 27.iii.1975, GBSRM, 1 ♀M, QM W5990; Coeran Plateau via Traverston, 28.iii.1975, GBSRM, 1 ♂P, QM W5902; Conondale at Bouloumba Creek, 29.xi.1974, GBSRM, 1 ♂M, QM W5933, 26.x.1974, GBSRM, 2 ♂M, QM W5936, 19.iv.1975, GBSRM, 1 ♂M, QM W5937, 23.viii.1975, GBSRM, 2 ♂M, QM W5938, 22.ii.1975, GBSRM, 3 ♀M 4 ♂M, QM W5939, 19.iv.1975, GBSRM, 1 ♀M, QM W5944; Cooloola–Teewah Creek, 13.vii.1973, R. Raven, 1 ♀M, QM W5784; Cunninghams Gap, 28.xii.1974, GBSRM, 1 ♂M, QM W5934; Dingo Creek via Traverston, 31.xii.1974, GBSRM, 1 ♀M 3 ♂M 1J, QM W5894, 27.iii.1975, GBSRM, 2 ♀M 1 ♂M 1J, QM W5895, 13.viii.1975, GBSRM, 1 ♂M, QM W5896, 9.xi.1974, GBSRM, 1 ♂M, QM W5898; Emuvale, at Bald Mountain, 17.xi.1974, GBSRM, 6 ♀M 7 ♂M, QM W5935; Gold Creek via Imbil, 31.xii.1974, GBSRM, 1 ♂M, QM W5889, 27.iii.1975, GBSRM, 5 ♀M 12 ♂M 1 ♀P 1 ♂P, QM W5891, 9.xi.1974, GBSRM, 3 ♀M 6 ♂M 1J, QM W5892, 16.vi.1975, GBSRM, 1 ♀M 2 ♂M 1 ♀P 1 ♂P, QM W5893, 23.viii.1975, GBSRM, 1 ♀M 1 ♂M, QM W5897; Granite Creek, Bulburin State Forest, 3.v.1975, GBSRM, 1 ♀M 2 ♂M 1 ♀P 1 ♂P 2J, QM W5881, 5.x.1974, GBSRM, 5 ♀M 2 ♂M 2 ♂P 5J, QM W5883, 29.xii.1974, GBSRM, 6 ♀M 3 ♂M 1 ♂P 6J, QM W5880, 3.v.1975, GBSRM, 1 ♀M 3 ♂M 2 ♀P 2J, QM W5885; Little Yabba Creek via Kenilworth, 27.iii.1975, GBSRM, 1 ♂M, QM W5798, 29.xii.1974, GBSRM, 1 ♀M 1 ♂M, QM W5799, 16.vi.1975, GBSRM, 1 ♀M, QM W5800; Mary Cairncross Park via Maleny, 16.vi.1975, GBSRM, 1 ♀M, QM W5791, 27.iii.1975, GBSRM, 1 ♀M, QM W5794, 9.xi.1974, GBSRM, 1 ♂M 2J, QM W5795, 27.iii.1975, GBSRM, 1 ♂M, QM W5797, 9.xi.1974, GBSRM, 1 ♀M 1 ♂M 3J, QM W5801, 9.xi.1974, GBSRM, 1 ♀M, QM W5806; Mount Cabinet via Jimna, 30.ii.1974, GBSRM, 1 ♂M, QM W5808; Mount Tenison Woods via Mount Glorious, 12.xi.1975, GBSRM, 1 ♂M, QM W5947; Numinbah Arch, Nerang Valley, 14.xii.1974 GBSRM, 1 ♂P, QM W5882; O'Reillys Guest House, Lamington, 11.iv.1976, GBSRM, 1 ♀M, QM W6891; Rathdowney at Philp Farm, Levers Plateau, 4.iii.1976, GBSRM, 1 ♀M 1 ♂M, QM W6892; Repeater Station, Springbrook, 13.x.1975, GBSRM, 1 ♀M, QM W5884; Rosen's Lookout, Beachmont, 14.xii.1974, GBSRM, 1 ♂M, QM W5899; The Palms, via Cooyar, 25.i.1976, GBSRM, 4 ♂M, QM W6895, 1 ♂M, QM W6898, 14.viii.1976, GBSRM, 1 ♂M, QM W6896, 1.v.1976, GBSRM, 1 ♂M, QM W6897, 17.x.1976, GBSRM, 2 ♂M, QM W6899; Tungi Creek, Jimna, 10.xi.1974, GBSRM, 1 ♂M, QM W5879; Water Park Creek, Corio Bay, 19.vii.1974, Littoral Society of Queensland, 1 ♂M, QM W5785; Wrattens Camp via Widgee, 29.xii.1974, GBSRM, 4 ♂M, QM W5985, 28.iii.1975, GBSRM, 5 ♀M 2 ♂M, QM W5986, 10.xi.1974, GBSRM, 1 ♂M, QM W5987, 2 ♀M 5 ♂M 1 ♂P, QM W5988. New South Wales: Brindle Creek,

FIG. 2: *Trochosa tristicula phegeia.* A, epigynum of a female from Deepdene Cliff, W.A.; B, epigynum of female from Brentwood, W.A.; C, F, G, median apophysis of males from Brentwood, W.A.; D, epigynum of female from Walpole, W.A.; E, embolus and embolic guide of male from Brentwood; H, internal genitalia of female from Churchman's Brook, W.A.; Q, lateral view of apical spermathecae of female from Brentwood, W.A.

Trochosa tristicula tristicula. J, epigynum of female from Bunya National Park, Qd.; K, median apophysis of male from Corio Bay, Qd.; L, median apophysis of male from Bunya Mountains, Qd.; M, internal genitalia; N–P, lateral view of apical spermathecae of 3 females from Queensland.

Trochosa alboguttulata. I, epigynum of female from Cooloola, Qd.

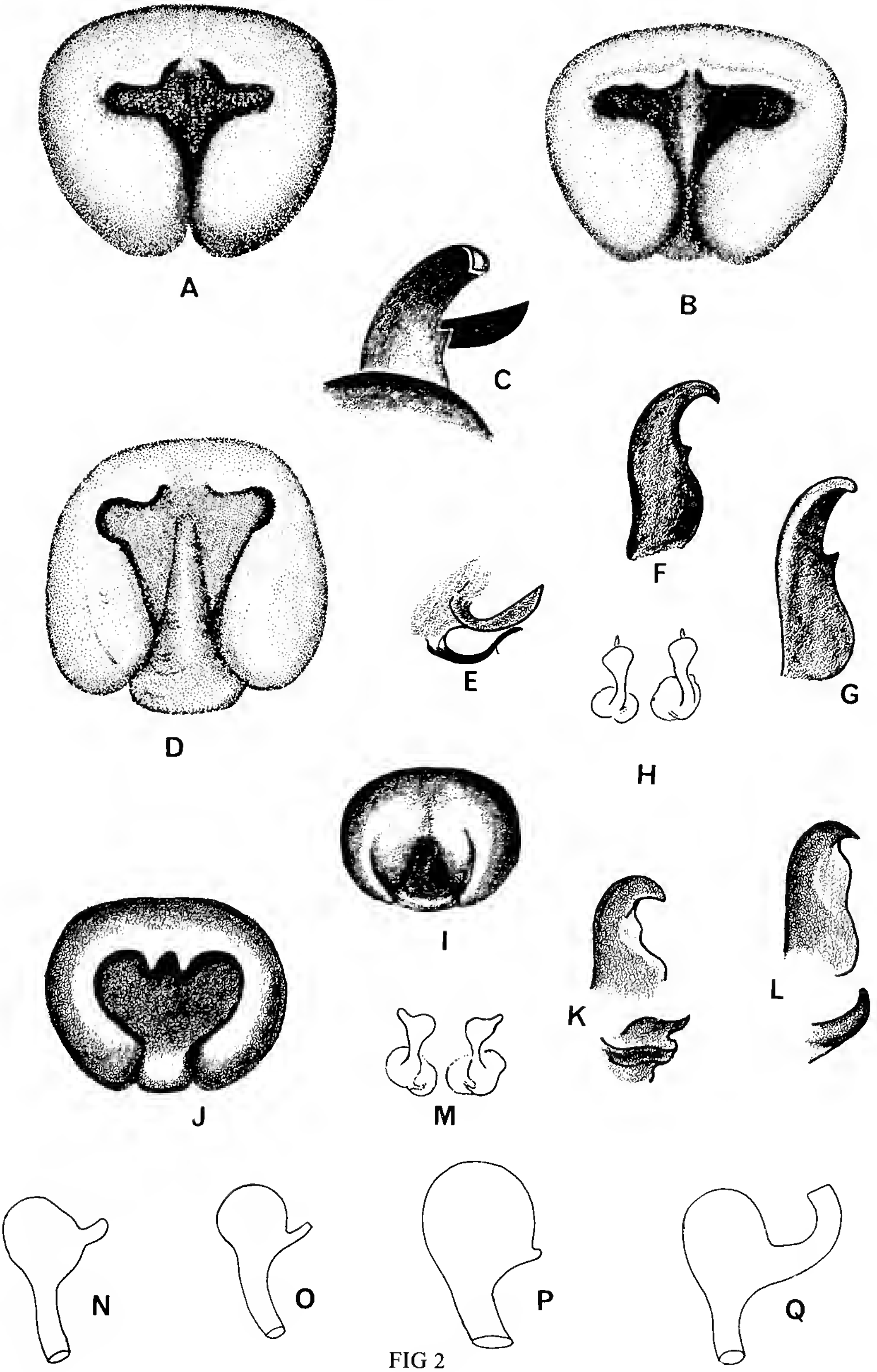


FIG 2

Wiangaree, 23.iii.1975, GBSRM, 1 ♀M 1 ♂M, QM W5989; Mount Nardi via Nimbin, 2.viii.1975, GBSRM, 1 ♀M 7 ♂M 1J, QM W5803, 1 ♂M, QM W5809; Mount Warning, 7.iii.1976, GBSRM, 1 ♂M, QM W6893, 7.xi.1976, GBSRM, 1 ♂M, QM W6894; Nightcap Range via Dunoon, 16.xi.1974, GBSRM, 1 ♀M 1 ♂M, QM W5903, 23.iii.1975, GBSRM, 1 ♀M, QM W5904; Tweed Lookout, Wiangaree State Forest, 16.ii.1974, GBSRM, 1 ♀M 2 ♂M, QM W5789, 27.xii.1974, GBSRM, 2 ♀M 5 ♂M 1J, QM W5793, 2 ♀M 1 ♂M, QM W5804, 23.iii.1975, GBSRM, 3 ♂M, QM W5796.

DESCRIPTION (after Koch 1877)

Female. Carapace dark red-brown with black-brown hair; parallel to the lateral margin is a narrow brownish-yellow band, serrated above; on either side of the lateral declivity are two short radiating striae; the boundary between the cephalic and thoracic part is indicated by a narrow stripe; a longitudinal stripe commences at the posterior declivity and stretches as far forward as the PL eyes, on each side of this stripe are two short longitudinal cephalic striae; paturon dark red-brown, lighter distally; maxillae and labium red-brown; sternum red-brown. Abdomen covered with yellow brown hair above and on the sides; a narrow lance-shaped brownish-yellow spot bordered with black at the anterior end dorsally; this spot does not reach the centre. Undersurface brownish-yellow with two blackish longitudinal stripes which converge towards the rear; between these a third blackish longitudinal stripe which commences immediately behind the epigynum but does not reach the spinnerets. Palpi and legs red-brown.

Anterior row of eyes recurved and considerably broader than the second row; eyes equidistant; the AM considerably larger than the AL; PM a radius apart.

Male: Similar in coloration to female.

VARIATION: Carapace light brown to dark brown with faint to very conspicuous brown or black lines or wedge-shaped marks radiating out from the centre of the carapace. The venter of the abdomen may be pale brown to dark brown without a pattern; brown with a light brown or very pale triangular area with darker blotches in the centre; pale brown with a vague W-shaped mark; pale brown with a darker brown triangular mark reaching the spinnerets; pale with two darker bars converging towards the spinnerets or fusing just before the spinnerets. Legs uniform brown in some specimens but normally banded or almost ringed with dark brown blotches or bands.

Chelicerae with three retromarginal teeth.

Male palpal organ with the median apophysis lacking a small spine on the concave side (Fig. 2K, L). Epigynum of female with a posterior median guide (Fig. 2J). Apical spermathecae with short fertilization tube on ventral surface (Fig. 2M–P).

The eye measurements of eight specimens are given below in Table 1 as a percent of the total width of the first eye row. Upper tangent of first eye row slightly procurved, wider than the second row in ratio 85:79, 80:77, 78:71, 85:78, 91:81, 80:73, 71:66, 83:79.

SIZE RANGE: Mature females C.L. 3·3 to 4·9 mm. Mature males C.L. 2·9 to 4·3 mm.

DIAGNOSIS: First row of eyes wider than second row; epigynum with the anterior margin of the depression with two small points; male palpal organ with a curved median apophysis without a spine on the concave side; legs normally banded or ringed with black-brown. Apical spermathecae with a small fertilization tube on the ventral or ventro-lateral surface.

LIFE HISTORY

Mature males and females have been collected throughout the year. The breeding season is unknown.

HABITAT

Forested areas, including rainforest, under logs, leaves and bark and near the margins of swamps and creeks.

BURROW

Unknown

DISCUSSION

See under *Trochosa tristicula phegeia.* This subspecies may be confused with *Trochosa alboguttulata* but the latter species has the epigynum with a well developed median guide and no points or cusps on the inner margin anteriorly. *T. alboguttulata* appears to be confined to sandy soils whereas *T. tristicula tristicula* is normally found on the heavy loams of forested areas.

Trochosa expolita expolita (L. Koch 1877)
(Fig. 3B–F, J–M)

Lycosa expolita L. Koch, 1877, pp. 917–19, pl. 79, figs. 4, 4a, 5, 5a, Port Denison (=Bowen), Brisbane, Queensland; Hogg, 1900, p. 77, Macedon, Victoria; Rainbow, 1911, p. 267; Bonnet, 1957, p. 2641.

Avicosa expolita: Roewer, 1954, p. 236.
Schizocosa expolita: McKay, 1973, p. 381.

MATERIAL EXAMINED

SYNTYPE: British Museum (N.H.), BM 1919.9.18. 337, ♂M, C.L. 4·0 mm, Brisbane.

OTHER MATERIAL: Queensland: Brisbane, Museum grounds, Bowen Hills, 10.vii.1975, RJM, 1 ♂M, QM W5732; Cabbage Tree Creek, Sandgate, from wasp nest, 1.i.1976, R. Raven, 33J, QM W5726; Emu Park via Rockhampton, 28.xi.1973, RJM, 1 ♀M, QM W5724; The Gap, Brisbane, 3.i.1973, RJM, 1 ♀M, QM W5734, 1.iv.1974, RJM 1 ♂M, QM S21, 28.iii.1974, 1 ♀M, QM S22.

Victoria: Eltham, xii.1923, S. Butler, 1 ♀M 1 ♂M, NM; Nunawading, 2.ii.1954, A. Neboiss, 1 ♀M 1J, NM.

DESCRIPTION (After Koch 1877)

Female: Carapace dark, covered with greyish-yellow hair; mandibles brown to black with yellowish hair; maxillae, labium and sternum dark red-brown, the latter with greyish-yellow hair. Abdomen basically black, with greyish-yellow hair, a lighter longitudinal stripe runs from the anterior base to the spinnerets and suddenly widens in its posterior half; on either side of this stripe posteriorly is a row of white dots. The femoral joint of the palpi and the femora of the legs brown-yellow, the remaining joints reddish-brown; on the femora of the third and fourth legs are two indistinct darker rings; the tips of all femora black; patellae shaded black above; tibiae of both anterior pairs of legs with three black spots below, those of the third and fourth pairs with two black rings; the terminal half of the metatarsi of the first and second pairs black, on these joints of the posterior pairs are two black rings; the lighter parts on the legs are covered with yellowish hair.

Anterior row of eyes procurved, not as broad as the second; AM slightly larger and further apart than the AL, almost adjoining the latter; AM about a diameter from the PM; PM over a diameter apart and almost twice this distance from the PL.

Male: Carapace dark, covered with greyish-yellow hair, and with a broad lighter coloured lateral band; mandibles and sternum black; maxillae and labium red-brown, lighter coloured at the anterior margin. Abdomen covered with black hair above and with a continuous longitudinal band covered with grey-yellow hair; on either side of the band in the posterior half, are two forwardly directed short branches; sides and ventral surface with yellow-brown hair. Palpi reddish-brown, the palpal organs darker. Legs reddish-brown; femora of the two anterior pairs black below and with a black, interrupted longitudinal stripe above, and posteriorly with black longitudinal spots; femora of the third legs with three black rings; femora of the fourth legs with three black transverse spots anteriorly and one black terminal spot posteriorly; tibiae and metatarsi with black spots; the hair on the legs greyish-yellow.

Anterior row of eyes slightly procurved, with the eyes about equal in size; AM about a diameter apart and a little further from the PM; AM about a radius from the AL; PM not very large, only slightly larger than the PL, and about a diameter apart. Three promarginal and three retromarginal cheliceral teeth.

VARIATION: The carapace is frequently dark brown with a well defined broad pale brown to cream longitudinal median stripe that extends to the posterior margin where it tapers to a point; a well defined lateral band, pale brown to cream in colour, extends around the margin of the thoracic slopes of the carapace but does not join posteriorly; lateral slopes of the carapace with black to black-brown wedge-shaped marks terminating just before or projecting slightly into the lateral band. Abdomen above with the anterior half lighter than the posterior half and with a very distinct white, cream or yellowish lanceolate longitudinal stripe commencing at the anterior slope and reaching the middle of the abdomen where it tapers to a point or blends imperceptibly with the broader posterior median longitudinal pale bar that may arise anteriorly in the pale area to continue to the base of the spinnerets or commence at about the middle of the abdomen behind a very conspicuous black-brown somewhat diamond-shaped mark that is bisected by the anterior pale stripe; the posterior median longitudinal bar is outlined by black-brown pigment that may extend over the posterior half of the abdomen or be confined to the margins of the posterior pale bar where it forms a somewhat parallel black-brown bar with an irregular lateral edge breaking up into blackish streaks extending anteriorly or laterally over the posterior half of the abdomen. The black-brown bisected diamond-shaped mark situated just before the middle of the abdomen may be longer than broad or broader than long and appear as two triangles with the bases on the margin of the pale anterior median longitudinal stripe. Legs light brown; the femora with dark brown lateral stripes or the complete ventral half dark brown; anterior patellae with a dark brown spot on each side, becoming reduced to brown smudges on the lateral tips of the posterior patellae; distal tips of femora with dorsolateral dark brown spots. The legs may have the above markings very distinct or quite faint. Undersurface of abdomen without markings or with a few small brown scattered spots laterally.

Anterior row of eyes slightly procurved (recurved in Koch 1877), shorter than the second row in ratio 46:61, 62:79, 49:58. Eye measurements for the syntype and two specimens are given below in Table 1 as a percent of the width of the first row of eyes.

Tibia of fourth leg with a dorsobasal bristle.

SIZE RANGE: Mature females C.L. 2·3 to 4·0 mm. Mature males C.L. 3·4 to 4·0 mm.

DIAGNOSIS: First row of eyes narrower than the second row; a distinctive epigynum; a dark brown to black diamond-shaped mark bisected by a longitudinal pale stripe on the dorsal surface of the abdomen. The median apophysis of the male is almost straight, gently curved or bent, but not hook shaped.

LIFE HISTORY

Mature females are found throughout the year and males are common from April to July. *T. expolita expolita* is active throughout the day and night.

HABITAT

Abundant on short grass, pastures and suburban lawns.

BURROW

A shallow retreat is constructed among grass roots.

DISCUSSION

See *Trochosa expolita impedita.*

Trochosa expolita impedita (Simon 1909)
(Fig. 3G–I, N–O)

Lycosa impedita Simon, 1909, pp. 187–88, fig. 6, Goosebery Hill (= Gooseberry Hill), Western Australia; Rainbow, 1911, p. 269; Bonnet, 1957, p. 2646; McKay, 1973, p. 379; 1974, pp. 10, 11, 12.
Allocosa impedita: Roewer, 1954, p. 206.

MATERIAL EXAMINED

HOLOTYPE: Not examined; location unknown.

OTHER MATERIAL. Western Australia: Australind at estuary foreshore, 22.x.1969, RJM, R. W. George, 1J, WAM 71–374; Bunbury Highway at Ludlow, 10.ix.1961, BYM, 1 ♀M, WAM 71–1565; City Beach Primary School, 16.ix.1968, I. Eliot, 1 ♀M, WAM 69–857, 1 ♀M 2 ♂M 1 ♀P, WAM 69–858–61; Collie, 23.x.1961, BYM, 1 ♀M, WAM 71–1566; Pinjarra, 10.ix.1961, BYM, 1 ♀M 1J, WAM 71–1567–69; Rossmoyne, Canning River, RJM, ix.1968, 1 ♀M 4 ♀M, WAM 69–846–50, xi.1968, 2 ♂M 1J, WAM 69–862–64, 1 ♀M, WAM 69–866, 9.xi.1968, 1 ♀M, WAM 69–870, x:1969, 1 ♀M 1 ♂M, WAM 71–706–07, x.1968, 3 ♀M 2 ♂M 2 ♂P, WAM 71–99–105, viii.1970, 1 ♀M, WAM 71–131, ix.1970, 2 ♂M, WAM 71–141–42, x.1970, 1 ♀M 3 ♂M, WAM 71–147–50, 12.i.1971, 1 ♂M, WAM 71–259, 4.xi.1970, 1 ♀M, WAM 71–260, 7.i.1971, 2 ♂M, WAM 71–261–62, xi.1970, 4 ♀M 8 ♂M 1 ♀P 1 ♂P, WAM 71–423–36, 4.xi.1970, 1 ♀M, WAM 71–548, 25.x.1970, 1 ♀M, WAM 71–549.

South Australia: Waite Institute, Claremont, 22.ix.1975, R. Cook, 1 ♂M 1 ♀P, SAM ARA535.

DESCRIPTION (After Simon 1909)

Female: Carapace black with a few white hairs towards the edge; a wide, golden, longitudinal, median band, pointed posteriorly; chelicerae dark chestnut with a few deep golden bristles; mouth parts and sternum black with a few black bristles and the layers at the top reddish-tinged.

Abdomen somewhat black above and covered with white hair; on the posterior half is a golden longitudinal band, rather narrow, and with a long point. Undersurface paler with a few white hairs, the belly with abundant golden hair, and irregular dark bands.

Legs deep yellowish-red, darker towards the extremities; femora with three black rings that are frequently broken; tibiae partly black-coloured and ringed.

Anterior row of eyes slightly curved forwards; AM not or barely larger than AL and are a little further from each other than from the AL; AL not much further from the edge of the clypeus than from the PM; PM about a diameter apart.

Epigynum twice as wide as long, semi-circular, and divided by a reddish, flat, wide, parallel-sided diaphragm; the epigynum is imprinted on both sides and is set apart by a thick slanting reddish edge.

Male: Similar to *T. expolita expolita.*

VARIATION: Similar to that of *Trochosa expolita expolita;* both sexes may have the legs uniformly coloured, and three converging dark bars may be present or absent on the ventral surface of the abdomen. Eye measurements were recorded for 8 specimens; each measurement is given below in Table 1 as a percent of the total width of the first eye row.

Variation in the shape of the epigynum is illustrated in Figure 3H–I, and the internal genitalia of WAM 71–423 is shown in Figure 3G.

The hook-like median apophysis and curved embolic guide of the male palpal organ of WAM 69–846 is illustrated in Figure 3O.

SIZE RANGE: Mature females C.L. 2·2 to 4·8 mm. Mature males C.L. 2·6 to 4·9 mm.

DIAGNOSIS: First row of eyes slightly narrower than the second row, a distinctive epigynum, and a dark brown to black diamond-shaped mark bisected by a longitudinal pale stripe on the dorsal surface of the abdomen. The median apophysis of the male palp is hook-shaped.

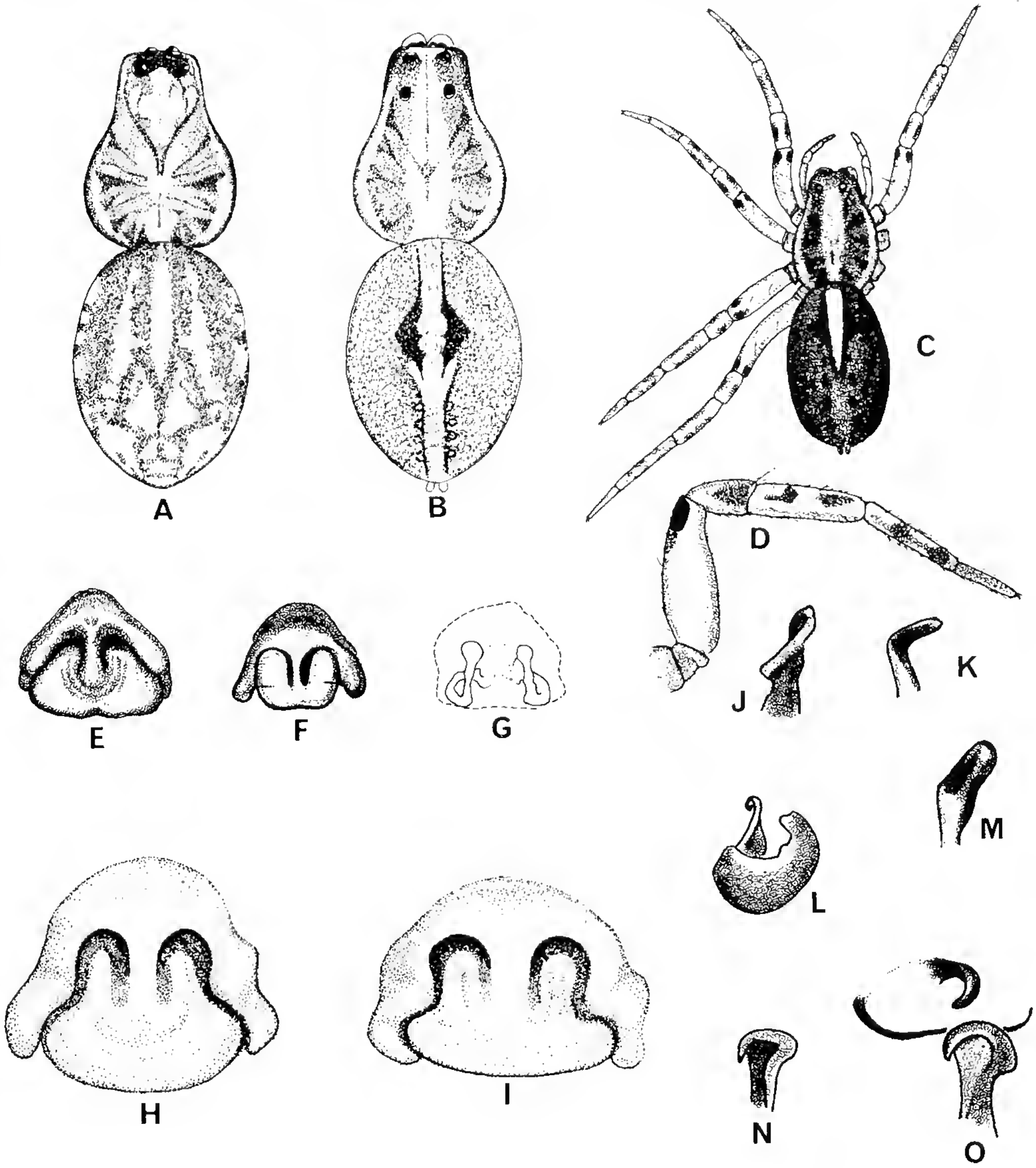


FIG. 3: *Trochosa tristicula tristicula.* A, female from Bulburin State Forest, Qd.

Trochosa expolita expolita. B, female from Brisbane; C, female from Nunawading, Vic.; D, foreleg; E, epigynum of female from Nunawading, Vic.; F, epigynum of female from Brisbane; J, median apophysis of male from Brisbane; K, M median apophysis of male from Eltham, Vic.; K, lateral view; M, ventral view; L, median apophysis of male from Brisbane.

Trochosa expolita impedita. G, internal genitalia of female from Rossmoyne, W.A.; H–I, epigyna of females from Rossmoyne, W.A.; N, male palpal organ from Waite Institute, S.A.; O, male palpal organ from Rossmoyne, W.A.

LIFE HISTORY

Mature females are found throughout the year but are most abundant during the summer months. Mature males commence courting in late October and are common during November and December. After courtship the males decline in numbers during late November but may persist in the field until late January. In the laboratory mature males cease feeding after mating in late October and many die during early November. The courtship display consists of rapid palpal drumming as soon as the female pheromone is contacted, with short forward jerks and short runs with the anterior pair of legs raised; some males make short jerky runs and then jerk the body forwards and backwards whilst the legs remain stationary. Mature males that had previously responded to the pheromone or presence of unmated *T. expolita impedita* females did not respond to the pheromone of *Lycosa pullastra* females (see McKay 1974, pp. 10–11). Females with egg-cocoons were collected during late November and early December.

This subspecies, like *L. pullastra* hunts during the day and at night. Field temperatures recorded 5 mm above the substrate adjacent to the spider ranged from 12·0°C to 36·0°C.

HABITAT

Areas with short grass, suburban lawns, and the banks of temporary creeks. This subspecies is most abundant on well-watered lawns or pastures. In Western Australia *T. expolita impedita* was collected from the estuary foreshore at Australind in association with *T. oraria*, *T. exculta phegia* and *Lycosa pullastra*. The South Australian specimens were collected from Lupins in an orchard at the Waite Institute.

BURROW

No burrows were located on suburban lawns; this subspecies shelters among grass roots and was found to be active during the day and night.

DISCUSSION

I have treated the Western Australian and South Australian populations as a subspecies of *T. expolita* due to a slight but apparently constant difference in the shape of the median apophysis of mature males of both subspecies. Further collecting from Victoria and South Australia is necessary to establish this relationship. Both subspecies appear to be identical in colour pattern and habitat requirements. The response of the mature males of the eastern subspecies to the pheromone of the western subspecies has not been tested.

Roewer (1954) placed *L. impedita* into the genus *Allocosa* Banks 1900, considered by Guy (1966) to be a subgenus of *Lycosa*. I have placed both subspecies into the genus *Trochosa* as although the first row of eyes is slightly smaller than the second row, the fourth tibia has the dorsobasal spine drawn out into a fine bristle or absent.

DISTRIBUTION

Western Australia and South Australia.

Trochosa martensii (Karsch 1878)
(Fig. 4A–C)

Lycosa martensii Karsch, 1878, pp. 812–3, Australia.
Diahogna martensii: Roewer, 1954, p. 239; 1960, p. 745.
Trochosa martensii: McKay, 1973, p. 381.

MATERIAL EXAMINED

HOLOTYPE: Zool. Museum Humboldt-Univ. Berlin, ZMB No. 756, ♀P, C.L. 5·1, Australia.

OTHER MATERIAL. Alexandra, Victoria. 7.xi.1927, collector unknown, NM, 1 ♀M, C.L. 6·3 mm; 7.xii.1954, A. Neboiss, NM, 2 ♀M, C.L. 5·5, 5·6 mm.

DESCRIPTION (After Karsch 1878)

Female: Carapace pale yellow-brown with a white longitudinal stripe commencing between the PL eyes on each side and curving in a concave line on the outside; these white lines continue posteriorly to the fovea and have in the middle two similar longitudinal stripes divided only in the anterior half by a narrow gap. Maxillae and labium covered with hair; fangs reddish-brown. Sternum covered with black hair.

Abdomen yellow-brown with a median longitudinal white line commencing on the dorsal surface at the base and extending posteriorly to the foremost depressed pair of spots; on the posterior half are 4 white spots decreasing in size towards the spinnerets; sides of abdomen dotted with small white specks. Undersurface of abdomen with a faint brown transverse curved stripe before the spinnerets, and separated from it by a narrow gap, a broader, almost rectangular brown transverse band; the middle part of the ventral surface with a pale yellowish-brown parallel trapeze with narrow yellowish margins, whose shorter side lies at the back and converges with the anterior yellow border of the broad brown transverse band. Spinnerets thick pale yellow. Colour of legs not given by Karsch.

Anterior row of eyes procurved, wider than second row, AM larger than AL. Ratio of eyes in micrometer units AM:AL:PM:PL=12:9:17:14; distance AM–AM 9, AM–AL 6, AM–PM 10, AL–PM 14 (between lens of eye), PM–PM 20. Clypeus to AM 10. Length of first eye row 63, length of second eye row 53. All measurements were difficult to obtain due to complete loss of pigment.

Chelicerae with three promarginal teeth; three retromarginal teeth of about equal size (not 4–5 as stated by Karsch).

Epigynum not completely formed but is stated by Karsch to have been an obliquely-oval yellow-brown plate, which on either side has a dark-brown pointed platelet directed posteriorly. The shape of the epigynum was not discernable in the holotype.

The palpi are almost spine-free above and wholly spine-free below. The distribution of the spines on the legs (from Karsch) is as follows: femora and patellae without ventral spines; tibiae of first and second pairs have one spine on the outer side of the anterior end, one spine on the inner side, one laterally next to the latter but slightly higher, and one in the middle; tibiae of the third pair have 4 on the outside and 3 on the inside; tibiae of fourth pair with 5 on the outside and 2 on the inside; metatarsi of all legs have on the ventral surface from rear to front 2+2+3 spines, the distribution of spines on the upper side is similar. An examination of the holotype shows the fourth tibiae to have the dorsobasal spine absent, the tibia of the first leg with one pair of apical ventral spines and one spine on the prolateral side.

The holotype is completely bleached without any discernable colour pattern.

VARIATION: Adult specimens have the carapace brown with a white to fawn lateral band and on the dorsal surface at the posterior margin two longitudinal white lines curve forwards to between the PL eyes where two short white lines extend posteriorly on the inside; some vague light and dark stripes radiate out from the foveal region.

Abdomen brown with a white longitudinal stripe extending from the anterior slope to about the middle of the dorsal surface where some white spots extend towards the spinnerets; on each side of this white stripe is a series of 3–4 white spots converging posteriorly on each side; sides of abdomen flecked with short, frequently broken, white lines; anterior slope of abdomen with white longitudinal lines and spots extending up on to the dorsal surface; undersurface of abdomen brown without markings; sternum brown; (Fig. 4A).

Legs and palpi brown with faint white stripes on the dorsal surface of the distal half of the femora, and the complete length of the tibiae. Palpi with 3 small spines on the dorsal surface of the femora. A dorsobasal bristle present on the fourth tibia; 2+2+2 ventral spines on the first tibia.

Eye diameters and interspaces given in Table 1, the anterior row, wider than the second row in ratio 85:71, 85:70, 80:68. The distance between the PM eyes slightly less than, equal to, or slightly greater than the diameter of the PM eyes.

Epigynum oval with a wide transverse guide and no median guide (Fig. 4B–C). Mature males are at present unknown.

Juveniles, prior to emerging from the egg cocoon, have a pattern of two wide longitudinal lines on the carapace and a pale longitudinal dorsal stripe on the anterior half of the abdomen.

DIAGNOSIS: *Trochosa martensii* is similar in colour pattern and eye measurements to *T. exculta,* but differs in having the white spots on the posterior dorsal surface of the abdomen converging towards the spinnerets instead of diverging and in lacking a median guide to the epigynum.

LIFE HISTORY

Mature females were captured in early November and December at Alexandra, Victoria. All three mature females had egg cocoons measuring 8·3 × 6·9 mm, 7·1 × 6·8 mm, and one of 7·8 × 6·8 mm had 132 developed young ready to emerge. Females possibly release young during early November through to late January. Mature males were not collected.

HABITAT AND BURROW

Unknown at present.

DISCUSSION

Trochosa martensii is the type species of the genus *Diahogna* Roewer 1954. This genus is characterised by having the first tibia with no more than 3 pairs of ventral spines; 3 retromarginal cheliceral teeth, anterior row of eyes procurved and wider than the second row; distance AM–AL shorter than distance AM–AM; distance PM–PM wider than the diameter of the PM eye. The holotype and one mature female fall into the genus *Diahogna* as defined above, and one mature female falls into the genus *Allohogna* using the key provided by Roewer (1959). Guy

TABLE 2: MEASUREMENTS OF LEG SEGMENTS OF *T. MARTENSII* IN MM FROM KARSCH

Leg	Femur	Patella and Tibia	Metatarsus and Tarsus
1	3·0	3·1	3·8
2	3·3	3·1	3·4
3	3·5	2·8	3·8
4	4·5	4·0	5·7

(1966) considers both *Diahogna* and *Allohogna* synonyms of *Trochosa* when eye diameters and interspaces are employed as generic characters.

DISTRIBUTION

Known from Alexandra, Victoria. Karsch (1878) gives no precise locality as the holotype was found by Professor E. von Martens of Berlin in a parcel containing Australian shells. Von

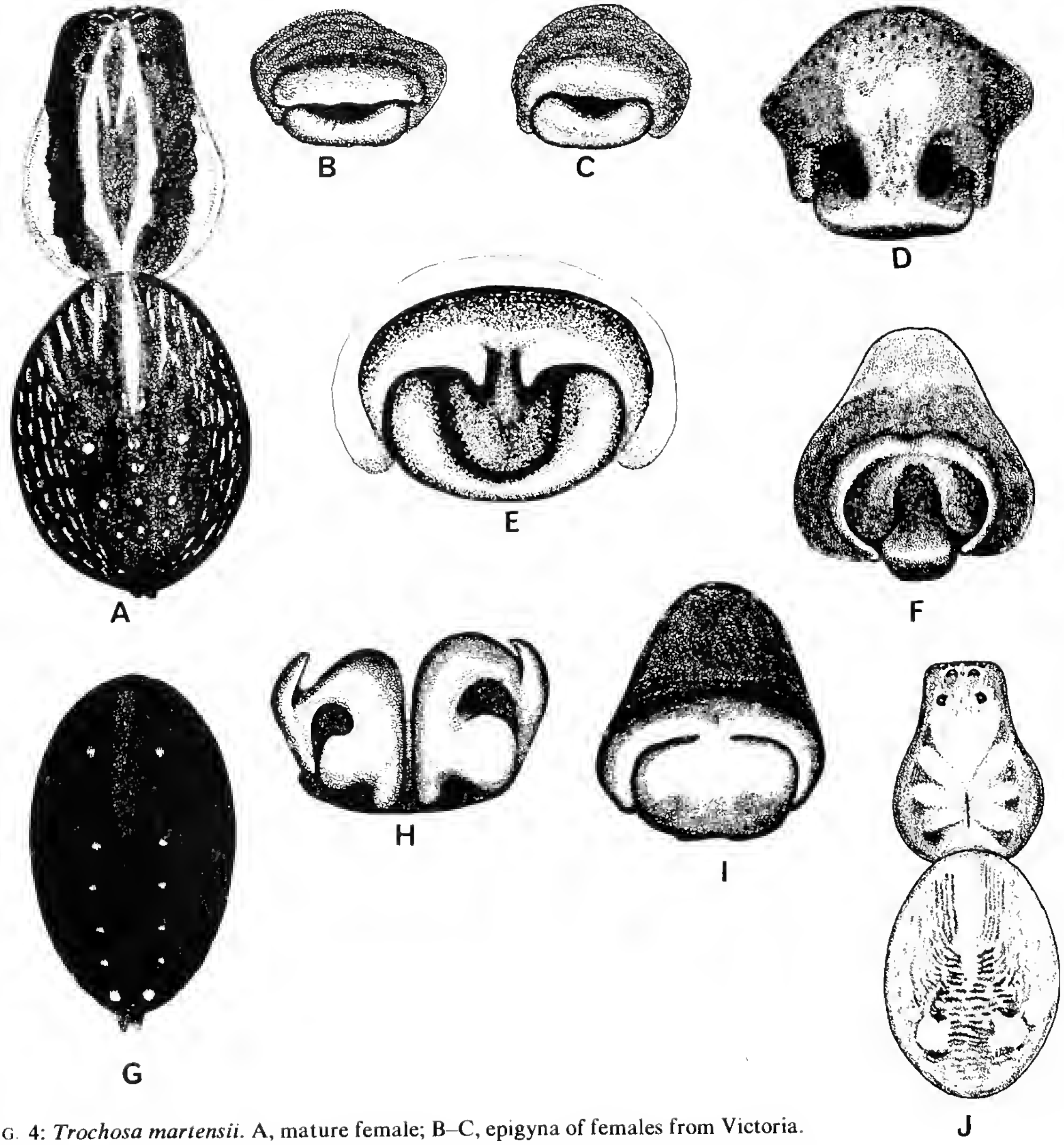


FIG. 4: *Trochosa martensii*. A, mature female; B–C, epigyna of females from Victoria.
Trochosa exculta. D, epigynum of lectotype.
Trochosa (?) *candicans*. E, epigynum of female from Reevesby Island.
Trochosa alboguttulata. F, epigynum of holotype.
Trochosa glarea. G, dorsal surface of abdomen; H, epigynum of holotype.
Trochosa wundurra. I, epigynum; J, holotype.

Martens worked on terrestrial molluscs in addition to marine molluscs.

Trochosa exculta (L. Koch 1876)
(Fig. 4D)

Lycosa exculta L. Koch, 1876, pp. 881–883, pl. 76, Figs. 1, 1a, 1b, 1c, Sydney, New South Wales; Rainbow, 1911, p. 267; Rack, 1961, p. 37.
Allohogna exculta: Roewer, 1954, p. 212.
Trochosa exculta: McKay, 1973, p. 381.

MATERIAL EXAMINED

SYNTYPE: British Museum (N.H.), BM 1919.9.18.333, ♀M, C.L. 7·2 mm, Sydney. Here designated as lectotype. The two syntypes present in the Zool. Inst. Zool. Mus. Hamburg (Rack 1961) are without precise data, and were not examined.

DESCRIPTION (After Koch 1876)

Female: Carapace dark reddish-brown with yellow-brown hairs, the pattern pure white. Lateral margin of thorax with a fairly broad border that is serrated across the coxae of the second and third legs; four short radial striae on the lateral declivity; two small dots on the lateral margin of the caput and behind the most posterior of these is a small crescentic dot; two curved longitudinal lines commencing at the posterior declivity and converging anteriorly and posteriorly to a point; these lines reach almost to the PM, and from their anterior point, two short lines extend posteriorly.

Abdomen brown-yellow, with the pattern white. A narrow longitudinal line commences at the base and continues almost to the middle; on either side of this longitudinal line, commencing at the base and running posteriorly is a longitudinal row of small spots; these spots become larger and more conspicuous at the base of the abdomen, and smaller and wider apart posteriorly; another pair of spots is sometimes present between the third and fourth spots; a longitudinal white line sometimes present on the lateral margin. The median longitudinal stripe is sometimes formed of yellowish hairs.

Palpi yellow-brown with a darker tarsal joint, and a white spot dorsally at the tip of the femur.

Legs yellow-brown or reddish-brown, with yellow-brown hair; femora sometimes with two blackish rings and a white line at the end; patellae and tibiae with a white line dorsally, on the tibiae this line is usually interrupted; in some specimens there are also two white spots at the rear; metatarsi with two white spots dorsally.

Anterior row of eyes straight, and considerably broader than the second row. Eyes equidistant by a radius; AM larger and a diameter from the PM. PM a diameter apart and 1½ times as far from the PL. PL barely larger than the AM.

Palpi shorter than the cephalothorax. Legs robust, without a well formed scopula. A spine at the anterior end of femur 1.

From Sydney; called by Mr Daemel a water spider probably because of its habitat near the water and its ability to run across the surface of the water. Live animals, according to Mr. Daemel, are light and dark green with brown and white lines and dots; the legs are dirty green. A young male, found at Gayndah, fully corresponds with the female.

An examination of the lectotype confirmed the presence of a dorsobasal bristle on the fourth tibia. The eye diameters and interspaces in micrometer units are AM:AL:PM:PL=22:17:30:26; distance AM–AM 12, AM–AL 8 between lens of eye 3 between base, AM–PM 18, AL–PM 20 between lens, 16 between base, PM–PM 30. Clypeus is about the width of AM. Length of first eye row 99, length of second eye row 84. All measurements recorded in Table 1 as a percent of the width of the first row of eyes.

Epigynum illustrated in Figure 4D.

DIAGNOSIS: *Trochosa exculta* is very similar to *Trochosa martensii* but differs in the white pattern on the dorsal surface of the abdomen and in having a median guide to the epigynum (Fig. 4D).

DISCUSSION

Karsch (1878) stated that *T. martensii* belonged to the group 1A *(Lycosa exculta)* of Koch, but did not discuss why he considered his immature female *(T. martensii)* to be a separate species. The discovery of fresh material of *T. martensii* allows a separation of the two species. Further collecting is necessary to describe the male palpal organ of both species and elucidate their relationship.

DISTRIBUTION

Sydney, New South Wales, and Gayndah, Queensland.

Trochosa candicans (L. Koch 1877)
(Fig. 4E)

Lycosa candicans L. Koch, 1877, pp. 888–890, pl. 76, Figs. 5, 5a, 6, 6a, 6b, Sydney, New South Wales; Rainbow, 1911, p. 266; Hickman, 1950, p. 5, Reevesby Island, South Australia; Bonnet, 1957, p. 2637.
Trochosula candicans: Roewer, 1954, p. 304.
Trochosa candicans: McKay, 1973, p. 381.

Material Examined

Holotype Not examined; location unknown.

Other Material (?) Reevesby Island, South Australia, xii.1936, J. Clark, ♀M, C.L. 3·6 mm, NM.

Description (after L. Koch 1877)

Female: Cephalothorax light yellow-brown with white hair; maxillae reddish-brown; labium dark yellow-brown; sternum brownish-yellow with white hair. Abdomen above and below white; from the base originate two diverging brown lines terminating in a small brown spot; two strongly diverging lines with inwardly curved ends follow, and posterior to these are additional spots covered by thick white hair. At the posterior half of the abdomen is a longitudinal row of brownish chevrons. Spinnerets, palpi and legs brownish-yellow with white hair.

Anterior row of eyes straight, wider than the second row. AM considerably larger than AL. AM almost a radius apart and the same distance from the AL and the PM. PM a radius apart and barely a diameter from the PL. PL considerably larger than AM.

Male: Cephalothorax as in the female. Abdomen white above and below, with four pairs of brown spots dorsally; the anterior pair at the base, the second and third connected by a brownish longitudinal stripe; the posterior pair small dots.

Legs and palpi white with cymbium yellow-brown and covered with yellow-white hairs.

Variation: The specimen from Reevesby Island (Hickman 1950, p. 5) agrees with the description of *Lycosa oraria*. The femur of the first leg has 1+1+0 spines dorsally, 1 anterolateral spine (not 2 anteriorly as recorded by Koch for *T. candicans*), and the first and second patellae lack spines (1 on each patellae in *T. candicans*). The mature female epigynum is similar in morphology in both species (Koch 1877, p. 886) and I am therefore unable to assign this specimen to *Trochosa candicans* with confidence. It is possible that *Trochosa oraria* extends across the Great Australian Bight into South Australia.

Habitat

Specimens from Shelly's Flats (about 19 km from Goulburn), and under joists above high water mark at Bondi Beach (Koch 1877).

Discussion

The identity of *Trochosa candicans* must await a comparison of males and females of *T. oraria* from Western Australia with the South Australian population *(T. oraria?)* and a series of *T. candicans* from the type locality (Sydney, New South Wales).

Trochosa alboguttulata (L. Koch 1878)

(Figs. 2I, 4F)

Lycosa albo-guttulata L. Koch, 1878, pp. 975–6, pl. 85, figs. 3, 3a Bowen, Queensland; Hogg, 1900, p. 77. Macedon, Victoria. Rack, 1961, p. 36.

Lycosa albo-guttata [misspelt]: Rainbow, 1911, p. 265. Queensland, New South Wales, Victoria.

Arctosippa alboguttulata: Roewer, 1954, p. 231.

Arctosippa alboguttata [misspelt]: Roewer, 1960, p. 759 (type re-examined).

Diapontia alboguttulata: McKay, 1973, p. 381.

Material Examined

Holotype: Zool. Inst. Zool. Hamburg, No. 14558, Cat. Araneae No. 446, ♀M, C.L. 4·7 mm, Bowen.

Other Material: Queensland: Myora Creek, North Stradbroke Island, 2.iii.1974, RJM, 1 ♀M, QM S23; Point Lookout, North Stradbroke Island, 2.iii.1974, RJM 2 ♀M, QM S24. Cooloola, Teewah Creek, 13.vii.1973, RR, 1 ♀M, QM W5784.

Description

Carapace dark yellow-brown, with a narrow median longitudinal stripe, covered with brownish-yellow hair, stretching from the posterior margin to the PM. A yellowish band on the lateral margin; this band disintegrates into small spots covered with yellow hair. On the lateral declivity of the thoracid part are two white hair-striae. Mandibles, maxillae and the labium reddish-brown; sternum brown-yellow, with yellow hair. Legs brown-yellow; the femora with two lighter coloured rings covered with white hair; on the middle of the tibiae above is a yellowish hair-spot; on the metatarsi of the 3rd and 4th pairs a longitudinal stripe of white hair dorsally. Palpi brownish-yellow, the tibiae and tarsal joints more vivid brown. Abdomen dark brown with a narrow longitudinal stripe covered with brownish-yellow hair on the dorsal side reaching to the middle of the abdomen. On each side of this stripe is a row of white hair-spots; on the posterior half these hair-spots are arranged in arched rows. Undersurface of abdomen brownish-yellow with two black longitudinal stripes beginning at the posterior margin of the epigastric furrow, converging posteriorly and reaching the spinnerets.

Anterior row of eyes slightly recurved, wider than the second row, equidistant by slightly less than a radius of an AM. AM considerably larger than AL, their distance from the PM more than their radius. PL as large as the AM.

Chelicerae with 3 small promarginal and 3 larger retromarginal teeth.

Labium more than half length of maxillae. Palp as long as the carapace. Legs dull with short hair; the metatarsi and tarsi of the first and second pair with a thinner scopula. On femur I, on the anterior end, two spines; all patellae of the anterior pairs lack spines. On the tibiae of the 3rd and 4th pairs 1 dorsal spine.

VARIATION: The yellow marginal band may be faint or absent in mature females. Legs uniformly coloured without rings, spots or stripes. The two black longitudinal stripes on the undersurface of the abdomen may be quite faint.

Eye measurements for the holotype and three mature females are recorded in Table 1 as a percent of the total width of the first eye row.

The epigynum of the holotype is illustrated in Figure 4G.

SIZE RANGE: Mature females C.L. 3·6 to 5·5 mm.

DIAGNOSIS: First row of eyes wider than the second row. Undersurface of abdomen brownish with two black longitudinal stripes coverging posteriorly. Similar to *Trochosa tristicula tristicula* but the epigynum has a well developed median guide and no points on inner margin anteriorly.

LIFE HISTORY

Mature females with egg cocoons were captured in March at North Stradbroke Island. Mature males have not been collected.

HABITAT

The holotype was collected from Bowen, possibly on coastal sands; the North Stradbroke Island material was collected during the day-time from below litter under trees growing on sandy soil; two specimens were collected on the beach below *Melaleuca* trees, the other specimen from below *Acacia* near the creek bank.

BURROW

Unknown.

DISCUSSION

Roewer (1954) placed *T. alboguttulata* into the genus *Arctosippa* Roewer, considered a subgenus of *Diapontia* Keyserling, a South American genus, by Guy (1966). In *Diapontia* the AL eyes are as large as the AM, whereas in *T. alboguttulata* the AL eyes are smaller than the AM. The fourth tibia of *T. alboguttulata* has a dorsobasal bristle.

Trochosa properipes (Simon 1909)

Lycosa properipes Simon, 1909, p. 189, Guildford and Subiaco, Western Australia; Rainbow, 1911, p. 271.
Allohogna properipes: Roewer, 1954, p. 212; 1960, p. 735.
Trochosa properipes: McKay, 1973, p. 381.

MATERIAL EXAMINED

The location of the holotype is unknown to me.

DESCRIPTION (After Simon 1909)

Male, 9 mm: Carapace dark, irregularly marked on the thoracic part by a golden longitudinal median line and by a long golden line on the edge; chelicerae reddish; sternum pale dark-reddish.

Abdomen somewhat black, covered with ash-grey to blackish hair and variegated with bent hairs; in the front it is decorated by a longitudinal, rather narrow and pointed band covered with golden hairs. Undersurface with dark hairs but black near the spinnerets.

Legs long (the front ones are obviously longer than the hind ones), dark-reddish, covered with very fine long, and closely growing bristles. The anterior tibiae armed with thin spines lower down 3 + 3, the middle tibiae with longer spines and a small spine on the inner side near the top. Metatarsi armed with stronger spines 2 + 2 and three smaller ones at the top. The fourth legs have numerous spines but the tibiae are protected by a single dorsal spine situated on the top half. Palpi with 1 + 1 + 3 dorsal spines on the femur, patella and tibia about equal in length; tarsus narrow, scarcely wider than the tibia, coming to a long point and exceeding the bulb; the small, somewhat round bulb (Cymbium?) is protected by a black apophysis at the top that is slanting and obliquely truncated.

Anterior row of eyes almost straight, slightly procurved, eyes almost equidistant, obviously wider than the second row; AM at least one third larger than AL which are at least three times more distant from the edge of the clypeus than from the PM; PM separated by a space almost a third smaller than an eye.

Retromarginal cheliceral teeth 3, almost touching, with the middle one a little larger.

DISCUSSION

The collecting station 103 was made at the townsite of Guildford near the Swan River on 19 May, and 28 August, 1905. The habitat is described as scrubland, flatland west of the Darling Ranges and much cultivated. Station 109 Subiaco, 6 August 1905 is described as garden and 'coastland' and probably refers to the margin of Herdsman's Lake. I found no *Trochosa* species at either locality despite at least four attempts to locate this species.

Simon states that the first pair of legs are obviously longer than the hind ones, a condition rare in lycosid spiders, therefore *'L. properipes'* may belong to the family Pisauridae. As Simon placed this species into *Lycosa* and it has most of the *Trochosa* characteristics I have retained it in this genus.

Trochosa glarea sp. nov.

(Fig. 4H, J)

MATERIAL EXAMINED

HOLOTYPE: Queensland Museum, S25, ♀M, C.L. 3·5 mm, Big Tuan Creek near Boonooroo, via Hervey Bay, Queensland, collected by R. J. McKay, 21 October 1976. In spirit.

DESCRIPTION

Carapace light brown covered with short dark hairs; a very faint trident-like pale pattern commences at the anterior tip of the fovea and runs anteriorly as a central longitudinal stripe with a mediolateral stripe running almost parallel from the base at the fovea; this pattern may not be evident in life; some dark marks radiate out from the foveal region; no pale lateral band; paturon, fang, maxillae and labium brown; sternum and coxae light brown. Abdomen light brown above with dark brown to black hairs and darker irregular blotches; an indistinct pale longitudinal stripe commences anteriorly and reaches the middle of the abdomen; a pair of white spots anteriorly followed by a pair of white spots almost at the middle of the abdomen, the four spots are followed by three pairs of white spots somewhat wider apart on the posterior half of the abdomen; just before the base of the spinnerets is a pair of bright white spots; sides of abdomen blotched with dark pigment. Undersurface of abdomen light brown with a darker somewhat mottled area before the spinnerets. Legs uniform pale brown.

TABLE 3: MEASUREMENTS OF LEG SEGMENTS OF *T. GLAREA* IN MM

Leg	Femur	Patella	Tibia	Metatarsus	Tasus
1	2·4	1·2	1·9	2·0	1·1
2	2·3	1·1	1·6	1·7	1·0
3	2·1	1·0	1·4	1·7	0·9
4	2·8	1·2	2·4	3·1	1·2

Anterior row of eyes with the upper tangent slightly recurved, wider than the second row in the ratio 84:78. Ratio of eyes in micrometer units AM:AL:PM:PL = 20:14:30:27; distance AM–AM 8, AM–AL 4, AM–PM 6, AL–PM 5, PM–PM 16. Clypeus to AM 15.

Chelicerae with three promarginal teeth, the middle one largest, three retromarginal teeth of equal size.

Tibia of first leg with 2+2+2 ventral spines. Tibia of fourth leg with a thin dorsobasal spine.

The epigynum is of characteristic shape, with a well developed chitinous hook on the antero-lateral surfaces (Fig. 4H).

VARIATION: Mature males were not collected.

DIAGNOSIS: Anterior row of eyes wider than second row; six pairs of white spots on the dorsal surface of the abdomen, those before the spinnerets most conspicuous; epigynum of characteristic shape, with a well developed chitinous hook on the antero-lateral surfaces.

HABITAT

The holotype was collected from among gravel and small pebbles on the damp edge of a flowing stream.

BURROW

Unknown.

DERIVATION

From the latin glarea meaning gravel.

Trochosa wundurra sp. nov.

(Fig. 4I, J)

MATERIAL EXAMINED

HOLOTYPE: Queensland Museum, S96, ♀M, C.L. 4·5 mm, Hyden Lake, Hyden, Western Australia, collected by R. J. McKay, 28 March 1970. In spirit.

DESCRIPTION

Carapace light brown; area within ocular quadrangle dark brown; some thin dark brown lines, terminating laterally in wedge-shaped brown marks radiate out from the foveal region; lateral margin of carapace dusky; paturon and fang dark brown; labium mid-brown; maxillae light brown; sternum and coxae pale brown to dark cream. Abdomen light brown to cream; dorsal surface with a distinct pale longitudinal stripe that commences at the anterior slope and terminates in a point about middle of abdomen; the anterior part has the longitudinal stripe outlined by a series of parallel dark brown to black streaks becoming transversely arranged on posterior two thirds where they demarcate two irregularly shaped blotches situated on each side of the dorsal midline; sides streaked with black-brown, the lower sides blotched or spotted with dusky marks. Undersurface of abdomen pale the lateral slopes spotted with dark brown marks. Legs uniform pale brown to cream.

Anterior row of eyes with the upper tangent slightly procurved, wider than the second row in the ratio 56:50. Ratio of eyes in micrometer units AM:AL:PM:PL = 12:9:18:17; distance AM–AM 5, AM–AL 4, AM–PM 3, AL–PM 4, PM–PM 14. Clypeus to AM 4.

Chelicerae with three promarginal teeth, the middle one largest; three retromarginal teeth of about equal size.

Tibia of first leg with one pair of apical ventral spines only, metatarsus of first leg with 2 + 2 + 2 ventral spines. Tibia of fourth leg without a dorsobasal bristle or spine.

The epigynum is of characteristic shape with the median guide expanded into a plate-like structure (Fig. 4I).

VARIATION: Mature males were not collected.

DIAGNOSIS: Anterior row of eyes wider than the second row; tibiae of the first pair of legs with a pair of apical ventral spines only; epigynum of characteristic shape.

TABLE 4: MEASUREMENTS OF LEG SEGMENTS OF *T. WUNDURRA* IN MM

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1	2·7	1·5	2·0	2·3	1·1
2	2·5	1·4	2·0	2·3	1·2
3	2·6	1·3	1·8	2·6	1·2
4	3·2	1·5	2·3	3·6	1·6

HABITAT

On the sandy shoreline of Lake Hyden.

BURROW

Unknown

DERIVATION

From the aboriginal 'wundurra' meaning warrior.

ACKNOWLEDGMENTS

Mr B. Campbell of the Queensland Museum offered valuable criticism of the manuscript, and Mrs Janet Byrne typed the final draft. Dr L. E. Koch and Dr A. Neboiss forwarded material for study.

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WABULAROO NAUGHTONI GEN. ET SP. NOV., AN ENIGMATIC KANGAROO (MARSUPIALIA) FROM THE MIDDLE TERTIARY CARL CREEK LIMESTONE OF NORTHWESTERN QUEENSLAND.

RESULTS OF THE RAY E. LEMLEY EXPEDITIONS, PART 4

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ABSTRACT

Wabularoo naughtoni gen. et sp. nov. is a middle to late Miocene kangaroo from the Carl Creek Limestone of Riversleigh Station, northwestern Queensland. The dentary morphology is potoroid-like but the molars are lophodont and therefore macropodid-like; the very large plagiaulacoid premolar shares characters of both groups. Its systematic and phylogenetic position are obscure. Although it may be structurally ancestral to either the potoroids or macropodids it post dates the appearance of both families in the fossil record.

Tedford (1967) summarizes the Riversleigh fauna from the Miocene Carl Creek Limestone noting three diprotodontid genera including *Bematherium angulum* Tedford 1967, and an undetermined genus of kangaroos. In 1976, the author and museum assistants Messrs H. Godthelp and R. Kohout made further collections from the Carl Creek limestone at the locality referred to by Tedford (1967, figs. 1–2) as 'D'. These collections included two additional genera of kangaroos, as well as crocodiles, birds, and diprotodontids.

The new kangaroo described here was found in an isolated block of the very hard Carl Creek Limestone. Using an electric jack-hammer, it was collected as part of a smaller chunk of limestone. Fine preparation was carried out in the laboratory using a compressed-air vibrotool.

Terminology of individual teeth follows Archer (1978a) and that of crown morphology follows Archer (1976a, b) or Bensley (1903). Registration numbers prefixed with F are in the palaeontological collections of the Queensland Museum.

SYSTEMATICS

Superfamily: MACROPODOIDEA
Family: Incertae sedis

Wabularoo gen. nov.

TYPE SPECIES: *Wabularoo naughtoni gen. et sp. nov.*

GENERIC DIAGNOSIS: It differs from all genera of the Potoroidae *(Hypsiprymnodon, Propleopus, Potorous, Caloprymnus, Bettongia* and *Aepyprymnus)* in having lophodont molars. It differs from all genera of the Macropodidae in having a combination of a short, shallow, swollen dentary with a greatly enlarged masseteric canal and a trenchant but wide and tall plagiaulacoid P_3. Of all known macropodid genera, it most closely resembles the monotypic *Hadronomas* but it also differs from the single species of this genus *(H. puckridgei)* as follows: the molars have narrower anterior cingula; the P_3 is proportionately much wider and taller-crowned, obliquely oriented in the tooth row, narrowed posteriorly, with recurved more numerous and finer serrations, and no buccal or lingual cingula.

Origin of the generic name: *Wabula* (wa'bula) means 'long-time-ago' in the Waanyi language as spoken by Ms Ivy George of Riversleigh Station; *roo* is a common non-specific Australian term for

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a kangaroo. The generic name is regarded to be masculine.

Wabularoo naughtoni sp. nov.
(Fig. 1; Pls., 1, 2)

Holotype: Queensland Museum F9177, broken right dentary with P_3, M_{2-3}, and part of M_4.

Type Locality: From an isolated boulder of the upper clastic arenaceous limestone member of the Carl Creek Limestone, site 'D' (of Tedford 1967), Riversleigh Station, northwestern Queensland.

Age: The absolute age is unknown but, based on faunal comparisons, the Carl Creek Limestone is interpreted to be mid to late Miocene in age (Tedford 1967, Archer and Bartholomai 1978).

Origin of the Species Name: In honour of Mr and Mrs E. Naughton, owners of Riversleigh Station, who graciously allowed us to work on the property as well as extended many kindnesses to us during our stay.

Diagnosis: That of the genus until additional species are known.

Description: The dentary is potoroine-like resembling for example *Bettongia* and *Aepyprymnus* in being short, heavy-bodied, with a marked inflection of the ventral border below the molar row, a prominent swelling of the lateral wall below P_3, and a large and laterally swollen masseteric canal. The point of inflection of the ventral border is below M_4 as in some

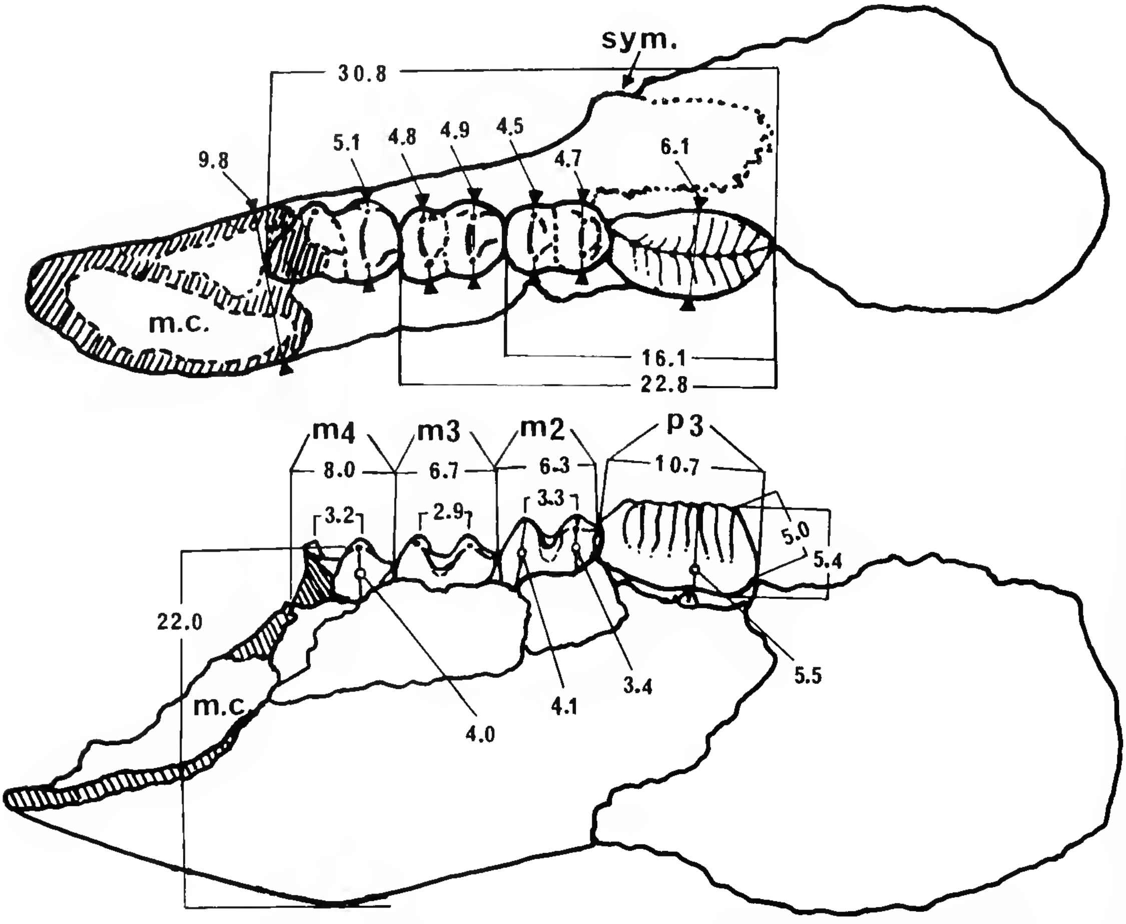

Fig. 1. Occlusal and buccal views of F9177, the holotype of *Wabularoo naughtoni*, showing measurements (in mm) and tooth nomenclature. In the buccal view, the intercusp distances 3·2, 2·9 and 3·3 were measured between the metaconid (lingual end of the protolophid) and entoconid (lingual end of the hypolophid) of each lower molar. In measurements involving length of the broken M_4, the posterior point is taken from the posterior edge of the posterior root. In measurements involving length of the P_3, the anterior edge is taken from the antero-most basal edge of the enamel. Molar widths were measured along axes passing transversely through the major cusps. Molar cusp heights involve only the protoconid (buccal end of the protolophid) and hypoconid (buccal end of the hypolophid). Abbreviations: *m.c.*, masseteric canal in section; *sym*, posterior end of the symphysis.

macropodids rather than below M_3 as in potoroids (when it occurs). The symphysis, although damaged, appears to extend posteriorly to the level of the trigonid of M_2.

P_3: This tooth is missing a small piece of enamel from the lingual face and a small piece from the basal anterolingual corner. Its morphology resembles the plagiaulacoid teeth of some potoroids such as *Aepyprymnus* and some macropodids such as *Hadronomas* but differs from these in that its occlusal outline is narrowed posteriorly, markedly swollen mesially, and again narrowed anteriorly. There is no evidence of basal cingula although the basal rim of the crown is buccally and lingually swollen. There are nine cuspules along the longitudinal crest, at least eight of which are the terminal points of paired buccal and lingual vertical crests. Only potoroids have this many serrations, the highest number in macropodids being approximately seven (in *Hadronomas)*. These vertical crests in *Wabularoo naughtoni* are sinuously curved on both sides of the tooth, but more complexly so on the buccal side. This type of curving is also pronounced in some potoroids, particularly *Propleopus*, but is not apparent in macropodids with serrated premolars perhaps because of their relatively brachydont premolar crowns. The vertical crests terminate occlusally in a subhorizontal longitudinal shearing crest. This crest also extends down the anterior and posterior ends of the crown. The posterior end of the crown is inflected lingually so that the longitudinal crest also turns lingually and contacts M_2 at the lingual edge of its anterior cingulid. This type of inflection is common in potoroids and macropodids. The buccal face of the tooth is approximately planar while the lingual side is mildly concave. This marked difference is not noticeable in macropodids but is in some potoroids. The whole tooth is set obliquely in the tooth row such that its anterior end is buccal to the longitudinal midline of the molar row. This is a characteristic of many potoroids but no macropodids.

M_2: This tooth is missing a piece of enamel from the lingual corner of the metaconid and some of the thin enamel on the posterior face of the hypolophid. It is low-crowned and broadly resembles molars of the simpler low-crowned macropodids such as *Setonix* and *Dorcopsoides*. The four major cusps are all subequal in height. A preprotocristid or paracristid connects the protoconid to the anterior edge of the anterior cingulid. The anterior cingulid is high, being higher than the midlink. The protolophid, although worn, shows a slight median flexure suggesting either a median vertical swelling such as occurs in some potoroids, a median crest such as occurs in the M_1 of some *Dendrolagus*, or a medially curved or interrupted crest such as occurs in potoroids. The protolophid is apparently not anteriorly concave, being more or less transverse and horizontal, a condition uncommon in most macropodids (exceptions include *Dorcopsis)*, but common in potoroids and sthenurines. The midlink or cristid obliqua is low and intersects the rear of the protolophid well buccal to its midpoint, a condition universal in potoroids but uncommon in most macropodids other than some of the low crowned forms such as *Dorcopsis*. The preprotocristid isolates a smaller buccal from a larger lingual region of the anterior cingulid. This character varies in most kangaroo subfamilies but its presence is more common in macropodines and sthenurines. The buccal median valley between the midlink, protoconid and hypoconid is transversely concave. The hypolophid is concave anteriorly, and with wear is also occlusally concave. The occlusal concavity is assymetric, the point of maximum concavity being lingual to the midpoint. There is no evidence of a posterior cingulum or cingular pocket on the posterior flank of the hypolophid. The metaconid is connected to the anterior cingulid by a lingual crest. The remnant of this crest suggests it turned buccally immediately anterior to the metaconid and then turned sharply lingually to form the anterolingual edge of the tooth. This character differs from a superficially similar condition in *Hadronomas* where there is a notch between the metaconid and the anterolingual edge of the cingulid, because in *Hadronomas* there is no crest linking the metaconid to the anterior cingulid, and the notch is near the base of the metaconid rather than up its flank as in *Wabularoo naughtoni*. The condition of the crest anterior to the metaconid also sets *W. naughtoni* apart from some of the otherwise similar low-crowned macropodids such as *Dendrolagus* because it evidently does not terminate immediately anterobuccal to the metaconid. No longitudinal linking crest connects the metaconid to the entoconid. There was evidently a short crest or swelling developed anterior to the entoconid such as occurs (but to a greater extent) in *Dorcopsis, Dorcopsulus* and *Dendrolagus*. The protolophid is markedly narrower than the hypolophid. The trigonid and talonid are subequal in width. The widest part of the tooth is across the anterior part of the midvalley.

M_3: The morphology of M_3 is as in M_2 except as follows: The whole tooth is larger; the protolophid is subequal in length to the hypolophid; the protolophid is symmetrically concave anteriorly and occlusally; the crest extending anteriorly from the metaconid to the anterior cingulid does not have an inflection immediately anterior to the metaconid; the anterior cingulid is lower such that its anterior edge is no higher than the midvalley of the tooth; the trigonid is noticeably wider than the talonid and is the widest part of the tooth; the anterior cingular shelf is longer; the swelling anterior to the entoconid is not as well-developed; and there is a poorly-developed but distinct lingual vertical crest on the posterior flank of the metaconid (this may also have been present in M_2, but the tooth is very worn in this area).

M_4: The hypoconid and posterior face of the hypolophid are missing. The morphology of M_4 is as in M_3 except as follows: There is a point of inflection between the anterolingual corner and the end of the anterior cingulid and the base of the metaconid; the anterior flank of the entoconid is not extended by a swelling, but rather projects anteriorly.

Meristic gradients along the tooth row: The protolophid and trigonid increase in width from M_2 to M_4; the hypolophid and talonid also increase in width at least from M_2 to M_3; the preprotocristid increases in length from M_2 to M_4; the anterior cingulid decreases in height from M_2 to M_4; and the protoconid increases in mass from M_2 to M_3, but is subequal in M_3 and M_4.

DISCUSSION

Wabularoo naughtoni is in most characters except molar morphology, a decidedly potoroid-like kangaroo. Its lophodont molars which also lack posterior cingula are however decidedly non-potoroid-like characters. Its systematic and phylogenetic position within the Macropodoidea are therefore very much in doubt.

Wabularoo naughtoni could theoretically represent any one of at least five evolutionary stages: (1) a potoroid developing into a macropodid; (2) a macropodid developing into a potoroid; (3) a specialized macropodid paralleling potoroids; (4) a specialized potoroid paralleling macropodids; (5) a representative of an as yet unrecognized group equivalent in rank to known kangaroo subfamilies but a derivative or ancestor of none of the other known groups. However, at least one undoubted potoroid occurs in the mid-Miocene Etadunna Formation (M. O. Woodburne, pers. comm.) and at least one high-crowned macropodid tooth is known from the mid-Miocene Namba formation from the Frome Embayment of South Australia (Archer and Rich, in preparation). These probably older occurrences discount the first two of the above possibilities. There is at present insufficient information to decide between the remaining three.

Speculations about kangaroo evolution and classification have been going on continuously since Bensley's (1903) comparative study of the teeth of marsupials. More recent speculation concerning the relative primitiveness of the known subfamilies (e.g. Pearson 1950, Ride 1971, Bartholomai 1972) has highlighted the fact that there is still no agreement about whether potoroids were ancestral to macropodids, macropodids were ancestral to potoroids, or both groups were derived independently from a common ancestor referable to neither group. There has even been renewed interest and uncertainty about the composition of the subfamilial groups (e.g. Woodburne 1967, Kirsch 1968, Archer 1978b). Elsewhere (Archer 1978b) I have proposed a speculative rearrangement of all kangaroo genera into two families: The Potoroidae containing the Hypsiprimnodontinae (*Hypsiprimnodon* and *Propleopus*) and the Potoroinae (all other potoroid genera); and the Macropodidae containing the Sthenurinae (possibly including the genera *Sthenurus*, *Procoptodon*, *Setonix*, *Dorcopsoides*, *Dorcopsulus*, *Dendrolagus* and *Hadronomas*) and the Macropodinae (containing all other previously described genera). The Sthenurinae, in the expanded form used by Archer (1978b), is essentially a plesiomorphic group and probably not monophyletic.

There are other different and as yet unnamed middle Miocene Kangaroos, from central South Australia (M. O. Woodburne, pers. comm.) that cannot be referred to any of the previously described subfamilies without significantly altering the current concepts of these subfamilies. There is a possibility that *Wabularoo naughton* and these other aberrant taxa are referable to a fifth subfamily of kangaroos. I have not proposed a new subfamily for *W. naughtoni* because of the limited information provided by the single dentary. It would be desirable to consider inciso and cranial structure as well, aspects of which are preserved in the Miocene material under study by M. O. Woodburne.

The diprotodontids of the Riversleigh loca fauna were concluded by Tedford (1967) to b contemporaneous with or slightly younger tha the Ngapakaldi diprotodontids from the Etadunna Formation. Pollens from the Etadunna Formation are regarded to be Batesfordian to Balcombian in age (pers. comm. from W. K. Harris *in* Callen and Tedford 1976). Therefore it can be suggested that the Riversleigh local fauna is probably middle to late Miocene in age.

ACKNOWLEDGMENTS

Dr Ray E. Lemley most generously supported all aspects of the field work in 1976 (as well as 1977) and the success of the whole project is in the first place the result of his help. Mr and Mrs E. Naughton, owners of Riversleigh Station, and Mr and Mrs J. Nelson, the managers, are owed many sincere thanks for permission to collect on the station and for courtesies extended to us while we were in north Queensland. Special thanks are also owed to Messrs H. Godthelp and R. Kohout (Queensland Museum) for their efforts as part of the 1976 field crew. Dr A. Bartholomai (Queensland Museum) read a draft of this paper. Mr A. Easton took the photographs. Ms Ivy George, of Riversleigh Station, kindly spent time communicating her language to the author as well as Dr J. G. Breen (Monash University). She is evidently the last living person who can speak the Waanyi language. Dr Breen kindly helped in the search for a suitable stem for the generic name.

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PLATE 1

Wabularoo naughtoni gen. et sp. nov., holotype F9177 × 2

FIG. A: Stereophotograph postero-occlusal view, showing P_3–M_4. The hopolophid of $M_{4\dagger}$ is broken.
FIG. B: Stereophotograph, occlusal view.
FIG. C: Stereophotograph, lingual-occlusal view.

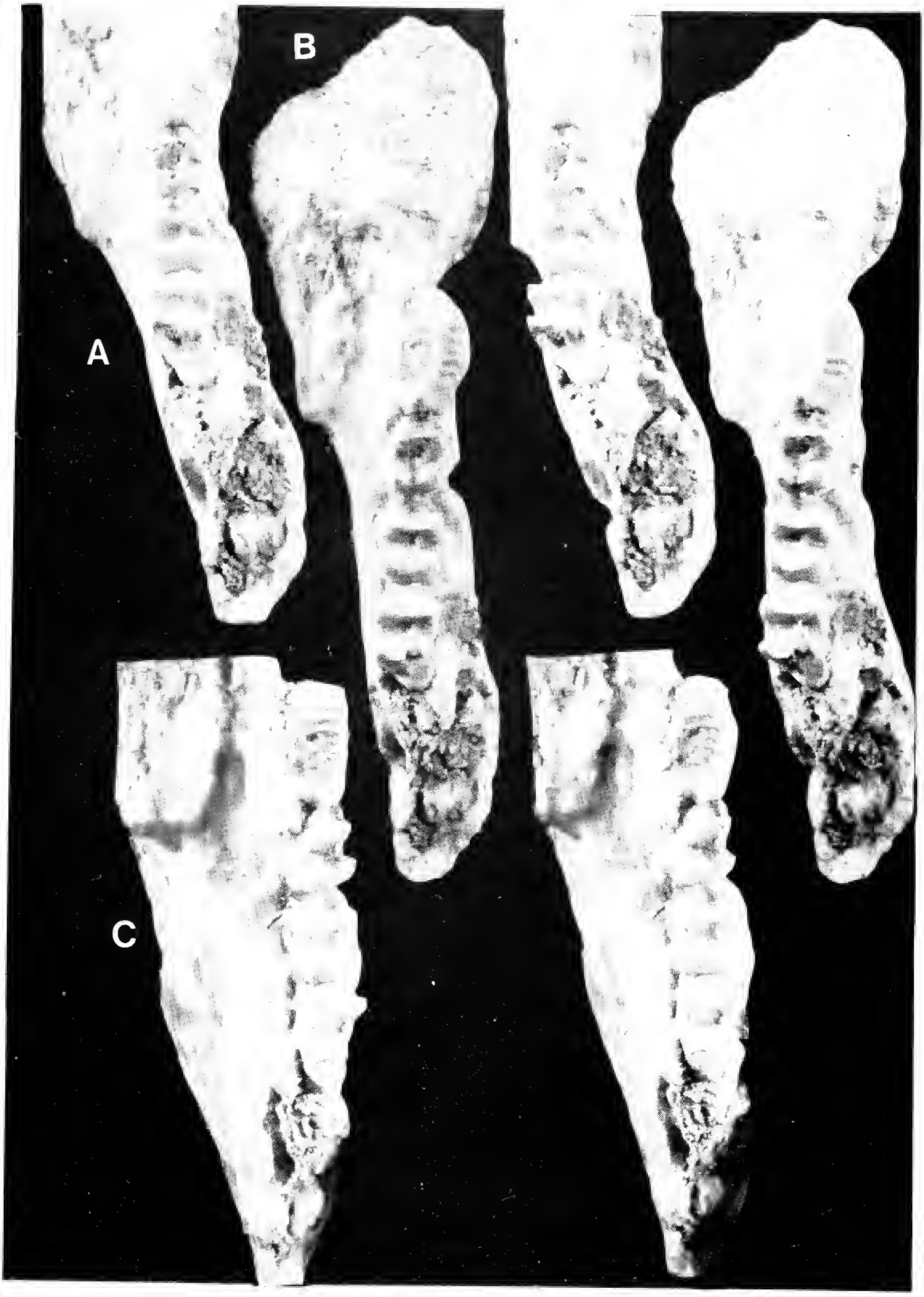
B
A
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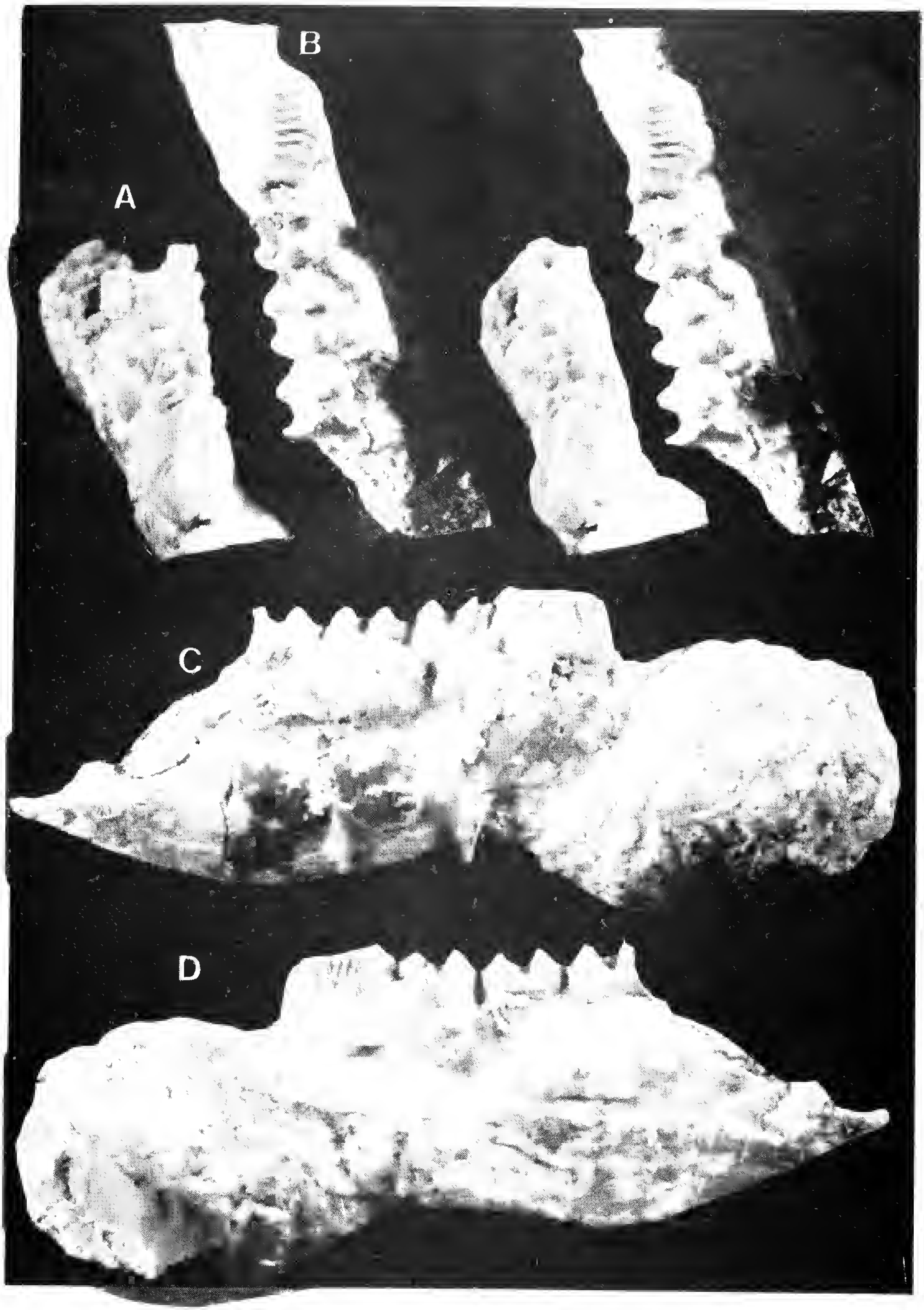
PLATE 2

Wabularoo naughtoni gen. et sp. nov., holotype F9177 × 2.

FIG. A: Stereophotograph, antero-occlusal view.
FIG. B: Stereophotograph, buccal-occlusal view.
FIG. C: Buccal view.
FIG. D: Lingual view.


A
B
C
D

Mem. Qd Mus. **19**(3): 309–17, pls. 1, 2. [1979]

WAKAMATHA TASSELLI GEN. ET SP. NOV., A FOSSIL DASYURID (MARSUPIALIA) FROM SOUTH AUSTRALIA CONVERGENT ON MODERN *SMINTHOPSIS*

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Queensland Museum
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ABSTRACT

Wakamatha tasselli gen. et sp. nov. is described from the modern unconsolidated bed load sediments of Billeroo Creek. The original provenance of the holotype and only known specimen (National Museum of Victoria, P33253) is uncertain. Adjacent formations exposed in the Creek bank include the middle Miocene Namba Formation and the Pleistocene Eurinilla Formation. *Wakamatha tasselli* differs from all other known dasyurids in the construction of the talonid of M_4 and the large size of P_3. The talonid structure is convergent on that of *Sminthopsis crassicaudata* and suggests an adaptation enabling greater transverse jaw movement, and finer commutation of foods.

New Cainozoic formations have been recently described from the Tarkarooloo Basin by Callen and Tedford (1976). They describe the Miocene Namba and Pleistocene Eurinilla Formations. The vertebrate faunas from the Namba Formation have been announced by Tedford *et al.* (1977) but no formal descriptions have been made. The vertebrate fauna from the Eurinilla Formation similarly has not yet been described.

In 1974, T. Rich, C. Tassell, and I. Stewart (all of the National Museum of Victoria) found vertebrate fossils in the bed of Billeroo Creek on Frome Downs Station, including the holotype and only known specimen of the dasyurid *Wakamatha tasselli* described here. Subsequent, extensive collections made in 1976 and 1977 by T. Rich, M. Archer, and I. Stewart at the type locality failed to produce any additional dasyurid material. On the occasion of all three visits, the site where the holotype was collected was under about 50 centimetres of water. Samples were taken from beneath the water wherever particles larger than sand size were felt when groping with bare hands through the bottom sediments, experience having shown that anything larger at that locality was likely to be bone.

Dental nomenclature follows Archer (1976, 1978).

SYSTEMATICS

Superfamily DASYUROIDEA
Family DASYURIDAE

Wakamatha gen. nov.

TYPE SPECIES: *Wakamatha tasselli gen. et sp. nov.*

GENERIC DIAGNOSIS: Differs from all known dasyurids in having a combination of the following three characters: (1) the P_3 was (based on alveoli) very large, probably longer than M_2; (2) the talonid of at least M_4 (M_{2-3} are missing) has a functional transverse crest developed between the hypoconid and entoconid that is formed by the posterior cristid of the entoconid being oriented posterobuccally and united directly with the lingual end of the hypocristid; (3) the talonid of M_5 is transversely compressed.

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ORIGIN OF GENERIC NAME: *Waka*, little; *matha*, bite; central South Australian Aboriginal words (Gason 1879) in reference to the small size of this marsupial carnivore.

Wakamatha tasselli sp. nov.

HOLOTYPE: National Museum of Victoria P33253, left dentary fragment with M_{4-5} and alveoli for $P_3 - M_3$.

TYPE LOCALITY 31° 11′S, 140° 16′E, on the bottom of a bend of Billeroo Creek, Frome Downs Station, South Australia.

STRATIGRAPHIC HORIZON Unknown. It was found in unconsolidated mud and silt at the base of Billeroo Creek. The formations exposed in the adjacent bank of the Creek are the Namba (Miocene) and Eurinilla (Pleistocene) Formations.

DESCRIPTION

Alveoli: The alveoli of P_3 suggest that P_3 was longer-crowned than M_2 and subequal in length to M_3. The anterior alveolus of P_3 is also wider than the anterior alveolus of M_2.

M_4: The trigonid is damaged with the tips of the protoconid and metaconid missing, as well as the occlusal edge of the metacristid. The paraconid is shorter than the metaconid which was probably shorter than the protoconid. The entoconid is subequal in height to the paraconid. The hypoconid is shorter than the entoconid. The paracristid is longer than the metacristid which is longer than the hypocristid. The short cristid obliqua extends from the hypoconid to a point below and buccal to the midpoint of the metacristid. A very tiny enamel swelling continues up the posterior face of the trigonid from the point of the intersection of the cristid obliqua and the trigonid. The hypocristid extends lingually across the talonid towards the posterior flank of the entoconid and terminates against the buccal end of a postentocristid that swings posterobuccally from the entoconid. The point of juxtaposition of the ends of these two crests occurs on the lingual half of the talonid, anterobuccal to the hypoconulid. The entoconid also has a preentocristid that extends anteriorly to the posterolingual edge of the trigonid. This crest provides a steep lingual wall for the talonid basin. The preentocristid and postentocristid form two halfs of a crescent with the median point represented by the entoconid, and the concave surface directed anterobuccally. The metacristid (although damaged) and hypocristid appear to have been oriented transversely with respect to the long axis of the tooth row. The hypoconulid is very low on the posterolingual corner of the talonid. No crest connects the hypoconulid to the hypocristid. The entoconid is only worn at the very tip while the hypoconid sustains a much larger and crescent-shaped wear facette. The posterior cingulum is short but continuous from the posterior base of the hypoconid to the buccal edge of the hypoconulid. The anterior cingulum is relatively longer. It descends anterolingually from the anterobuccal flank of the protoconid to the base of the crown and then ascends lingually to the hypoconulid notch. The lingual side of the hypoconulid notch is poorly-defined by the anterolingual basal corner of the paraconid. There is no buccal cingula around the base of the protoconid or hypoconid, although there is a slight cingulum at the buccal edge of the midvalley between the bases of those two cusps. The talonid is wider than the trigonid. The talonid basin is shallow but enclosed on all sides. The lingual side of the tooth is longer than the buccal side.

M_5: This tooth has the tips of the protoconid and metaconid missing. The paraconid is shorter than the metaconid which was shorter than the protoconid. The entoconid and hypoconid are closely approximated and only defined as the lingual and buccal ends respectively of a single, continuous crest. There is no hypoconulid. The paracristid is longer than the metacristid which is much longer than the very short hypocristid. The carnassial notch in the metacristid occurs lingual to the midpoint of the metacristid. The short cristid obligua descends steeply to the lingual half of the midvalley and then begins to ascend the posterior flank of the trigonid at a point below the carnassial notch in the metacristid. Half-way along the crest between the hypoconid and entoconid there is a small notch which presumably defines the boundary between the virtually transverse postentocristid and the transverse hypocristid, the two together functioning as a single transverse crest as in M_4. The entoconid and hypoconid sustain very small wear facettes (formed by wear with the postprotocristid on M^5) that are united across the transverse talonid crest. There is no posterior cingulum. The anterior cingulum is as in the M_4. A buccal basal cingulum appears to have extended across the midvalley between the bases of the protoconid and hypoconid, but has presumably been breached by wear from the paracone of M^5. The talonid basin is shallow but enclosed on all sides by the preentocristid, cristid obliqua, and posterior transverse crest. The trigonid is much wider than the talonid. The lingual side of the tooth is longer than the buccal side.

Meristic gradients between M_4 and M_5: The paracristids and metacristids are subequal in length. The posterior (composite) talonid crest is much shorter in M_5. The cristid obliqua is more lingually positioned in M_5. The talonid is much narrower on M_5. The entoconid and hypoconid of M_5 are much more reduced and approximated. The anterobuccal corner of the anterior cingulum is more gently and evenly convex in M_5 (in M_4 it is unevenly convex). The preentocristid is better-developed in M_4.

Dentary: The dentary is missing anterior to the P_3 although the posterior face of the P_2 posterior root alveolus is preserved. It is also missing part of the dentary posterior to the mandibular foramen. A mental foramen occurs below the anterior root of the M_2. The ventral rim of the dentary is slightly curved convexly below the M_5 and then ascends linearly and gradually anteriad. The depth of the dentary decreases gently anteriad. The remnant of the ascending ramus suggests its anterior edge formed an approximate angle of 120° with respect to the alveolar row.

DISCUSSION

The M_4 of *Wakamatha tasselli* reveals a unique talonid construction among dasyurids. In most dasyurids that have entoconids, the cusp is oval, or even laterally compressed (Archer 1976), not crescent-shaped. Further, with the exception of some *Sminthopsis*, the hypocristid of M_4 initially extends transversely or posterolingually across the talonid to ultimately contact the hypoconulid, not the entoconid. An exception (one other *Sminthopsis* approaches this condition) is *Sminthopsis crassicaudata*, but the structure of the talonid suggests it is convergent on the condition found in *Wakamatha tasselli*. In this highly apomorphic species of *Sminthopsis* (Archer 1976, 1977, and in preparation), the hypocristid extends transversely from the hypoconid to the posterobuccal corner of the entoconid and then turns sharply posteriad to merge into the hypoconulid. As this tooth in *S. crassicaudata* sustains wear, the minor posterior element of the hypocristid is rapidly overrun and a functional uninterrupted transverse shearing crest is developed between the hypoconid and the entoconid. In *Wakamatha tasselli* this transverse crest development is achieved but in a different way and without the requirement of occlusal wear. It is formed by the conjunction of a posterobuccally directed postentocristid and the hypocristid.

In both *Sminthopsis crassicaudata* and *Wakamatha tasselli*, the occlusal edge of this transverse talonid crest acts as a shearing counterpart to the postprotocrista of the M^4, while its posterior flank is worn by the anterior face of the metacone of M^4. The tip of the M^4 metacone would have worn the posterior cingulum of M_4 and anterior cingulum of M_5. All of these essential shearing counterparts are present in other dasyurids.

Convergence in this dental feature in two dasyurids suggests it has functional value. Although it is not clear what this value is, it may be that it facilitates the transverse movement of the dentary during which time food is crushed between the protocone and talonid basin. By removing the posterolingual limb of the hypocristid, the metacone can move transversely through a greater uninterrupted distance between the lower molars. Further, the upper and lower molars can occlude more closely, thereby being able to more finely commutate the food being crushed in the talonid basin.

Another unique dasyurid feature in *Wakamatha tasselli* is the very large size of P_3 as indicated by the alveoli. This is a common feature among didelphids, borhyaenids, thylacinids, and some peramelids but not dasyurids.

It is of course possible that the alveoli interpreted here to represent P_3 actually represent P_2, P_3 having been lost. Such reduction occurs in some modern species of *Antechinus, Planigale, Dasyurus, Dasycercus, Dasyuroides* and *Myoictis* (Archer 1976a). But even if this were the case in *Wakamatha tasselli*, none of the modern dasyurids that have lost P_3 have a P_2 that is longer than the M_2.

The alveoli interpreted here to represent P_3 could also represent a single alveolus for a reduced P_3, and the posterior alveolus for the posterior root of a P_2. Against this interpretation is the fact that the bony septum between these two alveoli has a median swelling and a slight longitudinal thickening, features characteristic of a septum formed between the two converging roots of a single tooth, but not of a septum developed between two adjacent teeth.

Laterally compressed M_5 trigonids are not found today among dasyurid species inhabiting high rainfall areas of New Guinea, but are universal among arid-adapted Australian dasyurids inhabiting the drier parts of central Australia. It is also not a feature of the middle Miocene *Ankotarinja tiranensis* (Archer 1976b) or of structurally primitive Cretaceous and Tertiary didelphoids. It appears to be an apomorphic state within the Dasyuridae. It normally correlates in modern dasyurids with complete reduction of a metacone on M^5.

The stratigraphic horizon from which *Wakamatha tasselli* originally came is unknown. Presumably it is either the middle Miocene Namba Formation, or the Pleistocene Eurinilla Formation, both of which are exposed in the adjoining banks of Billeroo Creek. Efforts to recover by wet sieving, more dasyurid specimens from the type locality, both from the soft muds, sands and silts that comprise the basal load of the Creek and from the sands and clays of the bank, were unsuccessful. We did recover fossil lungfish teeth, teleost spines, crocodile and turtle fragments, and an edentulous phalangeroid dentary. None of this material can at present be assigned with any confidence to either the Namba or Eurinilla Formations.

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PLATE 1

Wakamatha tasseli gen. et sp. nov., Holotype NMV P33253.
FIG A: Stereo-triplet of the LM_{4-5} in buccal–occlusal view.
FIG. B: Occlusal view of the entire dentary fragment with alveoti for P_3 to M_3, and M_{4-5}.
FIG. C: Anterior–occlusal view of the LM_{4-5}.
White line equals 0·05 mm.

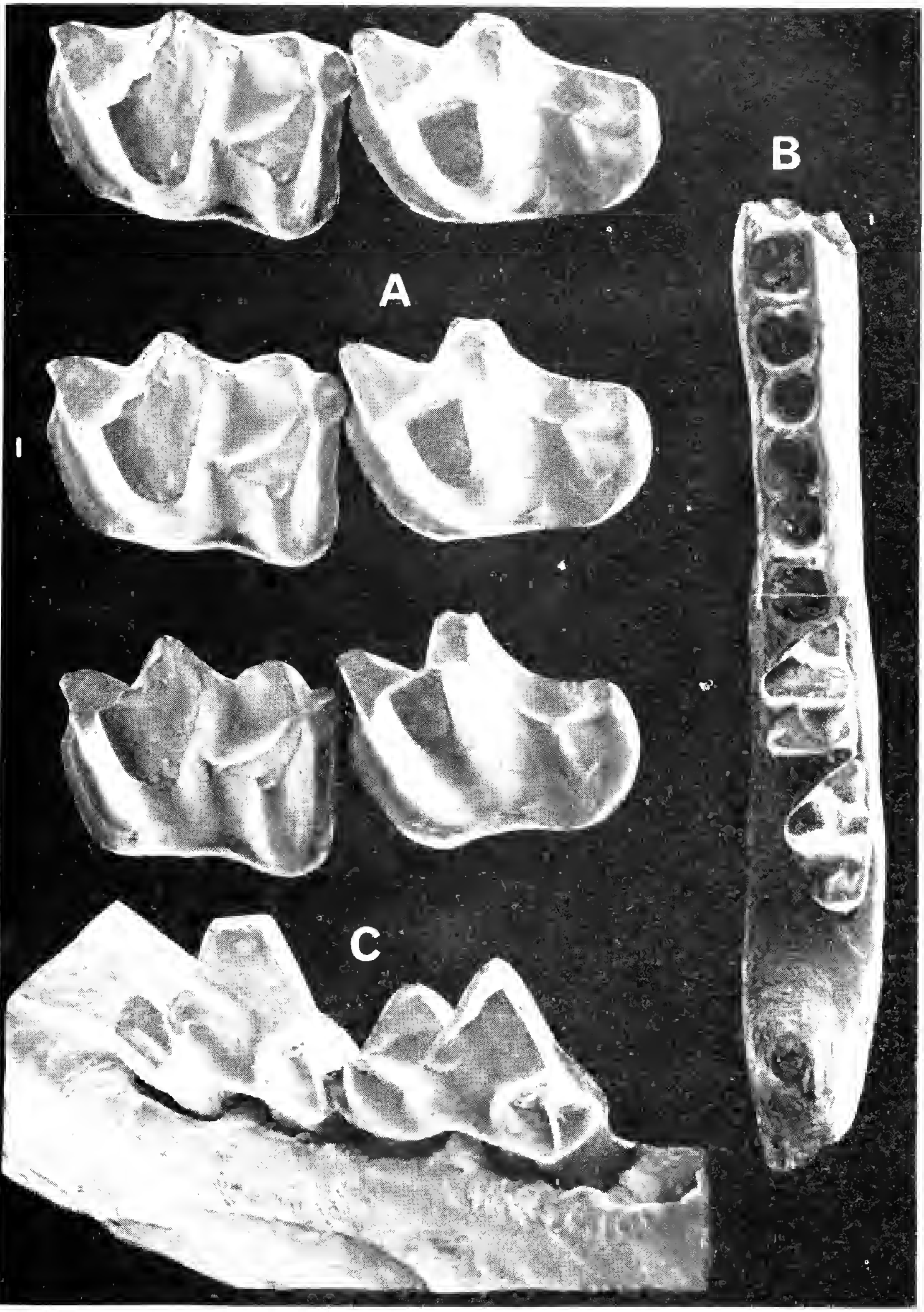
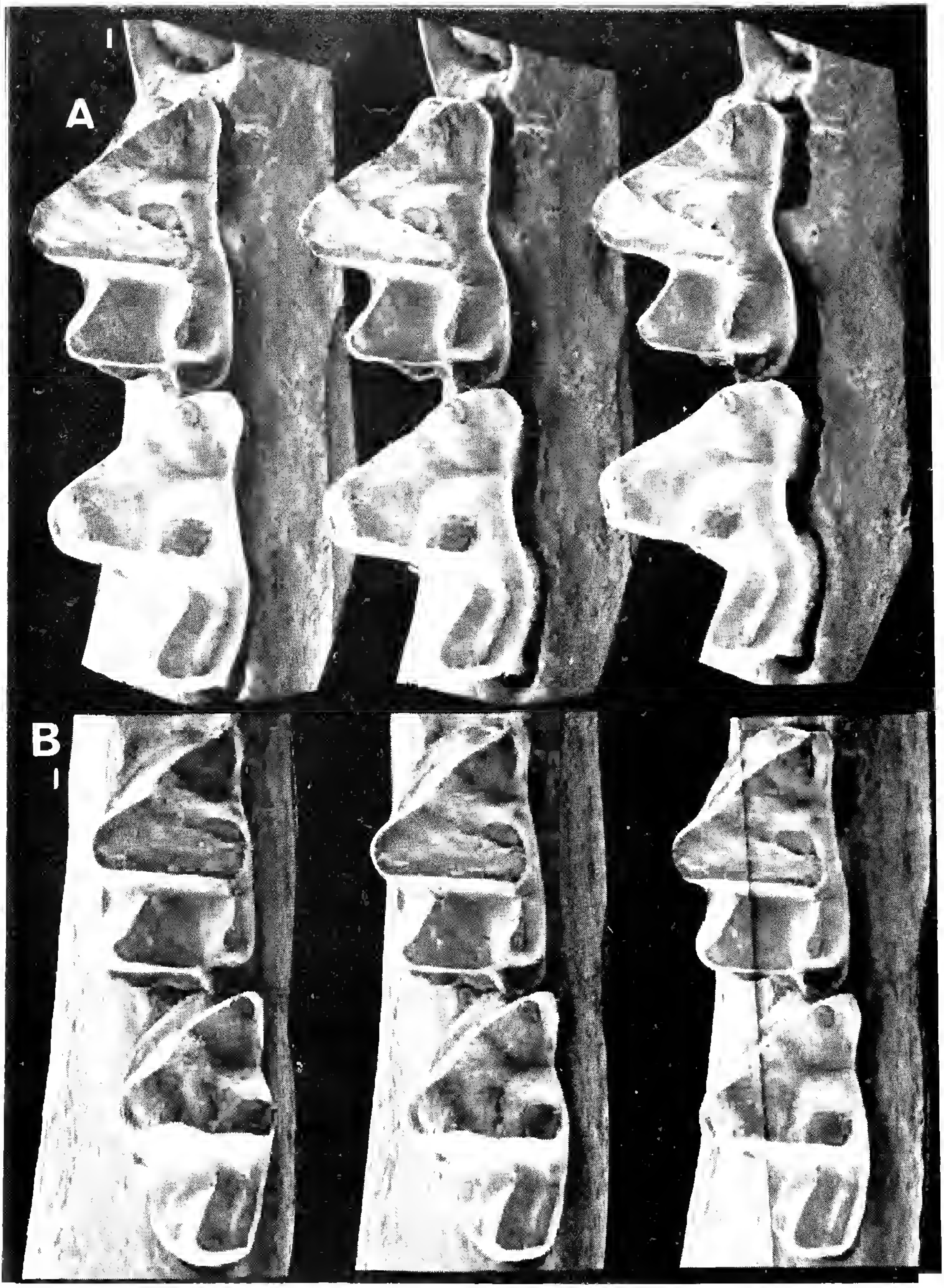

A
B
C

PLATE 2

Wakamatha tasseli gen. et sp. nov., Holotype NMV P33253.
FIG. A: Stereo-triplet of the LM_{4-5} in lingual – occlusal view.
FIG. B: Stereo-triplet of the LM_{4-5} in occlusal view.
White line equals 0·05 mm.


A
B

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ELECTROPHORETIC, ENZYME, AND PRELIMINARY TOXICITY STUDIES OF THE VENOM OF THE SMALL-SCALED SNAKE, *PARADEMANSIA MICROLEPIDOTA* (SERPENTES: ELAPIDAE), WITH ADDITIONAL DATA ON ITS DISTRIBUTION

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ABSTRACT

Parademansia microlepidota, a species recently resurrected from the synonomy of *Oxyuranus scutellatus*, has been collected live for the first time. The species occurs only in the Lake Eyre Drainage Basin and is confined to 'ashy downs' areas of the channel systems of Cooper Creek and the Diamantina River.

Electrophoretic and enzyme studies of its venom confirm that *P. microlepidota* is a distinct species. Two directional polyacrylamide gel electrophoresis patterns from *P. microlepidota* venom are clearly distinct from those of *Oxyuranus scutellatus, Pseudonaja textilis, Pseudechis australis,* and *Notechis scutatus*. The venom of *P. microlepidota* contains more hyaluronidase activity than venoms of other Australian Elapids examined.

Toxicity studies suggest that the venom of *P. microlepidota* is the most toxic terrestial snake venom known.

Parademansia microlepidota (McCoy) (the Small-scaled or 'Fierce' Snake) was described in 1879 from two specimens collected in north-western Victoria. A third specimen from 'Fort Bourke' (30°02'S, 145°49'E) was described in error by Macleay (1882) as a new species, *Diemenia ferox*. This specimen has since been lost, and only the two type specimens were known. *P. microlepidota* was recognised as a distinct but apparently 'lost' species for many years (Kinghorn 1923, 1929, 1955, 1956); it resembles *Oxyuranus scutellatus* (Peters), the Taipan, superficially and Worrell (1963a, b) treated *P. microlepidota* and *O. scutellatus* as conspecific. After freshly preserved specimens of *P. microlepidota* were donated to the Queensland Museum from southwestern Queensland, and additional specimens were collected by J. Wombey of the C.S.I.R.O., Darwin from mid-western Queensland, a search of state museum reference collections revealed more specimens, all in the South Australian Museum. Examination of all these specimens (fourteen) and the types of *Diemenia microlepidota* enabled confirmation of the specific status of *P. microlepidota* (Covacevich and Wombey 1976).

A serious case of snakebite in southwestern Queensland was attributed to *O. scutellatus* (Trinca 1969) but when the specimen concerned was examined and compared with both *O. scutellatus* and *P. microlepidota* (Covacevich and Wombey 1976) it proved to be *P. microlepidota.* At the time of the bite the specimen was regarded as one of the Brown Snakes, *Pseudonaja* spp., and *Pseudonaja textilis* antivenene was administered, but the patient's survival was attributed to readily available intensive medical care rather than a satisfactory response to *Pseudonaja textilis* antivenene.

P. microlepidota and *O. scutellatus* are both very large Elapids and, as such, are potentially dangerous to humans. The latter has been responsible for many fatalities and *P. mi-*

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crolepidota has been responsible for one known near fatality, despite the fact that it occurs in only sparsely settled areas. The largest *P. microlepidota* encountered to date measures 2·0 m and most preserved museum specimens and live specimens collected recently measure between 1·5 m and 1·8 m. *O. scutellatus* is alleged to attain a length of close to 3·5 m. The largest specimen in the Queensland Museum reference collection (J26935) measures 2·5 m and specimens of 1·5 m to 2·0 m are commonly encountered.

Live specimens of *P. microlepidota* were collected in late 1975 by two of us (C.T. and J.C.) and have been maintained successfully in captivity since. One specimen is illustrated in Plate 1. Collection of live specimens has permitted examination of the venom of *P. microlepidota* for the first time. Kinghorn (1956) regarded this species as 'deadly venomous' presumably because of its size and apparent resemblance to *O. scutellatus*, a known dangerous snake.

P. microlepidota is apparently confined to the Lake Eyre Drainage Basin of far southwestern Queensland and northeastern South Australia. No specimens have been collected from Victoria or New South Wales since the types of *P. microlepidota* and its synonym *D. ferox* were described late in the nineteenth century. It seems reasonable to assume therefore that the species no longer occurs in this area or, more likely in the light of recent field work, that it has never occurred there and that the museum records may be erroneous. The broad occurrence of *P. microlepidota* (and of its nearest relative *O. scutellatus)* has been described and mapped by Covacevich and Wombey 1976. The species is known from 120 km southeast of Boulia, western Queensland to just south of the Queensland-South Australia border and seems to be confined to the channel systems of Cooper Creek and the Diamantina River. In this area *P. microlepidota* favours the soft loams of the 'ashy downs' which are also favoured in the southwest by *Rattus villosissimus* (the Plague Rat). Populations of this latter species fluctuate dramatically (Covacevich and Easton 1974) and, when present in large numbers, the rats live in extensive interconnected burrow systems which are utilized by *P. microlepidota* as shelters and which also house their prime food source. When rat populations are very low, even appearing absent altogether, the burrows remain, and present evidence suggests that *P. microlepidota* continues to utilize the burrows but virtually stops feeding. The 'ashy downs' also crack extensively during dry periods and this provides additional shelter, enabling *P. microlepidota* to survive high temperatures apparently without food or water for long periods. The species does not occur continuously throughout its range but is found in isolated 'pockets', a characteristic shared with *O. scutellatus*. A population of *P. microlepidota* in the Windorah area is being studied by two of us (C.T. and J.C.) in an effort to obtain data on the biology of this highly specialised snake.

P. microlepidota has variously been referred to *Diemenia*, the genus which included the Brown Snakes (now *Pseudonaja* spp.); *Pseudechis* (the Black Snakes) and *Oxyuranus scutellatus* (the Taipan). It is easily distinguished from *Pseudonaja* spp. and *Pseudechis* spp. by external features such as head shape, head and body scales, and colour but is externally similar to *O. scutellatus*. The presence of 23 midbody scales, an unusually high count for Australian elapid snakes, in both *P. microlepidota* and *O. scuttellatus*, and other similarities, have apparently led to some of the confusion between these two species. The external and skull differences between *P. microlepidota* and *O. scutellatus* are summarised by Covacevich and Wombey (1976). Detailed analysis of the generic relationships between *P. microlepidota*, *O. scutellatus*, *Pseudonaja* spp., and *Pseudechis* spp. has not been completed but external and skull features suggest that *Parademansia* most resembles *Oxyuranus*, shares some characteristics with *Pseudonaja* spp., and least resembles *Pseudechis* spp. Examination of the venom of *Parademansia*, *Oxyuranus scutellatus*, *Pseudonaja* spp., and *Pseudechis australis* (the Mulga Snake) confirms this preliminary observation.

THE VENOM OF *P. MICROLEPIDOTA*

A two directional polyacrylamide gel electrophoresis (P.A.G.E.) system for characterising venom was developed by two of us (A.B. and S.S.) as an aid to the detection and identification of snake venom in clothing and biological fluids. The method was applied, in fact, only as an analytical procedure following the development of a more sensitive radioimmunoassay by Coulter et al (1974). It was considered that this improved P.A.G.E. system together with selected enzyme and toxicity studies would allow critical comparison of elapid venoms.

MATERIALS AND METHODS

VENOM COLLECTION

All snakes were housed in laboratory cages, one snake to a cage, and fed on freshly killed mice and day-old chickens. Individual snakes refusing dead food were fed minced whole animals through a catheter. The *Parademansia* were fed on mice only. The snakes, with one exception, were in excellent condition when the programme was started and remained so. The exception (No. 16) had been in captivity for some time and was very thin. This snake, the largest in the group, gave low venom yields.

The venom used for studies at the Commonwealth Serum Laboratories and for assessing yields was collected over a period of three months. Venom samples were obtained by inducing the snakes to bite a tightly stretched latex membrane over a glass container. The venom from each snake was frozen immediately and later dried under an ultimate vacuum of 5×10^{-3} torr, weighed, and then stored under vacuum.

The pooled venom used for toxicity and cross-protection studies was mixed in the liquid state after extraction, and then processed as above.

TWO DIRECTIONAL POLYACRYLAMIDE GEL ELECTROPHORESIS (P.A.G.E.)

The method used was based on that of Davis (1964) and Kochwa (1964), with modifications so that venom components can move to either anode or cathode according to the net charge of the individual components. To achieve this a separation gel was polymerised both above and below the venom sample.

REAGENTS: The following special reagents were required for the P.A.G.E.: Acrylamide, N,N'-methylenebisacrylamide (BIS), Riboflavin, Tris (hydroxymethyl) methylamine (TRIS), and Bromophenol blue from British Drug Houses Ltd.; Xylene Brilliant Cyanin G (Michrome No. 1224) from Edward Gurr Ltd.; N,N,N',N',-tetramethylethylene-diamine (TEMED) from Eastman Organic Chemicals; and 'Photo-flo 200' from Kodak.

The following stock solutions were prepared:

(a) 0·28% Ammonium persulphate (prepared weekly).

(b) 3·02 M TRIS pH 8·9, 0·46% TEMED. The pH was adjusted with HCl.

(c) 60% acrylamide. Before use the acrylamide was recrystallized from chloroform.

(d) 1·2% BIS. Before use the BIS was recrystallized from acetone.

(e) 0·988 M TRIS pH 6·7, 0·92% TEMED. The pH was adjusted with HCl.

(f) 3·6% BIS.

(g) 8 mg/ml Riboflavin. Insoluble material was removed by filtration with Whatman No. 41 filter paper.

(h) 64% sucrose.

(i) The electrode buffer consisted of 0·6 g/litre TRIS and 2·88 g/litre glycine.

PROCEDURE: Twelve clean glass tubes 140 mm long x 5 mm were rinsed in 1/200 dilution of 'Photo-flo 200' and without drying were set vertically in a stand with the lower ends closed. The lower small pore separation (anodal) gel (7%) was formed by mixing the following stock solutions at room temperature:

(a) 4 ml: (b) 2 ml: (c) 1·87 ml: (d) 2·45 ml: (H_2O) 5·68 ml

The tubes were filled to a height of 65 mm with this gel solution. Water was carefully layered on top of each 'liquid' gel to ensure a horizontal gel surface. Polymerization of the gel took approximately 20 min. The large pore spacer gel was made by mixing the following volumes of stock solutions:

(e) 0·5 ml: (c) 0·5 ml: (f) 2 ml: (g) 0·5 ml: (h) 2·5 ml: (H_2O) 2 ml

Aliquots of 200μ l were added to each tube and allowed to polymerize under a water layer which was then removed. The sample gel mixture was prepared as follows:

(e) 0·5 ml: (c) 0·5 ml: (f) 2 ml: (g) 0·5 ml: (h) 2·5 ml

For analysis of snake venoms, 200μ g of venom was dissolved in 190μ l of the sample gel mixture which was made up to 250μ l total volume with water. A total of 200μ l of this sample gel mixture was allowed to polymerize in the appropriate tube under water. The water was then removed and the upper cathodal small pore separation gel added to a height of 135 mm. This gel was of the same composition as the lower anodal gel.

Electrophoresis was carried out in 'LABQUIP' electrophoresis apparatus filled with the electrode buffer. Bromphenol blue (1 ml of 0·001% per 200 ml of buffer) was added to the upper or cathodal compartment of the apparatus as a marker. Tubes were electrophoresed at 3 ma/tube until the marker was 5 mm above the bottom of the tubes. Time of electrophoresis was 2·5 hours.

The gels are stained essentially by the method of Diezel et al (1972) but with the dye being prepared in 10% trichloracetic acid.

Assay of Hyaluronidase Activity

Hyaluronidase activity was determined by the method of Dorfmann (1955). Hyaluronic acid was obtained from Worthington Biochemicals, and the source of hyaluronidase was 'Rondase' as marketed by Evans Medical Ltd. Bovine Serum Albumin was purchased from Armour Laboratories. The results are expressed as units of hyaluronidase activity per mg venom.

Toxicity Studies, LD_{50} Determination*

Stock venom solutions of 1 mg/ml were prepared in 0·85% saline in appropriate aliquots and stored at -20°C. Samples of these stock solutions were thawed out and diluted with 0·85% saline as necessary prior to each toxicity determination, the dilution interval was 1:1·25. C.S.L. white Swiss mice in the weight range of 17 to 20 g were used in the assay. Four mice were used at each level which was given subcutaneously (S.C.) in a volume of 0·2 ml. Results were read as mice dead or alive at 48 hours.

The LD_{50} of each venom was calculated using the method of Spearman-Karber as adapted by Baxter and Gallichio (1976).

The formula employed was as follows:

$$\log_{10} LD_{50} = {}^{x}100 \pm \frac{d}{n}\left[(\Sigma r) - \frac{n}{2}\right]$$

where LD_{50} is the 50% lethal dose end point; ${}^{x}100$ is the $\log_{10}$ dose giving 100% deaths at that dose and all higher doses; d is the $\log_{10}$ dose interval; n is the number of mice at each dose interval; and Σ r is the total number of mice dying between and including the 0% and 100% response levels to increasing doses of venom.

Results

The venom yields obtained by regularly 'milking' individual specimens of *P. microlepidota* are shown in Table 1. The significance of these yields will be considered later in the light of the toxicity studies.

The P.A.G.E. patterns or 'finger prints' of a number of important elapid venoms are shown in Plate 2, fig. 1. The venoms studied were from a pool collected by milking many individual snakes. Venoms of different species have distinct patterns due to a variable number of components of differing mobilities and concentrations. The cathodal gel demonstrates the presence of positively charged proteins which further characterise the venoms. In the case of *N. scutatus* venom the cathodal moving proteins are known to be neurotoxins. Broad and Coulter at C.S.L. have also shown that the major cathodal band in the case of *P. textilis* venom is an important neurotoxin.

Plate 2, figs. 2 and 3 examine more closely the electrophoresed components of various *O. scutellatus* and *P. microlepidota* venom samples. Far greater uniformity can be seen amongst the individual single milkings of the latter species than in *O. scutellatus*. Because the sample B shown in Plate 2, fig. 2 was so different from other P.A.G.E. patterns of *O. scutellatus*, a further milking, sample H, was obtained from this particular specimen. As can be seen the same result was obtained. Toxicity studies on this particular venom showed it to be far less toxic than the other *O. scutellatus* venom samples.

Hyaluronidase activity of the venom of seven specimens of *P. microlepidota* ranging between 12·0 and 15·0 units/mg venom is shown in Table 1. For eight specimens of *O. scutellatus* it was considerably lower — 3·0, 3·0, 4·7, 5·0, 6·1, 8·2, 8·6, and 8·7. Hyaluronidase activity for large samples of pooled venom from *P. microlepidota* and *O. scutellatus* was 11·8 and 7·5 respectively.

The results of LD_{50} determinations on venom pools from the four most toxic Australian snakes were: 0·43 *(Parademansia microlepidota)*, 0·90 *(Pseudonaja textilis)*, 1·52 *(Oxyuranus scutellatus)*, and 3·82 *(Notechis scutatus)*. LD_{50} determinations for individual specimens of *P. microlepidota* are listed in Table 1 and confirm its extremely high toxicity in mice. Preliminary studies in guinea pigs suggest similar relative toxicities to those obtained in mice.

DISCUSSION

Two-directional electrophoresis of the principal Australian elapid venoms establishes their individual patterns or characteristic 'finger prints'. The innovation of displaying the cathodal moving components as well as those seeking the anode allows the comparison of the basic proteins which probably have neurotoxic activity.

Considerable uniformity is seen in P.A.G.E. patterns of the milkings from individual specimens of *P. microlepidota*. Initially we thought this was because the specimens were all collected from a limited area. It was not seen with individual milkings from specimens of *O. scutellatus* which come from diverse areas. Overseas experience has been quite different. Johnson et al (1967) found that milkings from individual specimens of

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* LD_{50} is the quantity of venom which kills 50% of a group of a specified animal receiving that amount of venom by a specified route.

Crotalus atrox could be clearly distinguished from each other by the use of one directional P.A.G.E. Taborska (1971) discovered similar variations amongst individual venom milkings from *Echis carinatus*. More recently Glenn and Straight (1977) reported similar studies on the venom of *Crotalus viridis* concolor. Not only were the electrophoretic patterns of the venoms collected from the 'same area' considerably different but they varied in lethality.

Further work is proceeding upon individual milkings from other species of Australian snakes from geographically remote areas as well as those found in close proximity to each other. It will be interesting to see if other species show the remarkable electrophoretic homogeneity seen with *P. microlepidota*. If they do not, then some explanation will have to be found for the lack of intraspecific variation in *P. microlepidota*.

It was interesting to find a specimen of *O. scutellatus* which yielded on two separate occasions a venom with only one major component and greatly reduced *in vivo* toxicity. This venom is being studied further to determine the properties of this major component. The specimen has a normal healthy appearance and its venom output is normal.

A further distinction between *P. microlepidota* venom and venom from *O. scutellatus* is seen by the much higher level of hyaluronidase activity or spreading factor seen in the former. Such activity will accelerate the onset of systemic toxic effects of the venom by facilitating its movement in the tissue.

The studies of *P. microlepidota* venom toxicity in mice are very significant as they suggest this snake is potentially the most toxic terrestrial snake. The average yield of 44·2 mg is enough venom to kill over 50,000 mice. The maximum yield of 110 mg would kill 125,000 mice. *Oxyuranus scutellatus* with an average yield on milkings of 120 mg (Garnet 1969) could account for some 47,500 mice. The average quantity of venom collected from *Notechis scutatus* is 35 mg, which could kill some 4,500 mice.

Ophiophagus hannah (the King Cobra) yields more venom than any other terrestrial snake — an average of 420 mg (Canthavorn 1969), with a subcutaneous LD_{50} for 20 g mice of 34·5 μ g (Minton 1974). This quantity would kill some 6,000 mice. Brown (1973) considered *O. scutellatus* (the Taipan) was the most 'deadly' snake in the world, presumably because of the combination of its high venom yield (average 120 mg) and high venom toxicity (LD_{50} of 1·52 μ g). In the light of the information above and in Table 1 this position appears to be challenged by *P. microlepidota*.

NEUTRALIZATION OF VENOM WITH ANTIVENENE.

We have found that *O. scutellatus* antivenene quite satisfactorily neutralized this venom *in vivo*. The Australian Polyvalent Antivenene made by C.S.L. is also quite satisfactory if the former antivenene is not available. *Pseudonaja textilis* or *Notechis scutatus* antivenenes are ineffective.

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Dr T. Houston (South Australian Museum) provided one of the live specimens of *Parademansia microlepidota* used in this study. Mr E. Bennett and Mr A. Anderson (Queensland Institute of Technology) and Mr A. Coulter (Commonwealth Serum Laboratories) have given helpful advice. Excellent technical assistance has been received from Miss A. Miller and Mrs M. Barbaro (Commonwealth Serum Laboratories).

TABLE 1: YIELD, HYALURONIDASE ACTIVITY, AND TOXICITY OF VENOM FROM SEVEN SPECIMENS OF *PARADEMANSIA MICROLEPIDOTA*

Specimen	Length (cm)	Sex	Venom yield* (grams dried)	Hyaluronidase activity+ (units/mg venom)	Toxicity^x LD_{50} μ g
7	155	F	0·03–0·04	13·2	0·31
13	160	F	0·03–0·06	12·8	0·35
14	165	M	0·02–0·04	13·0	0·61
5	170	M	0·02–0·03	15·0	0·35
3	178	F	0·04–0·07	13·0	0·50
11	180	M	0·06–0·11	14·7	0·39
16	193	M	0·02–0·03	12·0	0·28

* six milkings 16.11.1975 — 12.2.1976

\+ 11·8 for large venom pool

x 0·43 for large venom pool

Mr B. Campbell (Queensland Museum) constructively criticized the manuscript, and Mr A. Easton (Queensland Museum) took the photograph of the live specimen of *Parademansia microlepidota*.

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PLATE 1
Specimen of *Parademansia microlepidota* measuring approximately 170 cm, from southwestern Queensland

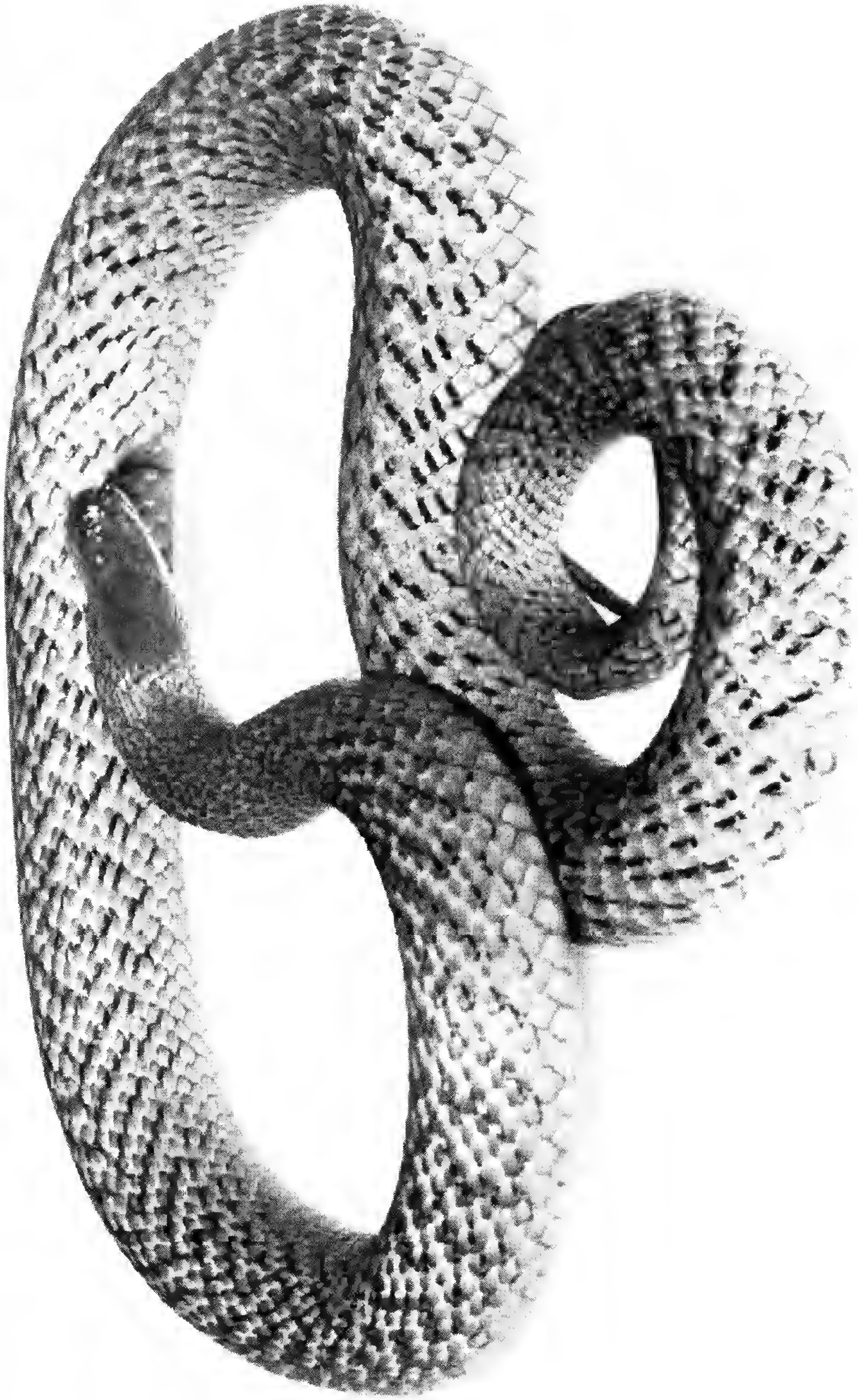


PLATE 2

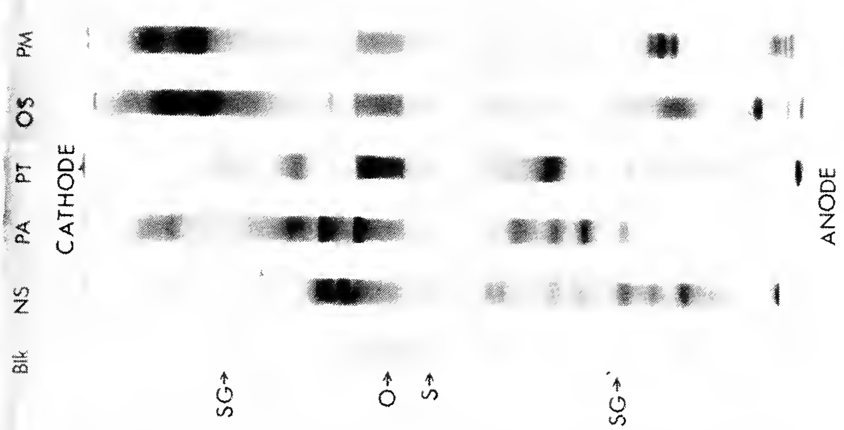
FIG 1. Two-directional 'P.A.G.E. patterns' of venom pools from five Australian elapid snakes.

Blk = Blank gel
NS = *Notechis scutatus*
PA = *Pseudechis australis*
PT = *Pseudonaja textilis*
OS = *Oxyuranus scutellatus*
PM = *Parademansia microlepidota*
O = *Application or sample gel*
S = *Spacer gel*
SG = *Separation gel*

FIG. 2. 'P.A.G.E. Patterns' of *Oxyuranus scutellatus*. Samples A to G are from individual snakes from different Queensland localities. Sample H was a requested second milking a month later from snake B. Sample OS is from a major venom pool. Blk is a blank gel.

FIG. 3. 'P.A.G.E. Patterns' of *Parademansia microlepidota*. The numbers indicate the snake (see Table 1) from which the single milking was collected. Sample PM was from a venom pool.

1


Blk
NS
PA
PT
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PM
CATHODE
ANODE
SG→
O→
S→
SG'→

2


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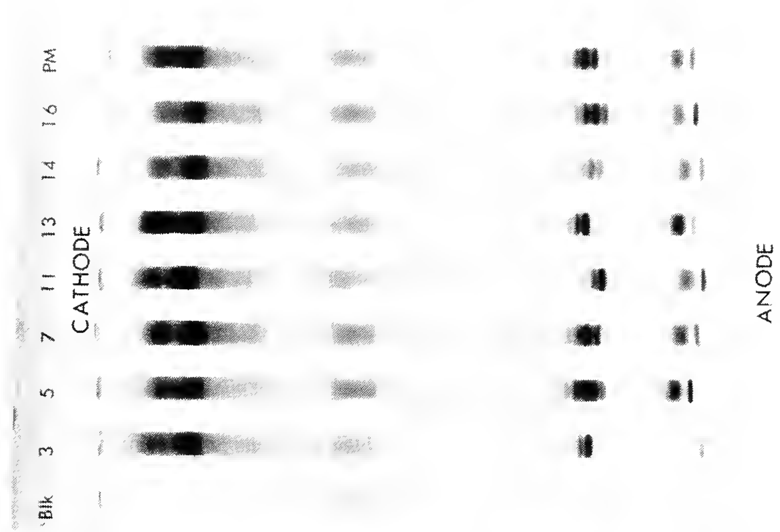
Blk
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14
16
PM
CATHODE
ANODE

Mem. Qd Mus. **19**(3): 331–55, pls. 1–5 [1979]

A PROTEROSUCHIAN THECODONT FROM THE REWAN FORMATION OF QUEENSLAND

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ABSTRACT

A new proterosuchian reptile, *Kalisuchus rewanensis*, is described on the basis of fragmentary skull and postcranial remains from the Lower Triassic (Rewan Formation) of SE Queensland. The classification of proterosuchians is briefly reviewed and *Kalisuchus* is referred to the family Proterosuchidae on account of its many resemblances with Chinese and African species of *Chasmatosaurus (Proterosuchus* auct.). *Kalisuchus* was an amphibious and superficially crocodile-like predator that probably reached a maximum body length of two or three metres. Its relationships with other proterosuchians suggest that the parent sediments may be correlated with the upper part of the S. African *Lystrosaurus* Zone (or, possibly, with the lower part of the *Cynognathus* Zone). This tentative correlation is supported by palaeobotanical evidence. The Rewan vertebrate fauna may be interpreted as a Palaeozoic relict in order to account for its surprising lack of synapsid reptiles (notably *Lystrosaurus)*.

The late Permian and early Triassic reptiles known as proterosuchians were probably the basal stock of the entire subclass Archosauria. They were, in other words, the remote ancestors of animals as varied as the crocodilians, the pterosaurs (or flying reptiles) and the two great groups of dinosaurs (saurischians and ornithischians). Remains of proterosuchians are known from South Africa, China, India, Russia, and possibly Argentina (see Charig and Sues 1976 for a comprehensive review). Despite their obvious importance for understanding of archosaur history the proterosuchians are still rather poorly known, most being represented by rare and fragmentary fossils. In such circumstances practically any new proterosuchian material will be of considerable interest.

This paper concerns a proterosuchian from the Rewan Formation of Queensland. While its remains are far from complete — in established proterosuchian tradition — they do nevertheless provide a good deal of significant new information, particularly with respect to dating of the Rewan Formation and to the relationship between proterosuchians and pseudosuchians. This proterosuchian is the earliest archosaur yet described from Australia.

MATERIAL

Most material comes from a single locality, known as the Crater, situated 72 km southwest of Rolleston and 11 km south of Rewan homestead. The Crater is a steep-sided basin, some 200 m across, which cuts into red beds at about the middle part of the Rewan Formation. The exposed sediments are red, brown, and green silts and mudstones with occasional sandy layers and strings of ironstone nodules. These beds are probably of Lower Triassic age and were apparently laid down by a system of meandering streams (Howie 1972a). Most specimens are isolated bone fragments that had been washed down on to the floor of the Crater by rain; very few specimens were found in the walls of the basin. Many of the bone fragments have been shattered by crushing and by weathering, and some seem to have suffered transport before burial. The bone itself is grey, cream or white in colour, but is usually stained black, brown or red by iron.

A few specimens were collected from a second locality, Duckworth Creek, which is situated southwest of the settlement of Bluff and about 127 km north-northeast of the Crater. This locality has been described by Howie (1972b), who explained that the sediments exposed there may be correlated directly with those of the Crater. In its preservation and appearance the Duckworth Creek material is virtually identical with that from the Crater.

All illustrated specimens were collected from the Crater and have individual QM catalogue numbers (see captions); non-figured material is catalogued under K10125 (from the Crater) or F9549 (from Duckworth Creek).

SYSTEMATICS

Class REPTILIA
Subclass ARCHOSAURIA
Order THECODONTIA Owen 1859
Suborder PROTEROSUCHIA Broom 1906
Family PROTEROSUCHIDAE Broom 1906

Genus **Kalisuchus** gen. nov.

Type and only species *K. rewanensis* sp. nov.

Kalisuchus rewanensis sp. nov.

HOLOTYPE: single right maxilla, QM F8998 (Plate 1, figs. A–C; Plate 2, fig. A).

REFERRED MATERIAL: an assortment of bone fragments from skull, vertebral column, limb girdles and limbs (QM catalogue numbers under 'Material').

LOCALITIES: the Crater, Rewan property, about 72 km southwest of Rolleston, SE Queensland (field locality L78 in QM records); a small amount of referred material was obtained from Duckworth Creek, near Bluff, SE Queensland.

HORIZON: lower beds of the upper part of the Rewan Formation, Mimosa Group; Lower Triassic.

ETYMOLOGY: the genus is named for Kali, goddess of destruction, in allusion to suspected predatory habits of the animal; the specific name refers to provenance of material.

DIAGNOSIS (genus and species): proterosuchid thecodontian with narrow and lightly constructed skull. Orbit large, pear-shaped or triangular (narrower below), set higher than lateral temporal fenestra, with rugose ornament on upper rim. Snout laterally compressed, with transversely expanded and downcurved tip, and with large antorbital fenestra roofed by lacrimal. Palate narrow, with long slit-like internal nares flanked by flat medial faces of maxillae. Jugal with blade-like process on ventral rim and with posterior ramus shaped like an inverted L-girder in cross-section. Rear edge of postorbital set into deep slit in leading edge of dorsal jugal ramus. Mandible robust, deeper than wide anteriorly, with splenial extending forwards almost to the loose symphysis; jaw wide and shallow at suspensorium, with unfused prearticular in front of glenoid fossa, and with prominent and straight retroarticular process. Near-isodont dentition of compressed, recurved and acutely pointed teeth having finely serrated rear edges; implantation subthecodont; upper tooth row interrupted at junction of maxilla and premaxilla. All centra spool-shaped, amphicoelous, longer than high and laterally compressed. Neck centra elongate, strongly keeled, perhaps with crescentic facets for small intercentra; trunk centra distinctly shorter than those of neck, weakly keeled or without keels; tail centra elongate, with weak paired keels or with smooth ventral surfaces. Neural spines of neck and trunk regions with dorsal edges swollen into very large spine tables. Posterior neck vertebrae with triple-headed ribs. Acetabulum imperforate; distal part of pubis twisted and transversely expanded. Limb bones thin-walled, with hollow or cancellous interior, resembling those of *Chasmatosaurus* spp. but noticeably less robust. Shaft of radius with well defined fossa for origin of deep digital flexors. Femur dorsally arched in distal two thirds, with deep intertrochanteric fossa, and with distinct fourth trochanter situated half-way down shaft. Calcaneum with stepped antero-medial face and posterior tuber.

DESCRIPTION

SKULL: The skull of *Kalisuchus rewanensis* is represented by fragments including a right maxilla (the holotype), a left jugal, a section of skull roof and portions of the mandibles. Evidently these fragments were derived from several animals: they are of disparate sizes and were collected on different occasions.

The maxilla is typically archosaurian in structure (Plate 1, figs. A–C; Plate 2, fig. A). It is cleanly broken at the back but is well preserved elsewhere and shows details of its contacts with lacrimal and premaxilla. The robust tooth-bearing portion is roughly semicircular in cross-section, with a flat medial face, and flares outwards a little beneath the antorbital fenestra. In advance of this the maxilla runs slightly inwards, indicating that the snout was relatively narrow. The lack of maxillary contribution to the palate makes it clear that the internal naris was a long slit adjoining the maxillary tooth row. At the rear of the maxilla a shallow groove in the dorso-lateral surface may have accommodated the anterior tip of the jugal beneath the antorbital fenestra. The anterior limit of the fenestra is defined by a thin ascending process; medial off-setting and inwards arching of this process indicate that the sides of the snout were recessed and overhung by the skull roofing bones. The upper rim of the fenestra was formed by the lacrimal, which met a narrow wedge-shaped facet on the ascending process of the maxilla. The junction between maxilla and premaxilla is extremely unusual: at the front of the maxilla a dorsal groove received the sub-narial ramus of the premaxilla in normal archosaur fashion, but lateral to this there was a more extensive secondary contact. Anteriorly the tooth-bearing part of the maxilla decreases in height and is drawn out laterally above the tooth row as a thick shelf. The shelf has a grooved outer margin and its upper and lower surfaces are marked with fine longitudinal striations. Evidently there was some complex interdigitation between this maxillary shelf and the premaxilla, with the two combining to form an expanded and hood-like tip to the otherwise narrow snout. The down and forwards slope of the maxillary shelf probably indicates that the intact skull possessed the downcurved premaxillae which are characteristic of proterosuchids in general.

The left jugal is incomplete at front and back but is nevertheless fully archosaurian in appearance (Figs. 1A–B). Its posterior ramus seems deceptively robust in lateral view; in fact it has a cross-section like an inverted L, with a broadly rounded rim between dorsal and lateral faces. A depression in the lateral face of the posterior ramus is the result of crushing, there being no discernible trace of an attachment surface for the quadrato-jugal. The stump of the anterior ramus is a compressed blade with its outer face looking slightly downwards; its medial face bears a shallow groove for the attachment of the ectopterygoid. The dorsal ramus is a stout, tapering and twisted blade which is slightly arched in cross-section (convex forwards) and has its outer face turned to the rear. At its upper end the dorsal ramus has a finely wrinkled surface, suggesting that the upper rim of the orbit carried rugose ornament (as it does in *Chasmatosaurus vanhoepeni).* The gracefully recurved bar between orbit and lateral temporal fenestra was constructed in standard archosaur manner of postorbital overlapping jugal, with the lower edge of the postorbital fitting into a deep slit in the leading edge of the dorsal jugal ramus. This interlocking between postorbital and jugal is apparently the reverse of that in *Chasmatosaurus vanhoepeni,* where the postorbital has been described as 'grooved on the hind surface to receive the dorsal process of the jugal' (Cruickshank 1972, p. 97).* None of the orbital margin has remained intact, though it is clear from the amount of bone between anterior and dorsal branches of the jugal that the ventral rim of the orbit lay somewhat higher than that of the lateral temporal fenestra. Backwards inclination of the dorsal jugal ramus indicates that the orbit was probably triangular or pear-shaped in outline (narrower below). The central part of the jugal, directly under the dorsal ramus, is thickened into a near-vertical buttress; this is damaged but seems, originally, to have extended into a prominent process on the lower edge of the jugal.

The skull roof is represented by a heavily crushed and plate-like piece of bone (Fig. 1C). Its asymmetry implies that it does not come from the mid-line, and it is tentatively identified as the left nasal with small portions of prefrontal and lacrimal still attached. This section of skull roof would have formed the dorso-lateral region of the snout immediately above the left antorbital fenestra. At the extreme postero-lateral margin of the specimen deep wedge-shaped impressions mark part of the coarsely interdigitating suture with the frontal. Lateral to this the nasal is overlain by a narrow slip of bone identified as part of the left lacrimal and this, in turn, is overlain by a tiny fragment of the left prefrontal. Lacrimal and prefrontal would have defined the antero-dorsal rim of the orbit, though none of this rim is preserved in the specimen. Along its antero-lateral edge the nasal is thickened and grooved for the attachment of the maxilla. Transverse arching of the nasal is very weak and has undoubtedly been reduced by crushing; in the intact skull that arching would have been considerably stronger, marking the break in slope between the roof and the side of the snout.

The mandibles are represented by fragments (Plate 2, fig. C; Plate 3, figs. A–F) identical with counterparts in *Chasmatosaurus vanhoepeni* and *C. yuani* (see Broili and Schroder 1934 and Young 1936 respectively). The forwards extent of the Meckelian canal implies that the splenial reached nearly to the unfused symphysis (Plate 2, fig. C; Plate 3, fig. A). In their anterior regions the mandibles are much deeper than broad, but the articular portion of a right mandible shows complete reversal of those proportions (Plate 3, figs. D–F). This antero-posterior shift in jaw proportions might seem unusual but is, in fact, matched in *Chasmatosaurus* and in crocodilians. The glenoid fossa is saddle-shaped and extends out and forwards at about 45° relative to the jaw axis. Shape and alignment of the fossa indicate that the condyle of the quadrate must have resembled that of *Chasmatosaurus* in its structure and orientation (see Cruickshank 1972, fig. 3a). The

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* Cruickshank's work (1972) relegated *Chasmatosaurus* Haughton 1924 to the synonymy of *Proterosuchus* Broom 1903 and employed the latter name throughout. My reasons for using the name *Chasmatosaurus* are explained in the discussion.

retroarticular process is robust, but it does not show the strong upwards curvature seen in *Chasmatosaurus*. In front of the glenoid fossa is a sheet-like portion of an unfused prearticular; this is perforated by a small foramen for transmission of the chorda tympani nerve (Plate 3, fig. E).

DENTITION: Maxillae and dentaries each carried a single marginal row of teeth; it is not known if *Kalisuchus* rivalled *Chasmatosaurus* in possessing premaxillary and palatal teeth. Implantation is subthecodont, according to the precise definition given by Romer (1956, p. 442),

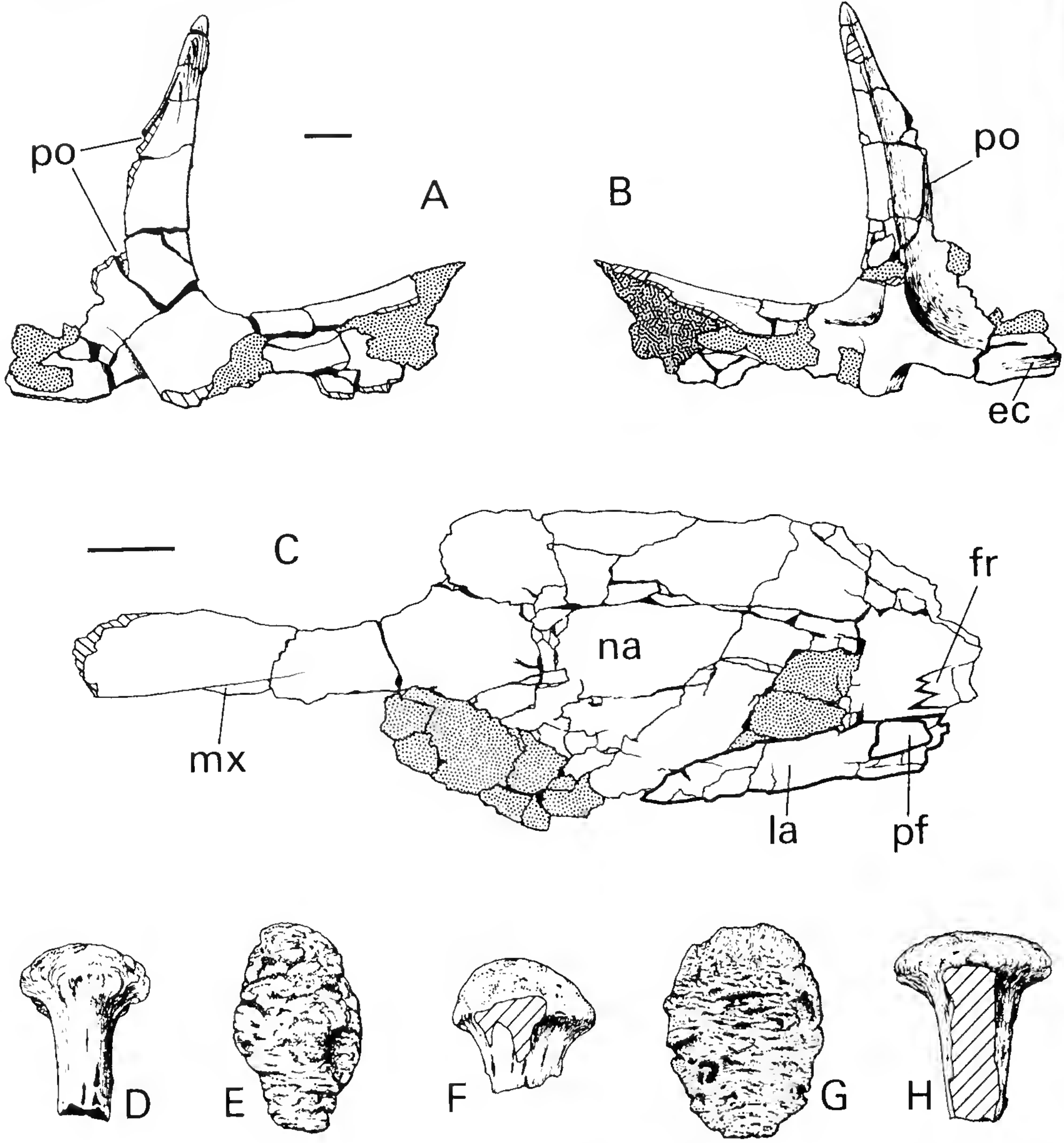

FIG. 1: *Kalisuchus rewanensis* gen. et sp. nov., referred specimens. Each scale indicates 1 cm; matrix indicated by stippling, and broken surfaces by oblique shading. A–B, left jugal (QM F9521) in lateral and medial views, (ec = groove for attachment of ectopterygoid; po = groove for attachment of postorbital). C, crushed section of skull roof (QM F9522) in dorsal view, (fr = impressed area of attachment of frontal; la = portion of left lacrimal; mx = groove for attachment of left maxilla; na = nasal; pf = portion of left prefrontal). D–H, crests of neural spines showing variable development of spine tables, all ×1 (D–E, QM F9523 in posterior (?) and dorsal views; F, QM F9525 in anterior (?) view; G–H, QM F9524 in dorsal and posterior (?) views).

but with the minor distinction that lateral and medial walls of the alveoli are equally high. The medial walls are thin and were apparently very susceptible to breakage (compare fig. C, in Plate 2, with fig. A in Plate 3). Few teeth are preserved in the material, and most of those are broken stumps. The type maxilla contains a near-complete tooth in the fourth alveolus, and a splinter of another tooth is lodged in the sixth and seventh alveoli. The latero-medially compressed, acutely pointed and recurved crowns of the teeth bear a close resemblance to those in *Chasmatosaurus*. The teeth of *C. vanhoepeni* are finely serrated on their rear edges (Gow 1975, p. 117) and so too are those of *Kalisuchus* (Plate 2, fig. B). In addition it is possible that some, or all, of the teeth in *Kalisuchus* were serrated on their leading edges. One replacement tooth has tiny serrations on the leading edge (Plate 2, fig. D); the displaced splinter of tooth in the type maxilla is clearly serrated (Plate 1, fig. B) and its longitudinal convexity implies that it represents a leading edge. The leading edges of the teeth are serrated, in a rather variable pattern, in *C. yuani* (Young 1936, fig. 5) and it seems likely that the teeth of *Kalisuchus* carried similar ornament.

From the limited variation in size of the alveoli it is reasonable to conclude that the dentition was near-isodont. The alveoli are closely packed in linear series and so, of course, were the teeth. In this respect *Kalisuchus* resembled both *C. vanhoepeni* (as figured by Broili and Schroder, 1934) and *C. yuani*. Cruickshank's reconstructions (1972) of *C. vanhoepeni* show decidedly irregular spacing of the teeth, but that irregularity probably stems from the composite nature of the reconstructions. The reconstruction of *C. vanhoepeni* by Broili and Schroder (1934, fig. 4) showed the upper tooth row extending without interruption across the suture between maxilla and premaxilla; but Cruickshank's reconstruction (1972, fig. 3a) shows the hindmost premaxillary teeth distinctly closer to the mid-line than the foremost maxillary teeth and separated from them by a short diastema. The type specimen of *C. yuani* has no diastema; the upper tooth rows diverge as they approach the front of the maxillae and then reconverge in the premaxillae (Young 1936, fig. 1). The arrangement of the upper teeth in *Chasmatosaurus* is either uncertain or variable. But in *Kalisuchus* their arrangement is highly distinctive. In front of its first alveolus the tooth-bearing part of the maxilla is smoothly rounded off (Plate 1, fig. B), implying the presence of a diastema or some other interruption of the tooth row at the junction of maxilla and premaxilla. The maxillary tooth rows converge towards the front while, at the same time, the maxillae increase in breadth at their anterior ends; this peculiar arrangement indicates that most of the contact between maxilla and premaxilla occurred lateral to the line of the maxillary teeth. It is difficult to escape the conclusion that the premaxillae were transversely expanded; and if the premaxillae did carry marginal teeth the hindmost of these are likely to have been situated outside the line of the maxillary tooth row.

VERTEBRAL COLUMN: The material includes many damaged and isolated vertebrae (most being represented by centra). It is impossible to estimate the vertebral formula, and composite descriptions of neck, trunk and tail vertebrae must suffice. In nearly all respects the vertebrae approach very closely to those of *Chasmatosaurus* (as described by Hughes 1963).

The cervical vertebrae have elongated and spool-shaped centra, each with a prominent ventral keel (Plate 3, figs. G-M). The centra are amphicoelous, having terminal faces which are gently excavated and slightly higher than wide. In some cases the antero-ventral and postero-ventral margins of the centra appear to be bevelled (suggesting the former presence of intercentra), but it is difficult to be certain of this on account of the poor preservation. In anterior neck vertebrae the diapophysis and the parapophysis are situated close together and low down at the anterior end of the centrum (Plate 3, figs. G-I); in succeeding neck vertebrae the rib facets are more widely separated owing to upwards, and slightly backwards, migration of the diapophysis (Plate 3, fig. J). One vertebra from the hindmost part of the neck (or possibly from the foremost region of the trunk) is of considerable interest in that the rib facets of the right side are perfectly preserved (Plate 3, figs. K-M). The parapophysis lies at the antero-ventral margin of the centrum; it is elliptical in outline (with the long axis running forwards and slightly down) and has a raised rim. The diapophysis is situated about half-way up the centrum, but is still close to the anterior margin; it has the outline of a figure 8 (the upper loop being the larger) and also has a raised rim. Duplex construction of the diapophysis clearly indicates the presence of triple-headed ribs in the neck (or anterior trunk) region of *Kalisuchus*.

The dorsal vertebrae are represented by poorly preserved centra (Plate 3, figs. N-O). These are amphicoelous, with terminal faces slightly higher than wide, and are all distinctly shorter than the neck centra. They have weak ventral keels or lack them entirely. Some broken and dissociated neural spines (Figs. 1D-H) were probably derived from the trunk region (or possibly from the hind part of the neck). They are robust blades of bone, and all have their dorsal edges thickened and expanded into very characteristic spine tables.

The caudal vertebrae (Plate 3, figs. P-R) are very similar indeed to those described and figured for *Chasmatosaurus yuani* by Young (1936).

PECTORAL GIRDLE: Several flat fragments of bone might possibly be portions of the shoulder girdle; that shown in Plate 4, figs. A and B, seems, for example, to be the upper part of a left scapula. None of these fragments can be identified with certainty, and none is well enough preserved to merit detailed description.

FORELIMB: The distal end of a right humerus (Plate 4, figs. C-F) resembles its equivalents in *Chasmatosaurus yuani* and in *C. vanhoepeni* (see Young 1963, fig. 2b, and Cruickshank 1972, figs. 6a-c, respectively). Its relative narrowness (from entepicondyle to ectepicondyle) cannot be regarded as a distinguishing feature and may be largely attributed to damage.

The radius is represented by two examples from the left side, the smaller one being nearly complete. The smaller radius (Plate 4, figs. H-K) is practically identical with that illustrated in *C. yuani* by Young (1936, fig. 9a). It is a slender bone, as it is in *C. yuani,* and is not so stoutly constructed as the radius of *C. vanhoepeni* (see Cruickshank 1972, fig. 6d). The original total length of this smaller radius was probably about 105 mm. The distal section of the second radius (Plate 4, fig. G) is clearly from a much larger animal; when complete this bone probably exceeded 160 mm in length (judging from the proportions of the smaller radius). On both radii the ventro-medial surface of the shaft carries a very distinct fossa for the attachment of the radial head of the deep digital flexors; an identical feature is illustrated by Young (1936) in the radius of *C. yuani.*

PELVIC GIRDLE: The only certainly identified part of the pelvis is the proximal portion of a right pubis (Plate 5, figs. A–B). This fragment consists of a massive buttress culminating proximally in a large facet to meet the pubic peduncle of the ilium. As it is traced distally the buttress curves forwards and down, diminishing in thickness, and becomes drawn out on the medial side into a transverse sheet. This sheet, or pubic apron, is crushed, but is still slightly arched to the front. Its entire medial margin is damaged, so that it is impossible to determine the extent of the symphysis or of any fenestration. In its general appearance this portion of pubis resembles its equivalents in pseudosuchians rather than in *Chasmatosaurus;* more specifically, it finds its closest counterparts in *Ornithosuchus longidens* and in *Euparkeria capensis* (see Walker 1964, fig. 11, and Ewer 1965, figs. 11, 12, respectively).

HINDLIMB: The femur is represented by a complete example (Plate 5, figs. C–G) and by two larger proximal ends, all of the left side. The femur is very similar to that of *C. vanhoepeni* (Cruickshank 1972, figs 9a–d) but is, like the radius, much less robust than in this African form. Cruickshank described the femur of *C. vanhoepeni* as 'almost straight' (1972, p. 108), but the femoral shaft of *Kalisuchus* shows a gentle and very distinctive S-bend (being upwardly arched in the distal two thirds). This curvature can hardly be attributed to post-mortem distortion; wherever the Rewan material has been distorted it has usually been crushed flat. The fourth trochanter is slightly better developed in *Kalisuchus* than in either *C. vanhoepeni* or *C. yuani* (in which latter Young 1963, p. 221, stated that there was 'no clear fourth trochanter'). Both *Kalisuchus* and *C. yuani* have the fourth trochanter situated about half-way down the femoral shaft; in *C. vanhoepeni* it has a more proximal situation.

The two ends of a single left tibia (Plate 5, figs. H–I) are virtually identical with equivalents in *C. yuani* (Young 1936, fig. 11a). So, too, is the distal end of a left fibula (Plate 5, fig. J; compare Young 1936, fig. 11b).

A single left calcaneum is very well preserved and strikingly like that of a crocodilian or of a pseudosuchian in its configuration (Plate 5, figs. K–L). Its antero-medial face is slightly abraded but is clearly 'stepped' to form part of a rotary joint against the astragalus; the postero-dorsal margin has been snapped off (Plate 5, fig. K) but seems originally to have been extended into a definite calcaneal tuber.

DISCUSSION

RELATIONSHIPS OF *KALISUCHUS*

Most Lower Triassic archosaurs are members of the suborder Proterosuchia (as defined by Charig and Reig 1970) and it is likely that the relationships of *Kalisuchus* lie within that taxon. The only well known Lower Triassic archosaur that may not be a proterosuchian is *Euparkeria* *capensis*, from the *Cynognathus* Zone of S. Africa (Broom 1913a, b; Ewer 1965; Gow 1970). *Euparkeria* has sometimes been regarded as an advanced proterosuchian that was nearing the pseudosuchian level of organization (e.g. Hughes 1963, Cruickshank 1972) but is best considered as a very primitive pseudosuchian newly descended from proterosuchian ancestry (the traditional view, endorsed by Reig 1970, Charig and Reig 1970). In nearly every feature of its skeletal anatomy *Kalisuchus* is characteristically proterosuchian. Some parts, such as the mandible and the radius, are practically indistinguishable from counterparts in the Chinese *Chasmatosaurus yuani*, while others, such as the femur, are closely matched in the African *C. vanhoepeni*. Still other characters, such as the subthecodont dentition, the triple-headed ribs and (if they are present) the intercentra, are virtually the hallmarks of proterosuchians. In only one or two respects (and notably in its possession of a 'crocodiloid' calcaneum) does *Kalisuchus* resemble pseudosuchians rather than proterosuchians. It is on account of its numerous and detailed resemblances with Chinese and African species of *Chasmatosaurus* that I regard *Kalisuchus* as a proterosuchian, rather than as a very primitive pseudosuchian comparable with *Euparkeria*.

Before attempting to pin down the more immediate relationships of *Kalisuchus* within the Proterosuchia it is necessary to mention two major problems. First there is the fact that the 'only well known genera are *Chasmatosaurus*, *Erythrosuchus* and *Shansisuchus*, and even of these our knowledge is far from complete' (Charig and Reig 1970, p. 140). In consequence it is not possible to make exhaustive comparisons with other proterosuchians; assessments of relationships within the Proterosuchia are, of necessity, very tentative ones. Second, the classification of proterosuchians has long been in a somewhat confused state. Charig and Reig succeeded in unravelling much of the complexity of proterosuchian taxonomy and drew up a useful classification (1970) wherein they recognized two families — the Proterosuchidae (comprising primitive forms) and the Erythrosuchidae (comprising more advanced forms). *Kalisuchus* is strikingly similar to *Chasmatosaurus*, the central genus of the Proterosuchidae, and plainly merits inclusion in the same family.

Within the Proterosuchidae there remains the long-debated possibility that the genus names *Proterosuchus* Broom 1903 and *Chasmatosaurus* Haughton 1924 might be synonyms. The problem of this possible synonymy is very complicated and has been well summarized, though inconclusively, by Charig and Reig (1970, p. 145 et seq.). More recently Cruickshank (1972) has included the genera *Elaphrosuchus* and *Chasmatosaurus* in the synonymy of *Proterosuchus* and has given a composite account of the latter. The unique type specimen of the genotype *(Proterosuchus fergusi* Broom 1903) had been lost for many years, but was rediscovered and was used by Cruickshank to support his conclusions regarding synonymy. That type specimen, a weathered portion of skull, could be compared with the type specimen of *Chasmatosaurus vanhoepeni* at only one or two points, as was explained by Haughton in 1924. Briefly, Cruickshank has attempted to uphold the synonymy of *Proterosuchus* and *Chasmatosaurus* on the basis of two similarities: in the palatal dentition and in the structure of the ectopterygoids. This is scarcely an overwhelming body of evidence. Moreover, Cruickshank has admitted that the type specimen of *P. fergusi* is less than adequate for comparative purposes (1972, p. 91): 'As the type of *P. fergusi* is such a poor specimen when compared with the other proterosuchians, it is impossible to refer these to the species *fergusi* . . . .It is unlikely that any other specimen will ever be assigned to *P. fergusi* in the future'. Apparently the type and only specimen of *P. fergusi* cannot serve as an adequate standard of reference for appraising the status of other specimens. Consequently I regard *P. fergusi* as being of uncertain status and have preferred to employ the very familiar name *Chasmatosaurus* in place of *Proterosuchus*. Recently Charig and Sues expressed a similar opinion (1976, p. 19) and rejected Cruickshank's placing of *Chasmatosaurus* in the synonymy of *Proterosuchus*.

The following classification of proterosuchians agrees in most respects with that recommended by Charig and Reig (1970) and by Charig and Sues (1976). It differs considerably from the classification advanced by Cruickshank in 1972, where *Garjainia* and *Vjushkovia* were regarded as synonyms of *Erythrosuchus*, and where *Euparkeria* was included in the Erythrosuchidae (see discussion by Charig and Sues 1976). In 1972 Romer suggested that the suborder Proterosuchia might be extended to encompass Middle and Upper Triassic thecodontians of the families Prestosuchidae and Proterochampsidae. His reason for including the prestosuchids is unknown; Charig wrote (1976, p. 100) that he could find 'no adequate justification for this extraordinary assignation, nor was Romer himself able to provide one when questioned verbally'. The relationships of the proterochampsids are uncertain; Reig (1959) and Sill (1967) both favoured crocodilian affinities for *Proterochampsa*, whereas Walker argued (1968) that the animal was a primitive phytosaur. Only Cruickshank (1975) has expressed any agreement with Romer's suggestion that proterochampsids are late-surviving proterosuchians. The following classification agrees with that of Charig and Sues (1976) in excluding prestosuchids and proterochampsids from the Proterosuchia.

SUBORDER PROTEROSUCHIA

A. Family Proterosuchidae

Chasmatosaurus. Lower Triassic.⁽¹⁾
- *C. vanhoepeni* Haughton 1924. *Lystrosaurus* Zone, Orange Free State and Cape Province, S. Africa. (Synonyms: *?Elaphrosuchus rubidgei* Broom 1946; *C. alexanderi* Hoffman 1965.)
- *C. yuani* Young 1936. *Lystrosaurus* Beds, Sinkiang, China.
- *C. ultimus* Young 1964. Ehrmaying Series, SE. Shansi, China. (Type and only specimen originally referred to *C. yuani* by Young in 1958.)

Chasmatosuchus. Lower Triassic.
- *C. rossicus* von Huene 1940. Zone V, northern Russia. (Synonym: ?*C. parvus* von Huene 1940.)

Archosaurus. Upper Permian.
- *A. rossicus* Tatarinov 1960. Zone IV, central European Russia.

Kalisuchus. Lower Triassic.
- *K. rewanensis*. Rewan Formation, SE. Queensland.

B. Family Erythrosuchidae

Erythrosuchus. Lower Triassic.
- *E. africanus* Broom 1905. *Cynognathus* Zone, Cape Province, S. Africa.

Garjainia. Lower Triassic.
- *G. prima* Ochev 1958. Zone V, southern Urals, European Russia.

Vjushkovia. Lower Triassic.
- *V. triplicostata* von Huene 1960. Zone VI, southern Urals, European Russia.
- ?*V. sinensis* Young 1973. Horizon IV, Sinkiang, China.

Shansisuchus. Lower Triassic.
- *S. shansisuchus* Young 1964. Ehrmaying Series, S.E. Shansi, China.

C. Incertae sedis

Proterosuchus. Lower Triassic.⁽²⁾
- *P. fergusi* Broom 1903. *Lystrosaurus* Zone, Cape Province, S. Africa.

Cuyosuchus. Lower Triassic.
- *C. huenei* Reig 1961. Cacheuta Beds, Mendoza, Argentina.

cf. *Garjainia (Chasmatosuchus vjushkovi* Ochev 1961), Zone V, Lower Triassic, southern Urals, European Russia (Tatarinov 1961).

cf. *Chasmatosaurus (Ankistrodon indicus* Huxley 1865; *Chasmatosaurus indicus* von Huene 1942), Panchet Group, Lower Triassic, India (Satsangi 1964).

cf. *Erythrosuchus*, Yerrapalli Formation, ? Lower Triassic,⁽³⁾ Godavari Valley, India (Robinson 1967; Chatterjee *et al.* 1969; Chatterjee and Roy Chowdhury 1974).

cf. *Chasmatosaurus*, N'tawere Formation, ? Lower Triassic,⁽⁴⁾ N.E. Zambia (Charig and Reig 1970).

cf. *Chasmatosaurus*, Knocklofty Formation, Lower Triassic, Tasmania (Warren 1972)⁽⁵⁾.

? 'proterosuchian', Yerrapalli Formation, ? Lower Triassic,⁽³⁾ Godavari Valley, India (Cruickshank 1972, p. 118; Charig and Sues 1976, p. 30).

⁽¹⁾ Cruickshank listed a specimen of '?*Proterosuchus*' (1972, table 1) possibly obtained from late Permian sediments (uppermost part of the *Kistecephalus* Zone).

⁽²⁾ *P. fergusi* came from sediments attributed to the '*Procolophon* Zone', but S. African sediments containing *Procolophon* are probably correlative with those of the *Lystrosaurus* Zone (Kitching 1972 and in Kitching *et al.* 1972).

⁽³⁾ The upper part of the Yerrapalli Formation is possibly of Middle Triassic age (Jain, Robinson and Roy Chowdhury 1964; Chatterjee and Roy Chowdhury 1974).

⁽⁴⁾ The N'tawere Formation may extend into the Middle Triassic (Cox 1969).

⁽⁵⁾ Proterosuchian material from the Knocklofty Formation of Tasmania has recently been described (Camp and Banks 1978) and named *Tasmaniosaurus triassicus*. *Tasmaniosaurus* has been referred to the family Proterosuchidae but is clearly not congeneric with *Kalisuchus*.

Of the adequately known and determinate proterosuchians listed above the closest relatives of *Kalisuchus* are *Chasmatosaurus yuani* and *C. vanhoepeni*, from the Lower Triassic of China and S. Africa respectively. Certain parts of the Queensland proterosuchian (notably the limb bones and the mandibles) are nearly identical with counterparts in the Chinese form. The resemblances with *C. vanhoepeni* are a little less striking but are nonetheless very impressive; the limb bones and the vertebrae of *Kalisuchus* have the same basic morphology as those in the African species, but the limb bones are distinctly less robust. While *Kalisuchus* differs from *Chasmatosaurus* in some minor details there are several more important differences which preclude assignment of the Australian material to the genus *Chasmatosaurus*.

First, there is a major difference in the structure of the snout. In having the front part of the maxilla flared outwards into a shelf *Kalisuchus* is unique among proterosuchians. This feature seems to indicate that the tip of the snout was transversely expanded and that much of the contact between maxilla and premaxilla was external to the line of the upper tooth row. In *Chasmatosaurus* the tip of the snout is narrow and the premaxilla meets the maxilla in fairly standard archosaurian fashion.

Second, there are some differences in the jugal. In *Kalisuchus* the interlocking between jugal and postorbital is the reverse of that described in *C. vanhoepeni* by Cruickshank (1972), and the L-shaped cross-section of the posterior ramus is almost equally distinctive (though the reconstructions of *C. vanhoepeni* by Broili and Schroder (1934) hint at a slightly similar development). No other proterosuchian matches *Kalisuchus* in having a projection on the ventral margin of the jugal.

Next, it is likely that the upper tooth row of *Kalisuchus* was disrupted by a gap, or by off-setting, at the junction between maxilla and premaxilla. The upper tooth row of *C. yuani* is certainly different (Young 1936, fig. 1); the arrangement of the upper teeth in *C. vanhoepeni* is either uncertain or variable (compare illustrations of Broili and Schroder 1934 with those of Cruickshank 1972) but is likely to have differed from that in *Kalisuchus* by virtue of the dissimilarity in snout construction.

The very characteristic spine tables of the *Kalisuchus* vertebrae seem to be much more strongly developed than in any other proterosuchian. No comparable structures are present in *C. yuani* (Young 1936, figs. 6, 7). Spine tables occur, on the fourth and subsequent neck vertebrae of *C. vanhoepeni*, but Cruickshank described these as 'lateral expansions' and stated that they were lacking from the typical thoracic vertebrae (1972, p.104). All the centra of *Kalisuchus* are amphicoelous, and so, too, are those of *C. yuani;* Cruickshank has ascertained (1972) that the trunk centra of *C. vanhoepeni* are procoelous.

The incompletely known pubis of *Kalisuchus* is broadly comparable in structure with that of *C. vanhoepeni* but seems to be most closely matched in the pseudosuchians *Euparkeria* and *Ornithosuchus*.

Last, the surprisingly 'crocodiloid' calcaneum of *Kalisuchus* is quite unlike that in *C. vanhoepeni* (see Cruickshank 1972, fig. 10, but note the revised identification of ankle bones by Gow 1975, p. 117). In possessing this complex tarsal structure *Kalisuchus* resembles pseudosuchians and crocodilians rather than any of the proterosuchians.

The conclusion that *Kalisuchus* is a close relative of *Chasmatosaurus* derives support from the fundamentally similar build of skeleton and skull. But superimposed upon that near-*Chasmatosaurus* framework of structure is a range of diagnostic differences in skull, dentition, pelvic girdle and limb bones. All those diagnostic differences in *Kalisuchus* may be regarded as advances from the structural conditions in *C. vanhoepeni* (and, to a lesser extent, from those in *C. yuani);* so, too, may the more subtle distinctive features in *Kalisuchus* (such as the more delicate limb bones and the more distal location of the fourth trochanter).

In every distinctive feature of its skull, dentition and postcranial skeleton *Kalisuchus* represents a definite advance on the basic proterosuchid pattern exemplified by *Chasmatosaurus;* and it seems that those advances were headed in the direction of pseudosuchians rather than in the direction of erythrosuchids. Proterosuchids were relatively slender animals that probably resembled crocodiles in outward appearance, but erythrosuchids were massive and stocky creatures that have been likened to hippos (see figs. 3 and 7 in Charig and Sues 1976). Some pseudosuchians retained the crocodile-like body form of the proterosuchids, but many tended to a more gracile, and eventually near-dinosaurian, body plan. The fact that *Kalisuchus* has relatively slender limb bones (by comparison with *C. vanhoepeni)* certainly hints at an approach to the pseudosuchian facies rather than to the erythrosuchid facies. And this suspicion of incipient progress towards pseudosuchians is reinforced by several features of the skeletal anatomy: the expanded tip to the snout, the rather delicate construction of the pubis, the upwards arching of the femoral shaft, and the 'crocodiloid' morphology of the calcaneum. Those distinctive features of *Kalisuchus* are matched in pseudosuchians of one sort or another, but they are not found in erythrosuchids. *Kalisuchus* also compares favourably with pseudosuchians in having a long neck (with cervical centra longer than wide) and a long tail; in erythrosuchids, both these sections of the vertebral column were shortened and the cervical centra were much wider than long.

To summarize, *Kalisuchus* is a close relative of *Chasmatosaurus*, the best known of proterosuchids, and is perhaps a little more closely related to the Chinese *C. yuani* than to the African *C. vanhoepeni*. The diagnostic differences between *Chasmatosaurus* and *Kalisuchus* testify that the latter is the slightly more advanced form. Nowhere in its skeletal anatomy does *Kalisuchus* show any obvious tendency towards erythrosuchid organization; instead it displays a small, but definite, advance towards pseudosuchians. That small advance is suggestive of a proterosuchid ancestry for pseudosuchians; it does not support the idea of an erythrosuchid ancestry (a widespread view, based on the evidence of *Euparkeria*), but accords fairly well with the suggestion that pseudosuchians evolved from animals transitional between proterosuchids and erythrosuchids (Reig, 1970).

Finally, the relationships of *Kalisuchus* give a useful indication of age for the Rewan Formation. The Rewan fauna is dominated by labyrinthodont amphibians (Bartholomai and Howie 1970; Howie 1972a, b; Warren 1972) but these are of limited value for purposes of dating and correlation. On the evidence of plant fossils Balme concluded (1969) that the Rewan sediments of the Bowen Basin extended from late Permian to early Middle Triassic; that conclusion was incorporated by Anderson and Anderson in their review of Gondwanaland biostratigraphy (1970, chart 21), and Warren showed the Rewan Formation as essentially Lower Triassic in age (1972, table 1). This consensus is reinforced by the presence of *Kalisuchus* in the Rewan fauna, because proterosuchids range from the uppermost Permian to the late Lower Triassic (Charig and Reig 1970, table 2). *Chasmatosaurus* is most abundant near the base of the Lower Triassic, with the majority of specimens having been found in the *Lystrosaurus* Zone or its equivalents. The Chinese *C. ultimus* came from sediments of the Ehrmaying Series (broadly the equivalent of the *Cynognathus* Zone) and may be regarded as a late survivor. Other possible occurrences of *Chasmatosaurus* outside the *Lystrosaurus* Zone (or its equivalents) are indicated in the classification given above (p. 20). In short, specimens of *Chasmatosaurus* are nearly all from the *Lystrosaurus* Zone and its equivalents or are, in some questionable cases, from levels immediately above or below; and the great majority of specimens is from the lower part of the *Lystrosaurus* Zone. As *Kalisuchus* is a little more advanced than *C. yuani* and *C. vanhoepeni* it is reasonable to conclude that its parent sediments are equivalent to the upper part of the *Lystrosaurus* Zone (or, possibly, to the lower part of the *Cynognathus* Zone). This tentative correlation is supported by recent studies of plant microfossils; Dr C. B. Foster has informed me (pers. comm.) that assemblages from the basal 120 m of the Rewan Formation in the Theodore-Moura area are closely comparable with those of the lowermost (Maitur) member of the Indian Panchet Group. The basal parts of both the Rewan and the Panchet can be identified with the *Protohaploxypinus reticulatus* Zone (uppermost Permian) of the Sydney Basin, N.S.W.

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Kalisuchus, like other proterosuchids, probably resembled a crocodile in outward appearance (see the restorations of *Chasmatosaurus* given by Broili and Schroder 1934, Charig and Sues 1976). The proximal articular surface of the femur is terminal in position, indicating that the thigh was not carried erect, but that *Kalisuchus* was a primitive 'sprawler'. Cruickshank estimated that *Chasmatosaurus vanhoepeni* would not have exceeded 1·5 m in overall length when fully grown (1972, p. 113), but *Kalisuchus* seems to have attained somewhat greater size. Using Cruickshank's illustrations and measurements of *C. vanhoepeni* it is possible to obtain estimates of total body length for several individuals of *Kalisuchus* (Table 1) — on the assumption, of course, that the two animals were roughly comparable in body proportions.

Chasmatosaurus has been envisaged as a rather crocodile-like predator that was equally at home in water and on land (e.g. see Broili and Schroder 1934, Tatarinov 1961, Reig 1970, Cruickshank 1972), and it is likely that *Kalisuchus* led a similar existence. Aside from *Kalisuchus*, the Rewan fauna comprised abundant labyrinthodont amphibians, occasional small reptiles (superficially lizard-like paliguanids, prolacertids and procolophonids), rare lungfishes (represented by tooth plates), and actinopterygian fishes and molluscs (both represented by fragments preserved in coprolites — see Plate 5, fig. L). Evidently *Kalisuchus* was the dominant predator in the Rewan environment; it presumably exploited the flourishing population of amphibians and might also have supplemented its diet by taking smaller reptiles and fishes.

Several structural adaptations of *Kalisuchus* are clearly those of a predator. The tip of the snout is likely to have been downcurved, though perhaps not to the extent that it was in *Chasmatosaurus*. Such curvature of the snout was probably an adaptation for grasping slippery prey and for reducing the risk of its escape.

The unfused, and seemingly very loose, mandibular symphysis probably allowed some spreading of the mandibles during feeding. Oblique orientation of the glenoid fossae would have caused the mandibles to splay apart as they were depressed; then, as the mouth was closing, left and right mandibles would have been drawn together. Latero-medial spreading and closure of the mandibles was automatic, and it ensured that the lower tooth rows shifted inwards, towards the mid-line, as they bit upwards into the prey. The upwards and inwards bite of the lower teeth would have afforded better purchase on slippery and wriggling prey.

Whether or not the skull of *Chasmatosaurus* was streptostylic is open to debate. Gow argued (1975) that streptostyly would have been possible only when the lower temporal bar had been breached (thus freeing the quadrate from linkage to quadrato-jugal and jugal); but Cruickshank (1972) maintained that quadrate movements were possible by virtue of a sliding contact between jugal and quadrato-jugal. The evidence from *Kalisuchus* is equivocal, but it is noteworthy that the maxilla and the jugal were found isolated and without attached portions of adjoining skull bones. That fact suggests that bones of the upper jaw and cheek regions were loosely connected in *Kalisuchus*. But whether or not those bones were capable of independent movements, and whether or not such movements were passive or voluntary, can only be resolved with the aid of better material. Nevertheless, cranial kinesis, whatever its nature, is characteristic of predators that kill and swallow relatively large prey, and the skull of *Kalisuchus*, with its seemingly loose construction, might well have been a kinetic one.

TABLE 1: ESTIMATES OF TOTAL BODY LENGTH FOR FIVE SPECIMENS OF *KALISUCHUS REWANENSIS*.

Specimen	Total length (m)*
left radius (QM F9541), c. 10·5 cm long	1·89
left radius (QM F9540), c. 17·0 cm long	3·06
left femur (QM F9543), c. 11·8 cm long	1·18
proximal end of left femur (QM F10126), c. 20·5 cm long	2·05
two ends of left tibia (QM F9544), c. 10·5 cm long	1·20

* Estimated using Cruickshank's (1972) data for *Chasmatosaurus (Proterosuchus) vanhoepeni.*

Other structural adaptations of *Kalisuchus* are less readily explained. First there is the transversely expanded tip to the snout. A somewhat similar structure occurs in another group of thecodontians, the stagonolepidids (or aetosaurids), which have been variously regarded as scavengers, carrion-eaters, herbivores or feeders on invertebrates. Walker suggested (1961) that the expanded premaxillae of stagonolepidids were useful for grubbing about in soft vegetation or for digging out invertebrates. But it is difficult to offer any comparable explanation in the case of a predator like *Kalisuchus;* its premaxillae are unknown, and the exact form of the snout remains to be seen.

Next there is the presence of triple-headed ribs in the posterior neck (or anterior trunk) region. There has been considerable debate about which early archosaurs did (or did not) possess triple-headed ribs (Tatarinov 1961, Hughes 1963, Charig and Reig 1970). They seem to have occurred in *Chasmatosaurus, Chasmatosuchus, Kalisuchus, Erythrosuchus, Garjainia* and *Vjushkovia* (though not necessarily in every species of polytypic genera). In addition Ewer reported (1965) the occurrence of virtually three-headed ribs in the early pseudosuchian *Euparkia*. Three-headed ribs would have been practically immovable (unless the three heads were arranged in a straight line), and they would effectively have stiffened the region of neck or trunk in which they occurred. In *Kalisuchus* and *Chasmatosaurus* stiffening at the base of the neck might be regarded as an adaptation for a near-crocodilian method of swimming (see Cruickshank 1972, p. 113 and p. 119).

The swollen crests of the neural spines (Fig. 1, D–H) also merit brief comment. These were probably embedded in a dermis of considerable thickness, but they do not seem to have supported any dermal armour (there being no scutes in any of the Rewan material). Lack of dermal armour is apparently a primitive characteristic common to all proterosuchians (except, possibly, the South American *Cuyosuchus*). Thornley (1970) made a detailed examination of skin remnants preserved in one specimen of *Chasmatosaurus vanhoepeni* and found traces of epidermal structures resembling scales.

The Rewan vertebrate fauna is ecologically distinct from faunas of comparable age in other areas of Gondwanaland. Early Lower Triassic faunas in Africa, India, China and Antarctica are dominated by synapsid reptiles including the very characteristic *Lystrosaurus*. The Rewan fauna has all the constituents of the typical *Lystrosaurus* Zone (or equivalent) assemblage in other continents — *except* synapsids. Instead of being dominated by synapsids the Rewan fauna is dominated by labyrinthodont amphibians, a fact that lends the fauna a decidedly Palaeozoic cast and makes reliable correlation with other Lower Triassic sequences very difficult.

Lystrosaurus was an amphibious herbivore, something like a modern hippo, that thrived in lakes, rivers and marshes in other continents during the early part of the Lower Triassic. Rewan sediments exposed at the Crater represent a fresh-water environment that would seemingly have been an ideal habitat for *Lystrosaurus*. Yet the abundant vertebrate material from the Crater contains no recognizable fragment of any synapsid. Even the broken vertebral centra of *Lystrosaurus* are very characteristic in appearance (e.g. see Colbert 1974, fig. 12) and would not be easily overlooked. In early Triassic times *Lystrosaurus* and its allies were widespread and abundant in most areas of Gondwanaland, so that their absence from the Rewan fauna is very perplexing. It is difficult to explain the absence of synapsids by arguing that the Rewan fauna is earlier or later than Lower Triassic. Palaeobotanical evidence establishes a late Permian age for the base of the Rewan Formation, so that the Crater horizon (which is about the middle of the formation) can scarcely be earlier than Lower Triassic. In any case, it seems unlikely that *Kalisuchus* should ante-date the somewhat less advanced *Chasmatosaurus*. If, on the other hand, the Crater horizon were Middle Triassic one would expect to find few labyrinthodonts, progressive and near-dinosaur thecodontians (rather than a proterosuchian) and, again, synapsids. There seems little doubt that the Rewan fauna from the Crater is Lower Triassic; but I suspect that it is a relict Palaeozoic fauna with a sprinkling of newly-introduced Mesozoic forms (such as *Kalisuchus* and, perhaps, some of the smaller reptiles). Such an explanation would account for the oddly archaic aspect of the fauna and, hence, for the problem of obtaining a satisfactory estimate of age. Exactly why synapsids such as *Lystrosaurus* had not invaded the Rewan environment remains a mystery; it is not easy to conceive of any barrier that would have permitted passage of one amphibious reptile *(Kalisuchus)* and barred the entry of another *(Lystrosaurus)*.

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PLATE 1

Kalisuchus rewanensis gen. et sp. nov. Holotype (QM F8998), a right maxilla, in lateral (A), ventral (B), and dorsal (C) views. All ×2.

PLATE 1

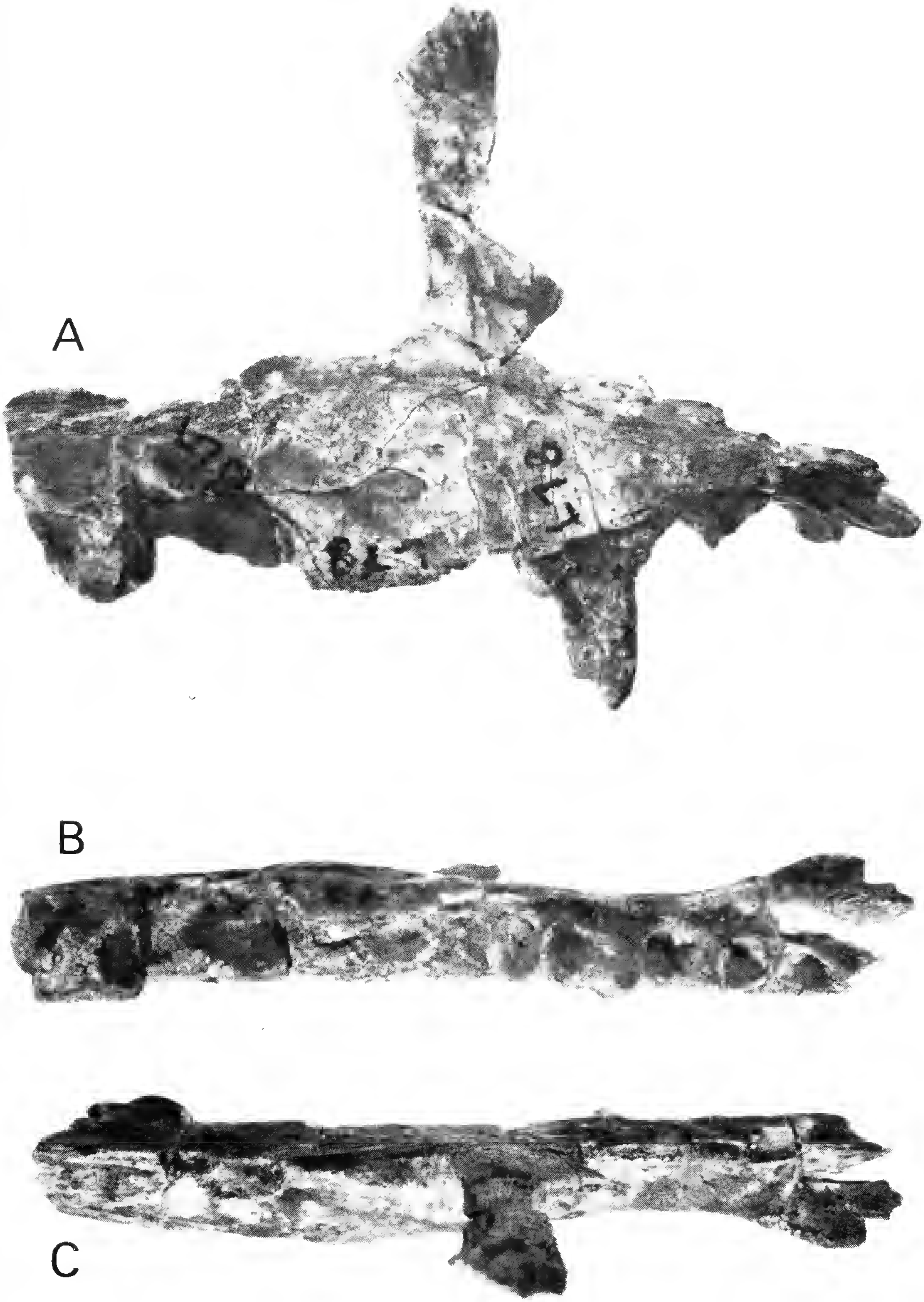

PLATE 2

Kalisuchus rewanensis gen. et sp. nov. Holotype and referred specimen.

FIG. A: holotype, right maxilla (QM F8998), in medial view, ×2.

FIG. B: tooth in 4th alveolus of holotype; in medial view, ×6, to show fine serrations on rear edge.

FIG. C: referred specimen, the symphysial portion of a right mandible (QM F9526), in medial view, ×1. Note remnants of thin bony walls medial to alveoli.

FIG. D: close-up view (×5·5) of replacement tooth indicated by arrow in Fig. C; note fine serrations on front edge.

PLATE 2

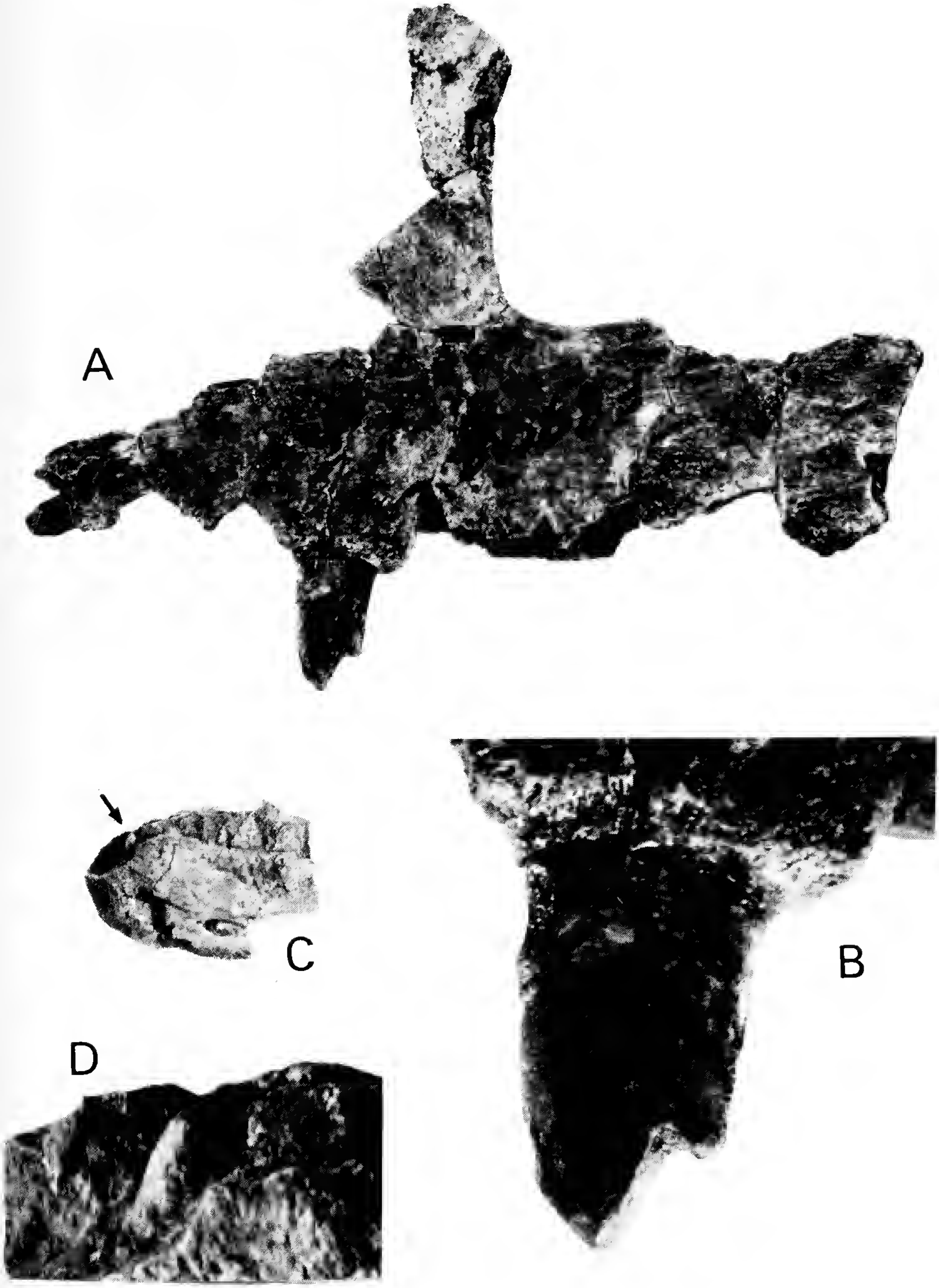

PLATE 3

Kalisuchus rewanensis gen. et sp. nov. Referred specimens. All ×1.

FIGS. A–C: symphysical portion of right mandible (QM F9527) in medial (A), dorsal (B) and lateral (C) views.

FIGS. D–F: articular portion of right mandible (QM F9528) in lateral (D), dorsal (E) and medial (F) views.

FIG. G: cervical centrum (QM F9529) in anterior view, showing parapophysis and diapophysis close together and low down on anterior rim.

FIG. H: anterior portion of cervical centrum (QM F9530) in posterior view, showing cancellous interior and strong ventral keel.

FIG. I: anterior portion of cervical centrum (QM F9531) in posterior view, showing parapophyses, diapophyses, cancellous interior and rather weak ventral keel.

FIG. J: cervical centrum (QM F9532) in right lateral view, showing slightly abraded parapophysis and diapophysis.

FIGS. K–M: posterior cervical centrum (QM F9533) in right lateral (K), ventral (L) and anterior (M) views. Areas of rib attachment outlined in ink; note 'figure 8' construction of diapophysis.

FIGS. N–O: dorsal centrum (QM F9534) in left lateral (N) and ventral (O) views.

FIG P: anterior caudal vertebra (QM F9535) in left lateral view; the neural arch is incomplete.

FIG. Q: mid-caudal centrum (QM F9536) in right lateral view.

FIG. R: posterior caudal centrum (QM F9537) in left lateral view.

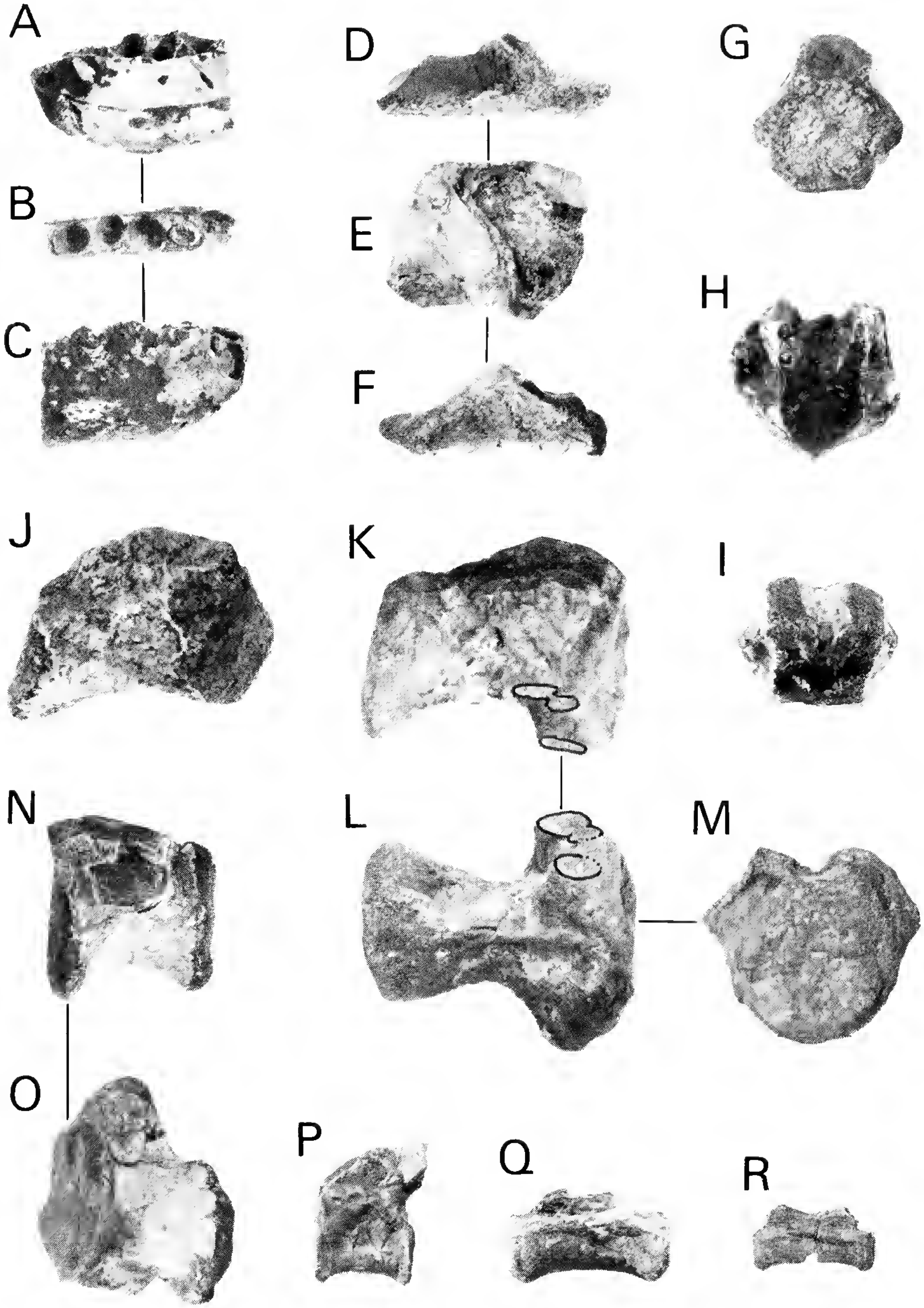
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PLATE 4

Kalisuchus rewanensis gen. et sp. nov. Referred specimens. All ×1.

FIGS. A–B: ? upper part of left scapula (QM F9538) in dorsal (A) and lateral (B) views.

FIGS. C–F: distal portion of right humerus (QM F9539) in proximal (C), dorsal (D), ventral (E) and distal (F) views.

FIG. G: distal portion of left radius (QM F9540) in medial view, showing fossa for attachment of deep digital flexors.

FIGS. H–K: left radius (QM F9541) in anterior (H), medial (I), proximal (J) and distal (K) views; part of proximal articular surface is preserved, but distal end is lacking.

FIG L: coprolite from the Crater (QM F9547), possibly attributable to *K. rewanensis*.

PLATE 4

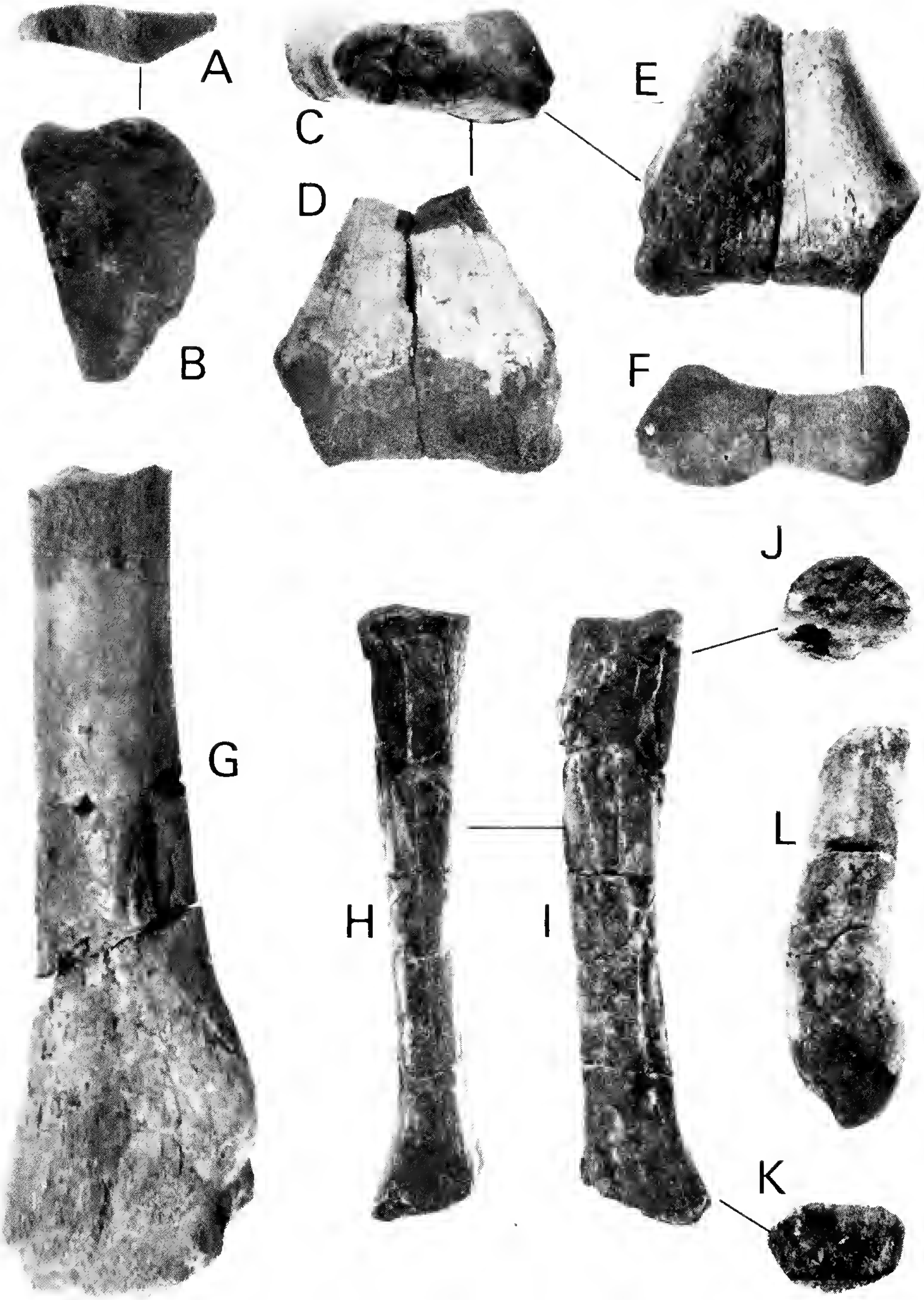


PLATE 5

Kalisuchus rewanensis gen. et sp. nov. Referred specimens. All ×1.

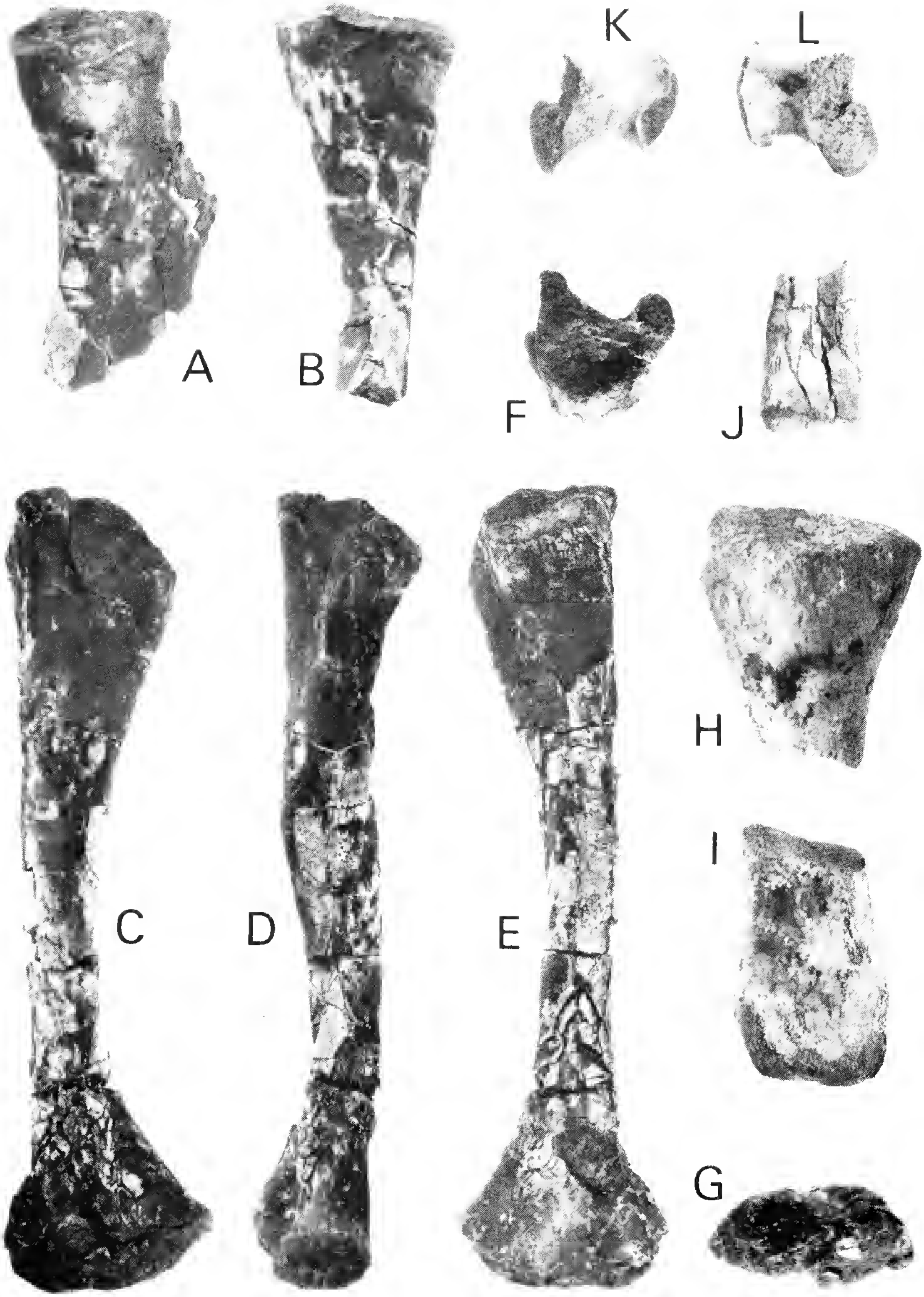
FIGS. A–B: proximal portion of right pubis (QM F9542) in antero-medial (A) and postero-lateral (B) views.

FIGS C–G: left femur (QM F9543) in ventral (C), anterior (D), dorsal (E), proximal (F) and distal (G) views.

FIGS. H–I: proximal (H) and distal (I) ends of a single left tibia (QM F9544) in anterior view; a considerable portion of the shaft is missing.

FIG. J: distal portion of left fibula (QM F9545) in medial view.

FIGS. K–L: left calcaneum (QM F9546) in proximal (K) and distal (L) views.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Mem. Qd Mus. 19(3): 357–65, pls. 1–3. [1979]

CROCODYLUS POROSUS FROM THE PLIOCENE ALLINGHAM FORMATION OF NORTH QUEENSLAND.
RESULTS OF THE RAY E. LEMLEY EXPEDITIONS, PART 5

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ABSTRACT

An incomplete crocodilian snout from the Bluff Downs local fauna of the Allingham Formation of northern Queensland is identified as *Crocodylus porosus*. The Allingham Formation is, at the latest, of early Pliocene age and this specimen is the oldest attributable to *C. porosus*. It indicates that *C. porosus* has been present in Australia for at least 4 million years, and is one of the oldest known of living crocodilian species.

Whilst collecting material from the Allingham Formation of northern Queensland (Archer and Wade 1976) in 1975, M. Archer uncovered a fragmentary crocodilian snout. The base of the Nulla basalt, which overlies the Allingham, is dated as 4·0 to 4·5 million years old (Wyatt and Webb 1970), and hence the Allingham is at least that old. Thus this snout represents a crocodile of early Pliocene age.

The specimen shows no significant differences from modern *Crocodylus porosus* of comparable size, and hence its early Pliocene age is of interest. *C. porosus* has been reported from the Pleistocene (e.g. Lydekker 1888, Deraniyagala 1958), and whilst the *Zoological Record* (1970) reports *C. porosus* from the Miocene of Alcoota, central Australia, this is based on a specimen formally described as *Crocodylus* sp., which is clearly not referable to *C. porosus* (Woodburne 1967). Thus the Allingham specimen represents the oldest occurrence of *C. porosus*.

Material referable to several living mammal species dates into the Pliocene (e.g. Kurten 1968, 1972), but only one living crocodilian species known to me, *Gavialis gangeticus*, is represented by pre-Pleistocene material (Steel 1973). Thus the Allingham crocodile is also of interest as indicating that a second living crocodilian species dates from the Pliocene.

The Bluff Downs local fauna (from the Allingham Formation) contains considerable crocodilian material, mostly teeth, as well as remains of other reptiles, mammals and birds (Archer in Archer and Wade 1976), and apparently sampled an environment including temporary water bodies. The snout was discovered in the main quarry, in bed b of section 2 or the type section of the Allingham Formation. This section is figured by Archer and Wade (1976, figs. 1B, 2).

DESCRIPTION

The specimen (Queensland Museum F9229) comprises the right premaxilla (nearly complete), the incomplete left premaxilla, and the anterior two-thirds of the right maxilla. The palatal portions of both premaxillae and maxilla are less complete than the dorsal portions. Three teeth are present. The plates clearly portray the appearance and form of the specimen so the description will not be exhaustive but will be restricted to those features useful in establishing the taxonomic assignment of the specimen.

PREMAXILLA: The right premaxilla is almost complete dorsally but lacks the palatal portion bounding and posterior to the incisive foramen: the left is less complete. Five alveoli are present in the right premaxilla, and a foramen for the first mandibular tooth. The constriction (maxillary-premaxillary notch) posterior to the last premaxillary alveolus is abrupt and marked. The posterior process of the premaxilla is broad.

MAXILLA: The right maxilla is broken posteriorly at the ninth alveolus, and is complete dorsally to the nasal and premaxillary contacts.

Most of the palatal process, however, has been lost. The delicate internal partitions are absent. A pronounced swelling is present over the root of the fifth tooth, as is common in crocodylids, and the maxilla is expanded laterally at this alveolus. The sculpture of the dorsal surface is less developed than in modern *Crocodylus* skulls of comparable size. At its nasal margin the maxilla is slightly upturned, suggesting the presence of the median ridge characteristic of *Crocodylus porosus*.

TEETH: Preserved are the fourth left premaxillary, and the fifth and eighth right maxillary teeth in situ. The former two are round in cross-section, whilst the eighth maxillary exhibits some lateral compression. All three teeth show marked anterior and posterior carinae and ridging (or fluting) of the crowns. They differ in no features from those of *C. porosus* or *C. novaeguineae* of comparable size.

COMPARISON

Comparison will be carried out first with Plio-Pleistocene crocodilians now extinct, and then with modern crocodilians of the Queensland region. The two now extinct crocodilians are the Pliocene or Pleistocene *Crocodylus nathani* (Longman 1924) and the Pliocene *Pallimnarchus pollens* (de Vis 1885). Unfortunately the type material of *C. nathani* does not include any portion of the snout, and so is not directly comparable to F9229. Comparison of the type material with material of *C. porosus* reveals no significant differences between *C. nathani* and *C. porosus*.

The material ascribed to *Pallimnarchus pollens* by de Vis (1885) contains little comparable with F9229, only a left premaxilla, and so comparison will also be made with the snout from 'Lansdowne' assigned to this species by Longman (1925). As pointed out by Longman, the premaxillae of that specimen differ in no significant features from the premaxilla included in the type. Comparison of the type premaxilla with F9229, reveals many differences, almost all of which can reasonably be attributed to the difference in size between the two specimens. Comparison of the type, F9229, the 'Lansdowne' snout, and a large *C. porosus* suggests that F9229 (and *C. porosus*) differ from the type of *P. pollens* in that the latter has a recess for accommodation of the first dentary tooth just posterior to the second premaxillary alveolus. F9229, *C. porosus* and *C. novaeguineae* have such a recess between the first and second premaxillary alveoli. In the 'Lansdowne' premaxilla this recess is immediately posterior to the second premaxillary alveolus (Longman 1925) as in the type premaxilla of *P. pollens*.

A second difference of F9229 from the 'Lansdowne' snout, probably unrelated to the difference in size, is that in the 'Lansdowne' specimen the fourth maxillary tooth is the largest in the tooth row (Longman 1925). In F9229, as in both *C novaeguineae* and *C. porosus*, the fifth maxillary tooth is the largest. These features suggest that F9229 is not referable to *Pallimnarchus*.

Of the two modern crocodiles that inhabit Queensland, *Crocodylus porosus* and *C. johnstoni*, the latter is a narrow-snouted form obviously distinct from F9229. In addition to comparison with *C. porosus*, however, comparison has also been made with *Crocodylus novaeguineae*. This is appropriate because of the proximity of Niu Gini to Queensland, and also because the *Crocodylus* sp. from the Miocene Alcoota local fauna (Northern Territory) has some similarity to *C. novaeguineae* (Woodburne 1967).

Comparisons were made with modern crocodile skulls that ranged in size from that of F9229 to about 30 percent larger in linear dimensions. This choice of skulls restricted the sample available, but eliminated the necessity for consideration of allometric effects. Three skulls of *Crocodylus porosus* were used (University of New South Wales, School of Zoology teaching collection (unnumbered), and QM J14478 and J29021) and one of *C. novaeguineae* (QM J5332).

In the region of the snout *Crocodylus porosus* differs from *C. novaeguineae* in five features (Schmidt 1928, 1932): the presence of a median (nasal) ridge in *C. porosus;* a marked groove on the dorsal surface of the maxilla just lateral to the nasal contact in *C. novaeguineae;* a slender posterior premaxillary process in *C. novaeguineae* five premaxillary teeth in *C. novaeguineae*, and four to five in *C. porosus;* and a more pronounced maxillary-premaxillary notch in *C. porosus* than in *C. novaeguineae*. Taking these in order; the slight upturning of the medial margin of the maxilla of F9229 suggests the presence of a nasa ridge as in *C. porosus*, but does not demonstrate it. On the other hand, a maxillary groove like tha of *C. novaeguineae* is clearly absent in F9229, and the posterior process of the premaxilla is as broad as in *C. porosus*. Five premaxillary alveoli are present in F9229, and the premaxillary-maxillary notch is not only more pronounced than in C *novaeguineae*, but also more pronounced than i the specimens of *C. porosus* available to me.

Thus, of the five features, two are not helpfu whilst the other three suggest attribution to th species *C. porosus*. None resemble the characters of *C. novaeguineae*. It may be concluded that the Allingham crocodile, F9229, represents the earliest material of *Crocodylus porosus*, and that this species has been present in Australia at least since the early Pliocene.

DISCUSSION

The Allingham locality is just west of Emu Valley homestead, which is about 120 kilometres from the coast, and a much longer distance up the Burdekin River and Allingham Creek. This is rather far upstream for a crocodile often thought to be estuarine. It has been noted, however, that *Crocodylus porosus* often travels some distance up rivers (Neill 1971) definitely up to the first major waterfall or barrier (G. W. Webb., pers. comm., 1978). 'Bluff Downs' however is well upstream of the first waterfall, and suggests that either the Pliocene geography had less relief than the present, or that *C. porosus* navigated well beyond the waterfalls.

ACKNOWLEDGMENTS

Dr Ray E. Lemley kindly provided the funds which enabled the discovery of this specimen. The specimen was made available for study by the Queensland Museum, and the photographs were prepared by the Biomedical Photography Unit of the Univ. of New South Wales and Teaching Hospitals. The Queensland Museum, the Australian Museum and the School of Zoology, Univ. of New South Wales made available specimens for comparison. In addition, Drs M. Archer, A. Greer and G. Webb provided helpful comments and other assistance in the preparation of this note.

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PLATE 1

The Allingham and modern crocodile skulls in lateral aspect.
A: *Crocodylus novaeguineae*
B: The Allingham crocodile
C: *Crocodylus porosus*
Line represents 5 cm.

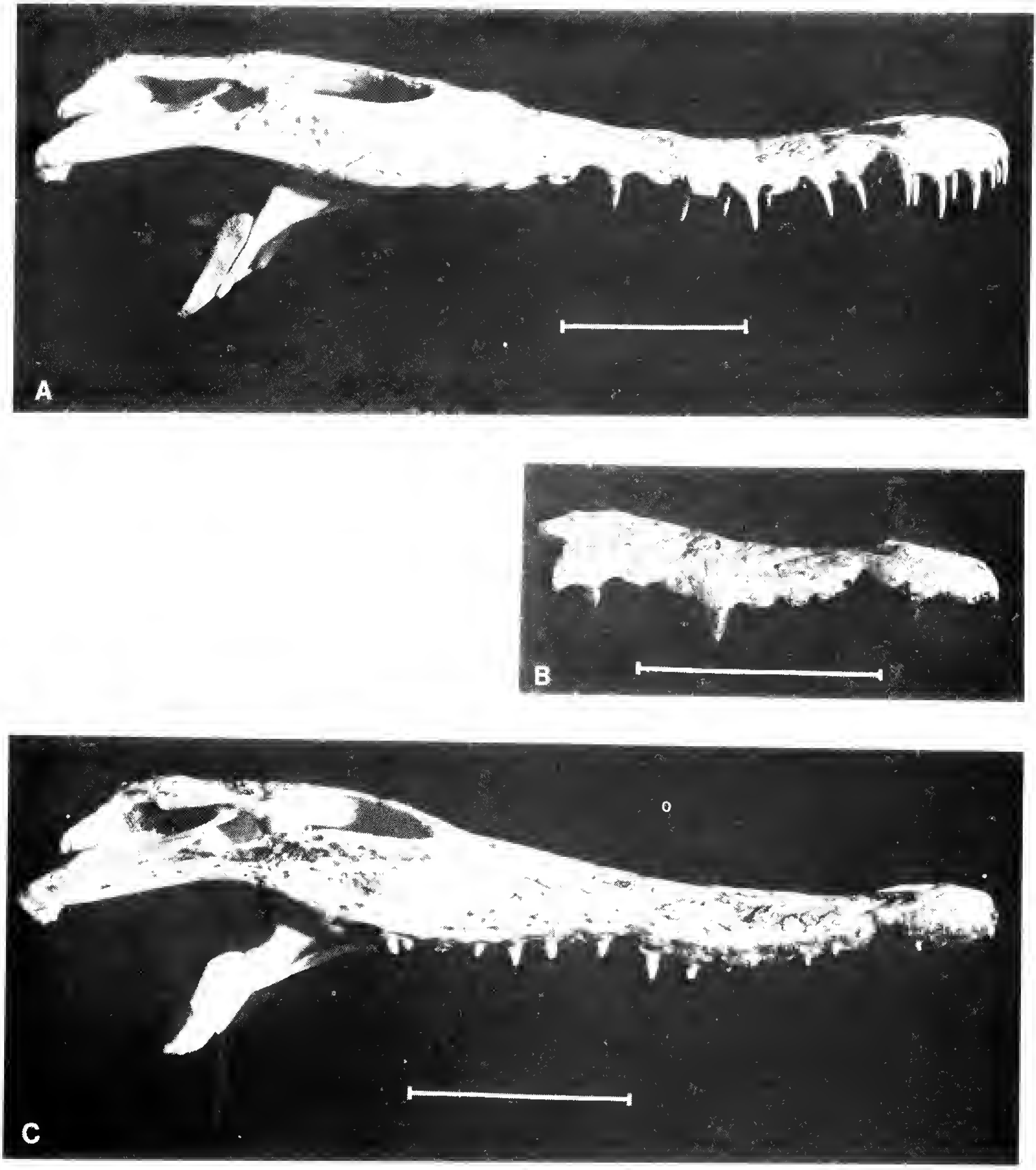
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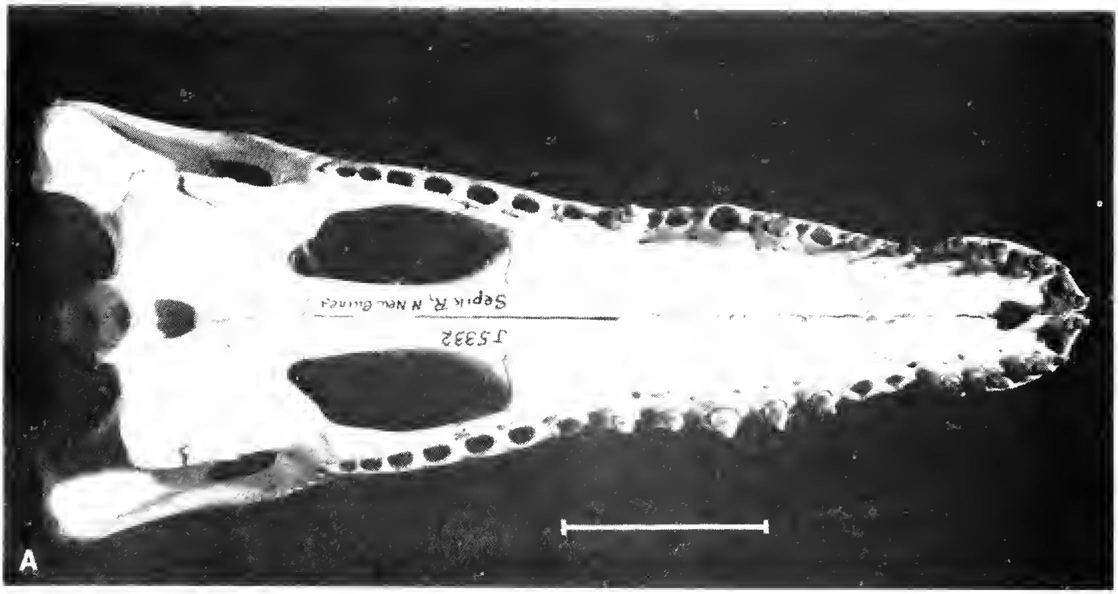
PLATE 2

The Allingham and modern crocodile skulls in palatal aspect.

A: *Crocodylus novaeguineae*
B: The Allingham crocodile
C: *Crocodylus porosus*
Line represents 5 cm.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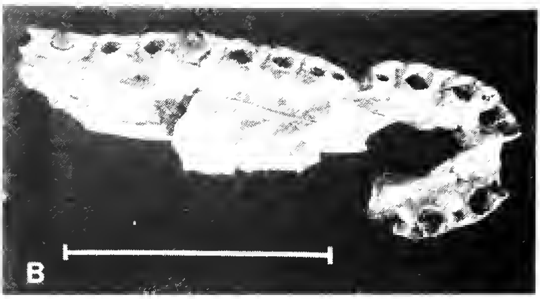
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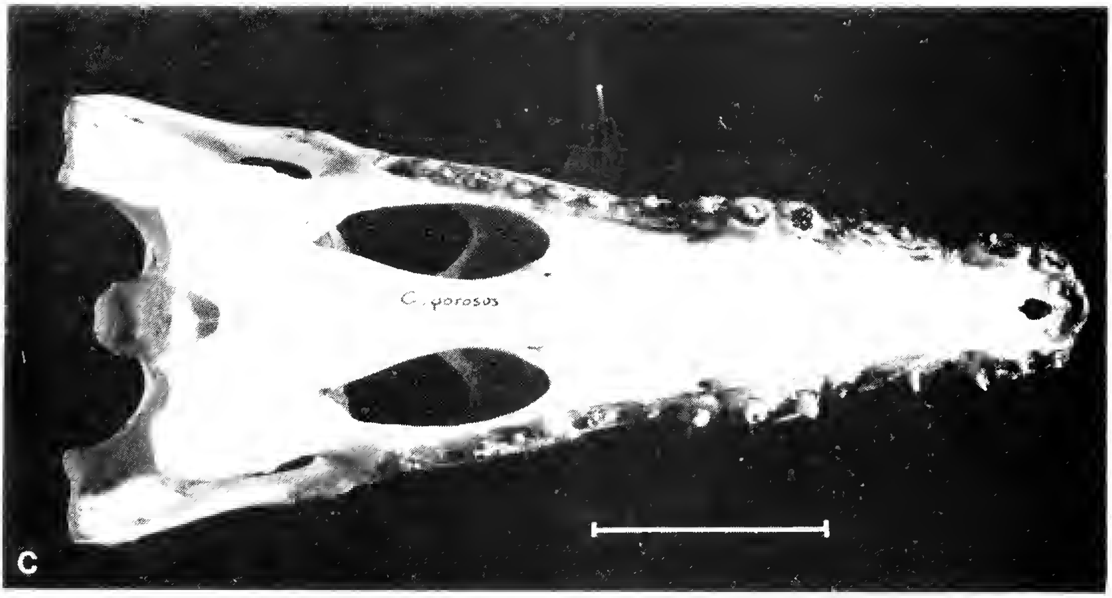
C. porosus
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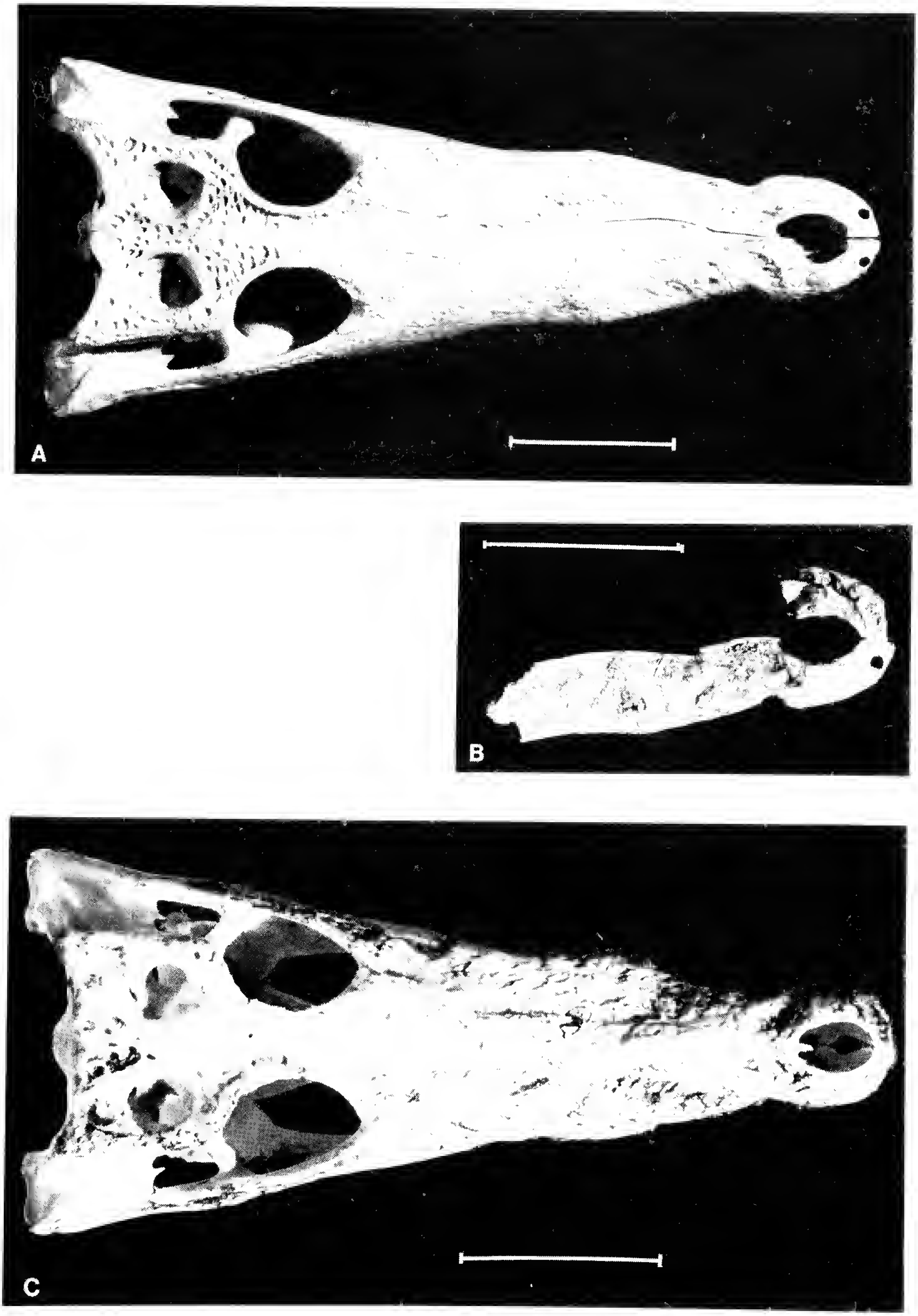
PLATE 3

The Allingham and modern crocodile skulls in dorsal aspect.

A: *Crocodylus novaeguineae*
B: The Allingham crocodile
C: *Crocodylus porosus*
Line represents 5 cm.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Mem. Qd Mus. **19**(3): 367–71, pl. 1. [1979]

DESTRUCTION OF WILD TOBACCO TREES *(SOLANUM MAURITIANUM* SCOPOLI) BY MOUNTAIN POSSUMS *(TRICHOSURUS CANINUS* OGILBY)

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Queensland Museum

ABSTRACT

The feeding activities of Mountain Possums *(Trichosurus caninus)*, in the Conondale Range, southeastern Queensland, led to the defoliation and collapse of a stand (approximately 0·5 ha) of Wild Tobacco trees *(Solanum mauritianum)*. It is unknown how the possums are protected from the highly toxic steroidal alkaloids present in the bark and leaves. It is proposed that the sudden absence of the Wild Tobacco trees will result in the area becoming overtaken by *Lantana camara*.

The Wild Tobacco tree (*Solanum mauritianum)*, Plate 1, Fig. 1, is one of the most prominent pioneer shrubs in tropical and subtropical areas of northern New South Wales and Queensland. It grows rapidly into a small soft-wooded tree of up to six metres, and the large flannel-textured leaves and purple flowers make it a conspicious feature of cleared rainforest patches and abandoned paddocks. Opinions differ as to whether the plant is native to Australia (Everist 1974, p. 470; Webb, Tracey and Williams 1972, p. 681). It is regarded as a noxious weed in many coastal rural areas because it invades rapidly, is difficult to eradicate once established, and seriously reduces pasture carrying capacities. However its ecological importance as a nursery shrub in disturbed forests is emphasized by Williams *et. al.* (1969, p. 531) who state that 'The building phase which follows [the pioneer phase] is primarily characterized by the persistance of two pioneer shrubs — *Omolanthus* and especially *Solanum mauritianum* — which together form what is in effect a preliminary canopy under which the shade tolerant plants of the mature forest can regenerate'.

The Mountain Possum *(Trichosurus caninus)* is common, but restricted to subtropical rainforests in Queensland and northern New South Wales, and wet sclerophyll and temperate forests throughout the rest of its range in eastern New South Wales and in Victoria. Owen and Thomson (1965) report that these possums spend considerable time feeding on the ground and on understorey plants. They found its diet to consist mainly of herbaceous plants, fungi, leaves of shrubs and trees and occasionally lichens. In many areas of southeastern Queensland this possum has commonly been observed raiding council rubbish bins and household compost heaps. It is also regarded as a pest in many fruit orchards, particularly those containing bananas and pecan trees.

In the Conondale Range of southeastern Queensland where the observations reported here took place, the Mountain Possums restrict their activities to understorey trees and shrubs. The canopy feeders in this area are the Common Ringtail Possum *(Pseudocheirus pereginus)*, usually occurring in the rainforest, and the Greater Glider *(Schoinobates volans)* and Yellow-bellied Glider *(Petaurus australis)* which utilize the edge of the rainforest and emergent trees.

The destruction of the small, pure stand (approximately 0·5 ha) of Wild Tobacco trees mentioned here, occurred along the disturbed edges of logging roads and on an overgrown disused road in subtropical rainforest bordering Tragedy Creek (152° 35'E, 26° 42'S) in the Conondale Range of southeastern Queensland.

No more than three or four adults were seen feeding at any one time in the Tobacco Trees. This contrasts with unnaturally high densities found in some suburban areas of outer Brisbane such as Mt Glorious, where as many as ten or twelve adults often congregate in single small trees, (eg. *Acacia* spp.) before descending to feed on compost scraps. Both males and females have been observed feeding on the Tobacco trees. The area was visited four times in eight months during 1977–8. The first observations were during the winter months. The Mountain Possums at this time fed on the bark, terminal branches and the leaves but appeared to prefer the bark, which was eaten to ground level and as far out on the branches as the animals' weights would permit them to reach (Pl. 1, Figs. 2 and 3). Their continued browsing over the next three months led to the eventual defoliation of shrubs over most of the area. Those shrubs (approximately 90% of the stand) that had been completely de-barked had dehydrated and had either been toppled over by wind or remained upright as dead sticks (Pl. 1, Figs. 4 and 5). In one small area some partially eaten trees had begun to sprout new shoots from the main trunk. Subsequent visits during the following summer, revealed Mountain Possums eating the leaves of such trees that had regrown (Pl. 1, Fig. 6).

DISCUSSION

Australian *Solanum* plants contain steroidal alkaloids in the form of solasodine. Collins, Eastwood and Swan (1976) comment that three species (*Solanum aviculare, S. laciniatum* and *S. similie)* contain high enough concentrations of solasodine to be considered suitable for possible cultivation as part of an Australian steroid industry. Solasodine has a very similar structure to diosgenin, a plant steroid extracted from the yam *Dioscorea*, grown extensively in Mexico. This steroid is chemically converted into sex steroids used in oral contraceptives throughout the world. Solasodine can similarly be converted into marketable sex steroids.

An assay of the steroidal alkaloids found in *Solanum mauritianum* (J. M. Swan pers. comm.), revealed 0·18, 0·09 and 1·11% of solasodine in the dried leaf, stem (bark and core of terminal branches) and green fruits respectively. These figures refer to the aglycone obtained after acid hydrolysis, the alkaloid actually occurring as the glycosides, solasonine and solamargine. Solasodine glycosides are very toxic. Everist (1964) reports a few cases of fatal poisoning in pigs and cattle in Queensland. As part of a demonstration of the toxic effects of these glycosides, A. A. Seawright (pers. comm.) fed a 5–10 ml homogenate of ground green berries of *S. mauritianum* to guinea pigs and the animals died within an hour after ingestion. Everist (1974, p. 471), reporting similar demonstrations by Seawright, noted that the 'Symptoms and post mortem appearance were those of acute gastrointestinal irritation'. He also notes a case of fatal human poisoning that followed ingestion of the fruits of this plant.

The berries of the Wild Tobacco are commonly eaten by rainforest birds such as King Parrots (*Alisterus scapularis*), Brown Pigeons *(Macrophygia amboinensis)* and Satin Bowerbirds *(Ptilinorhynchus violaceus)*, but there are few reports of native mammals eating these fruits. J. Winter (pers. comm.) has observed Spectacled Fruit Bats *(Pteropus conspicillatus)* squeezing and consuming the juice but discarding the fibre and seeds of the berries. J. A. Lamberton (pers. comm.) points out that in another species, *S. aviculare*, the concentration of solasonine is highly variable, the greatest concentrations being formed in under-ripe fruit. The alkaloid disappears rapidly as the fruit ripens.

The leaves of the Wild Tobacco tree are sometimes eaten by native mammals. In his discussion of the Coppery Brushtail *(Trichosurus vulpecula)* Russell (1977) states that 'They also eat the leaves of the Wild Tobacco bush, almost defoliating a particular bush at times. Again this is the only possum I have seen eating this plant.' J. Winter (pers. comm.) also reports individuals of *T. vulpecula* eating these leaves in areas of the Herberton Range of northeastern Queensland. M. Archer (pers. comm.) reports Mountain Possums eating leaves from the same species on Mt Glorious, 30 km west of Brisbane.

This is the first report of a mammal or bird eating the bark of the Wild Tobacco tree.

It is surprising that possums should find the tree edible. No tests have been made to determine the manner in which Mountain Possums are protected from the potentially toxic effects of this food but it is possible that some protection is afforded by the action of microsomal enzymes (see Freeland and Winter (1975) on feeding in *T. vulpecula)*.

It is not yet known if this tree is a preferred food of the Mountain Possum or something eaten only when no other more appetizing foods are available. In 1977, when the observations were made the area was suffering a drought. The destruction of the patch of Wild Tobacco trees would no doubt affect patterns of succession in that area. Immediately adjacent to the study area were well established patches of *Lantana camara*. Williams *et al.* (1969, p. 531) point out that as soon as the 'preliminary canopy' dies and the canopy opens then succession follows one of two paths depending on whether ' . . . more advanced plants than *Solanum mauritianum* are already forming a canopy which will occur only on litter-intact sites. On such sites such shade tolerant species of e.g. *Urtica*, *Sambucus* and *Laportea* are to be expected, since they are able to outgrow *Lantana* and prevent its establishment; but in the bare and well lighted sites . . . where the advanced species are not yet established, disappearance of the preliminary canopy will favour the growth of *Lantana* even more strongly'.

The lack of more advanced plants than *Solanum mauritianum* in the study area suggests that the area will eventually become overtaken by *Lantana*.

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PLATE 1

FIG. 1: Uneaten Wild Tobacco tree *(Solanum mauritianum)*.
FIG 2: Bark eaten from main stem.
FIG. 3: Partially eaten Wild Tobacco trees.
FIG. 4: Stake left after debarked limb had dehydrated and collapsed.
FIG. 5: Defoliated Wild Tobacco trees.
FIG 6: Mountain Possum *(Trichosurus caninus)* eating leaves of Wild Tobacco tree.

1

2

3

4

5

6

Mem. Qd Mus. 19(3): 373–9, pl. 1. [1979]

A NEW SPECIES OF BIOLUMINESCENT EARTHWORM FROM NORTH QUEENSLAND BELONGING TO THE SUBGENUS *DIPLOTREMA* (OLIGOCHAETA: MEGASCOLECIDAE)

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ABSTRACT

A new species of the Acanthodriline earthworm genus *Microscolex (Diplotrema)* from the Townsville district of north Queensland is described and figured. The species exhibits alternation of nephropore position, a condition elsewhere within the Acanthodrilinae approached only by members of the endemic New Zealand Neodrilacea. This mutually-shared character is more likely to represent a convergence rather than real phyletic affinity. The new species was found to exude bioluminescent coelomic fluid when agitated, a phenomenon tenuously linking it to the North American genus *Diplocardia*, at least one species of which is known to exhibit a similar reaction.

The endemic Australian subgenus *Diplotrema* is known to occupy a range extending from a southeasterly limit near Narrabri, New South Wales (Dyne 1978), through southern Queensland to Cape York Peninsula, and across to the Northern Territory (Jamieson and Dyne 1976), with an isolated record from SW Australia. The new species described in the present study adds a further link to the discontinuous distribution of *Diplotrema* species which follows the Queensland coastline.

Populations of worms were found to be restricted to open, comparatively dry, grassy areas, often in the surrounds of semi-perennial creeks (the Townsville region is itself considered to lie in an arid corridor). Such habitat 'preferences' are shared by a large number of *Diplotrema* species, possibly indicative of a predominantly geophagous, rather than phytophagous, feeding strategy.

The observation of marked bioluminescent activity in the coelomic fluid of live individuals prompted a detailed systematic study of the species prior to an investigation into the biochemical system involved.

The following abbreviations are used in text and figures:

AM	Australian Museum
BM	British Museum
♀	Female pore
GD	Author's collection
l	Length
♂	Male pore
pr.p	Prostatic porophore
QM	Queensland Museum
s	number of segments
sem.gr	seminal groove
sp.amp	spermathecal ampulla
sp.d	spermathecal duct
sp.div	spermathecal diverticulum
sp.p	spermathecal pore
w	width
U	total circumference

SYSTEMATICS

Genus **Microscolex** Rosa, 1887

Subgenus **Diplotrema** Spencer, 1900 Emend.

Diplotrema heteropora sp. nov.
(Figs. 1A–D, Table 1, Plate 1)

MATERIAL EXAMINED

HOLOTYPE: Queensland Museum G8890, 147° 02'E, 19° 30'S, Palm Creek, approx. 33 km south of Townsville, under bladey grass in sandy soil, about 30 meters up the creek bank, coll. G. Dyne, 10 Feb 1975.

PARATYPES: QM G8932, AM W6634–5, BM 1978.1.16., same data as holotype; QM G8892–3, AM W6636, BM 1978.1.17, 146° 55'E, 19° 36'S, 7 km E of

Woodstock, on road to Giru, approx. 40 km south of Townsville, in moist to saturated sandy loam under grass and open eucalypts, coll. W. Nash, 13 Mar 1977; QM G8891, 8894, AM W6637, GD 1977.1–2, 146° 49'E, 19° 17'S, 100 m from ring road, James Cook University, Townsville, towards Mt Stuart, in moist sandy soil, coll. W. Nash, 20 Mar 1977; GD 1978.3, BM 1978.1.18, AM W6638, QM G8895–6, 0·5 km from ring road, towards Mt Stuart, in moist black clayey soil.

DESCRIPTION

l 83+, 154 mm; w (midclitellar) 5·9, 7·8 mm; s 134, 264 (Holotype (posterior amputee), Paratype QM G8932). Form circular in cross-section throughout; pigmentless buff in alcohol, clitellum purplish-grey. Prostomium pro-lobous, peristomium much furrowed. First dorsal pore 18/19; setae 8 per segment, commencing in II in regularly spaced longitudinal rows throughout; setae *a* and *b* of XVII and XIX modified as penial satae, those of VIII and IX as genital setae, setae *a* and *b* absent from XVIII.

Nephropores visible externally only on the clitellum, alternating between *c*-lines (sometimes a little shifted towards *b)* and a position far lateral of *d,* near the mid-dorsal line; the pores discharging in the intersegmental furrows. Clitellum annular, encompassing, with the exception of the male field, segments XIII–XIX, slightly encroaching into XX. Setae and intersegmental furrows only partially obscured on the clitellum. Male pores small points lateral of *b* in XVIII, close to 17/18, located slightly lateral of a pair of well-defined seminal grooves. Prostatic porophores 2 pairs, the trans-segmental pairs conjoined by the somewhat sinuous seminal grooves. The central region of the male field (demarcated by the intersegments 17/18, 19/20, and the seminal grooves) is depressed, with the raised porophore mounds projecting ventrally into it; there is a similar ventralwards extension of the male field margin in mid-XVIII. Female pores are conspicuous as a pair of small slits immediately anterior of *a,* in XIV. Spermathecal pores 2 pairs, inconspicuous, situated in 7/8, 8/9, obscured by segmental overlap. A broadly diffuse tumescence associated with the genital setae is discernible in the ventral seta surrounds of segments VIII and IX.

Septation: 5/6–9/10 strongly muscularized and thickened, 7/8 the thickest; 10/11 moderately strengthened, 11/12 slightly so. Dorsal blood vessel single; last hearts in XIII. Supra-oesophageal vessel present, traceable only in X–XV; only those commisurals in X–XIII may be regarded as heart-like, with connectives to both the dorsal and supra-oesophageal vessels; the

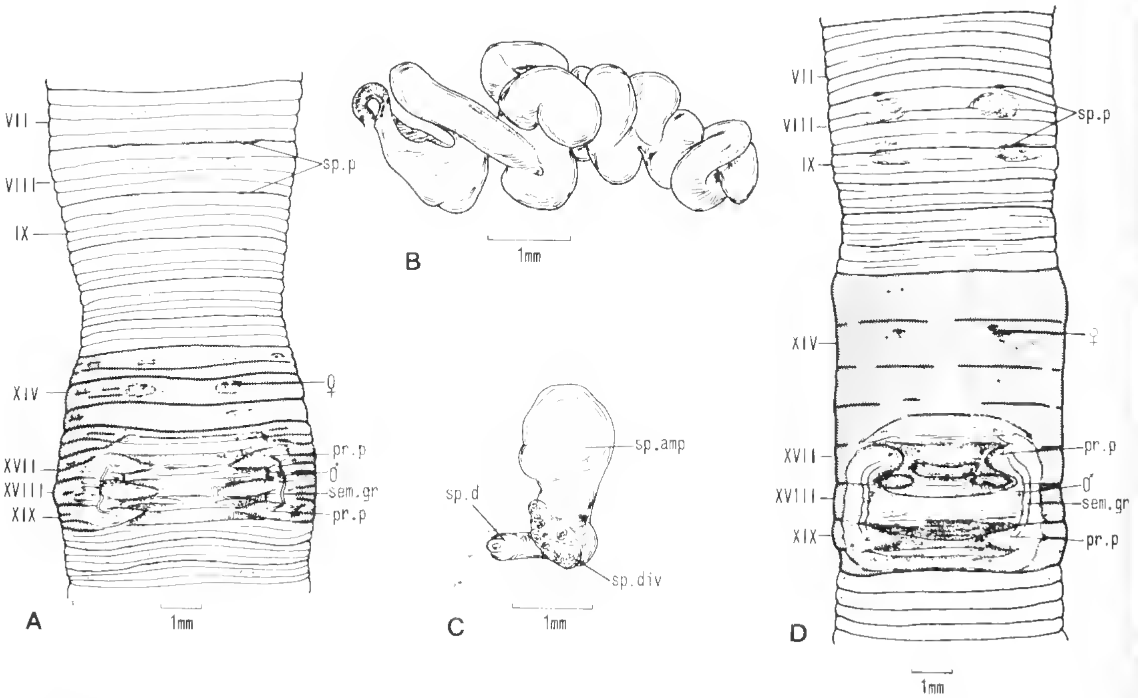

FIG. 1: *Diplotrema heteropora:* A, Genital field of Holotype; B, Dorsal aspect of right prostate gland of Holotype; C, Right IX spermatheca of Holotype; D, Genital field of QM G8892.

remainder are dorso-ventral only, decreasing in size anteriorly. Gizzard large, firm and muscular, in V; oesophagus narrow, internally rugose, lacking pouching or calciferous glands; intestine commences in XIX, typhlosole developed as a low ridge after XXIX, intestinal walls somewhat thickened and folded.

Simple stomate holonephridia present throughout, with conspicuous ducts alternating regularly in the position of exit to the exterior; alternation internally appears to be from *cd* to far dorsal of *d*, though the duct apparently travels a short distance within the parietes. Nephridial bladders absent. A large pair of tufted nephridia present in IV, with a well-defined composite duct passing anteriorly. In III, the duct bifurcates, sending one branch dorsally, the other continuing along the ventrolateral body wall; the fate of the two respective ducts was not definitely determinable, though in all probability, they terminate enteronephrically in the buccal cavity. Holandric; 2 pairs of medium-large iridescent sperm funnels present in X and XI, and 2 pairs of racemose seminal vesicles with distinct component loculi in IX and XII. Two pairs of tubular, highly coiled, yet compact, prostate glands in XVII and XIX, each with a muscular, medium length duct passing to the exterior. Vasa deferentia not demonstrable in H., but in QM G8892 (Woodstock Popn.) they are obvious as a pair of iridescent tubes winding on the body wall on each side, turning dorso-laterally to skirt the internally glandular manifestation of the male field, becoming slightly more swollen, finally entering the parietes, unfused, in XVIII. Two pairs of conjoined (*a* and *b*) penial seta follicles are associated with the prostatic ducts in XVII and XIX, each containing a number of small, curved, reddish setae, in varying stages of growth; the shaft of mature setae are more or less regularly ornamented with series of very shallow circumferentially orientated indentations; length of mature seta = 1·87 mm; midshaft diameter = 32·5 μm (mean of 2).

Ovaries, composed of fan-shaped egg-strings, together with plicate funnels in XIII. Spermathecae 2 subequal pairs in VII and IX, each composed of a sacciform ampulla, with sessile diverticulum at the junction of ampulla and duct, the diverticulum internally partitioned into numerous iridescent intramural sperm chambers; the duct long and slightly sinuous; ratio, length spermatheca: length of duct = 3·0. Two pairs of genital seta follicles are associated with the spermathecal ducts; these follicles are themselves embedded in discrete lobulated glandular tissue. The setae are, but for the proximal and distal extremities, ornamented with a regularly arranged pattern of distally sloping concavities, giving the seta a serrated appearance; the tip is sometimes further elaborated by a pair of longitudinally directed grooves. Length of mature seta = 1·02 mm; midshaft diameter = 44·2 μm (mean of 2).

PARATYPIC VARIATION: Small interpopulational differences in the configuration of the genital field were observed: one of the specimens from the type locality, AM W6634 and particularly some Woodstock paratypes, e.g. QM G8892, possessed three additional tumescences within the male field; one elongate marking intermediate between the anterior pair of porophores, the remaining two

TABLE 1: INTERSETAL DISTANCES IN *DIPLOTREMA HETEROPORA* EXPRESSED AS PERCENTAGES OF THE PERIPHERY

	aa	ab	bc	cd	dd	dc	cb	ba	U (in mm)
HOLOTYPE	10·90	1·96	8·42	1·67	66·3	1·67	7·07	2·06	14·93
QM G8932	12·98	1·70	8·37	1·41	62·9	1·37	9·68	1·61	19·64
AM W6635	11·91	1·56	9·23	1·73	63·7	1·71	8·58	1·54	18·25
QM G8892	11·29	1·60	8·90	1·66	64·9	1·47	8·59	1·60	19·09
QM G8893	12·66	1·64	9·6	1·22	62·8	1·36	9·55	1·21	16·85
AM W6636	10·70	1·65	9·24	1·22	66·3	1·10	8·33	1·49	19·68
BM 1978.1.11	12·17	1·75	8·28	1·48	64·3	1·33	8·96	1·70	18·70
$\bar{x}$	11·80	1·69	8·86	1·48	64·5	1·43	8·68	1·60	
S_x	0·87	0·13	0·52	0·21	1·45	0·21	0·87	0·26	
$S_{\bar{x}}$	0·33	0·05	0·20	0·08	0·55	0·08	0·33	0·10	
Townsville Population									
QM G8894	13·95	1·91	9·08	1·64	61·5	1·56	8·5	1·89	14·45
AM W6637	11·72	1·47	8·96	1·37	63·2	1·59	10·20	1·49	15·88
GD 1977.1	13·86	1·63	10·15	1·35	60·7	1·40	9·27	1·60	15·77
$\bar{x}$	13·18	1·67	9·40	1·45	61·8	1·52	9·32	1·66	

elliptical, immediately below the porophores; in some specimens, there are additional markings in 19/20 and/or 20/21. Unlike the type, in most specimens, the median ventralwards projections of the male field are produced as to form a single raised median ridge. Considerable variation also exists as to the degree of development of the swelling associated with the genital setae in VIII and IX.

Internals: In QM G8892–3 and AM W6636, the supra-oesophageal vessel is more highly developed than the condition described for the Holotype, extending from VIII–XIV; the origin of the intestine may vary from XIX(H.) to XVII (as in QM G8932) or XVIII (AM W6634, QM G8892–3); muscular thickening observed in the Holotype was not found developed to the same degree in any other specimens examined.

REMARKS

Nephropore alteration distinguishes *D. heteropora* from the remainder of the genus. The configuration of the genital field is also unique. The occurrence of the first dorsal pore in the clitellar region is not elsewhere recorded for *Diplotrema*, though an even further posteriad position is described for *D. eremia* (Spencer 1896), in which the pores commence in the postclitellar region (confirmed in Jamieson and Dyne 1976).

BIOLUMINESCENCE OBSERVATIONS

Live worms from Townsville were found to exude copious bioluminescent coelomic fluid on electrical stimulation (using a 50 volt magneto) or prolonged mechanical agitation. Addition of dilute peroxide greatly enhanced the emission of light, producing a 'flash-peak', and thereafter, rapidly waning activity. The emitted light appeared yellow-green to the dark-adapted eye.

Similar activity was recently recorded by Jamieson (1977) for a species of *Digaster, D. keasti*, though this species did not exhibit spontaneous luminosity. The stimulation, by peroxide, of increased activity, particularly in the spontaneously luminescent *Diplotrema heteropora*, suggests the existence of a peroxidase-type bioluminescence system, as demonstrated for the North American acanthodrile *Diplocardia longa* (Bellisario et al. 1972). In this species, the luciferin substrate has been found to be a relatively simple aldehyde (Ohtsuka et al. 1976).

Jamieson (1977) discusses the adaptive significance of bioluminescence in earthworms. Nash (pers. comm.) has found that the Townsville worms do not demonstrate luminosity throughout the entire year. Such seasonality could be correlated to a breeding cycle, in which case the bioluminescence may be a functional component of a mate recognition system.

DISCUSSION

Within the Acanthodrilinae, nephropore alternation as seen in *Diplotrema heteropora* has previously been confined to the Neodrilacea, an apparently homogeneous aggregate of four genera restricted to New Zealand. The type genus of the group, *Maoridrilus*, was originally partitioned from *Acanthodrilus* on the basis of alternating nephropore series by Michaelsen in 1899, and later united with *Neodrilus* and *Plagiochaeta* in a group termed the 'Maoridrilacea' (Michaelsen 1928). Stephenson (1930), in reviewing the acanthodrile genera, reasserted the integrity of the group as his 'Sectio Neodrilacea' a name retained by Lee (1959), at the hierarchical level of Tribe, when revising the New Zealand earthworm fauna, and incorporating a further new genus, *Neochaeta*.

In *Maoridrilus* the nephropores alternate between the dorsal and ventral setal couples, whereas in *D. heteropora*, the alternation is between the dorsal setal couples and a position yet further dorsal by a distance exceeding *bc*. The vast majority of members of the Neodrilacea possess nephridial bladders, often differing in shape according to the position of the nephridial body; such structures are totally lacking in *D. heteropora* or any other known Australian acanthodrile.

It is probable that the evolution of the condition seen in *D. heteropora* has been a completely independent event, and indicates no direct affinity with the New Zealand forms other than, perhaps, common retention of genetic pre-adaptation inherent in primitive, mutually-shared Pan-Gondwanan ancestors.

In overall morphology (e.g. arrangement of the male terminalia, possession of penial and genital setae, the number and general appearance of the spermathecae) *D. heteropora* is an unremarkable *Diplotrema* species. Though the fixation of nephropore alternation amounts to a morphological apomorphy (phyletic advance), with respect to the numerically dominant single-series acanthodriles, it is difficult to envisage a satisfactory adaptive advantage deriving from such a configuration. In forms with large nephridial bladders (e.g. *Maoridrilus*), such a condition may represent the most parsimonious solution to a 'packing' problem; no such adaptive pressures apply, however, in the avesiculate *D. heteropora*, unless one accepts the remote possibility that ancestral forms of this species originally possessed bladders, and have since lost these. A further hypothesis might be that in the event of the excretory fluid acting as a locomotory lubricant, an alternating nephropore arrangement would provide a more satisfactory distribution of the fluid. Alternatively, the condition may have arisen simply as a pleiotrophic effect of genes encoding for other characters, which are, themselves, under considerable selective pressure.

The affinities of *Diplotrema* with the extra-Australian *Diplocardia* are discussed in Jamieson and Dyne (1976); the mutual possession of bioluminescence systems with at least partially compatible cross-reactivity (Wampler, pers. comm.) may be interpreted as further evidence of a definite relationship between these two genera.

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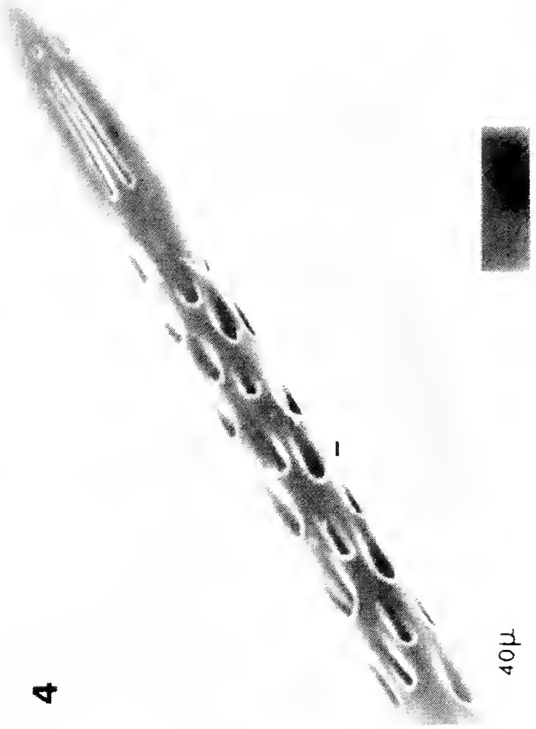
PLATE 1

FIG. 1: Midshaft region of penial seta from right XIX follicle;
FIG. 2: Genital seta from right VIII follicle of Holotype;
FIG. 3: Detail of midshaft region of 2;
FIG. 4: Genital seta from right VIII follicle of QM G8892.


1
20μ


2
100μ


3
20μ


4
40μ

Mem. Qd Mus. **19**(3): 381–91, pls. 1, 2. [1979]

THREE SPECIES OF *LINGULA* FROM THE QUEENSLAND COAST

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ABSTRACT

On the basis of new taxonomic characters, *Lingula* species common on the Queensland coast are shown to belong to three species: *L. anatina, L. rostrum,* and *L. adamsi.* All three are described and illustrated on the basis of these new characters. The understanding of the taxonomy of the genus has been advanced in the present work. *L. bancrofti* is shown to be a synonym of *L. rostrum,* and *L. murphiana* of *L. anatina.* Collections studied are principally located in the Queensland Museum and these have been compared with material in the British Museum, the Museum National d'Histoire Naturelle de Paris, and the Australian Museum.

Johnston and Hirschfeld (1920) recognized the following species of the genus *Lingula* on the Queensland coast: *L. anatina* Lamarck>*L. rostrum* (Shaw); *L. tumidula* Reeve; *L. hians* Swainson>*L. hirundo* Reeve; *L. murphiana* Reeve; *L. exusta* Reeve; *L. bancrofti* Johnston and Hirschfeld. These species were all distinguished on the basis of the valve characters. However these show such a high degree of variability that they are unreliable as taxonomic criteria. Hedley (1909) considered that all Australian specimens should be assigned to a single species, although in 1916 he recognized the possibility that they represented more than one species. Recently, Hammond and Kenchington (1977), using morphometric characters, assigned the Queensland *Lingula* to only two species, *L. anatina* and *L. tumidula.*

As the *Lingula* species are not easy to distinguish from one another, they are often misidentified and confused. Queensland is the type locality for several of the species that have been designated in the genus. The present study was undertaken in an attempt to resolve some of the problems.

The taxonomic characters that are available on which to base taxonomy of the genus are reviewed and the Queensland specimens are redescribed.

TAXONOMIC CRITERIA

The most commonly used features are on the shell (i.e. colour, convexity, calcification, opacity, general form, ratio length to breadth). They vary throughout the life of each individual, between different populations, and within a population of the same species. The peduncle also varies in length owing to its capacity to regenerate, as well as its degree of contraction, and the amount of shrinking during fixation. All these criteria have been assigned some taxonomic value (Chuang 1962, Emig 1977c, Hammond and Kenchington 1977).

The shell ratios proposed by Chuang (1962) must be considered cautiously. The width/length ratio of the protegulum may be helpful in identification of juvenile specimens, but has been tested in only 3 species (Emig 1977c). The width/length ratio of the dorsal larval valve shows too great a variability (Emig 1977c). The width/length ratio of the whole shell, studied by Hammond and Kenchington (1977) cannot be used, since different species identified according to the two new criteria (set out below) have a similar w/l ratio. It appears, therefore, that all morphometric characteristics previously used to designate species must now be considered as inadequate for taxonomic purposes.

The validity of the morphology of deltidial regions and the arrangement of musculature, as distinguishing characters, has been demonstrated recently by Emig (1977a, 1977c). These two major features are used in this work to distinguish the Queensland species of *Lingula.* A third characteristic appears to be the disposition of the two main mantle canals. Information on the other non-taxonomic characters is also given.

Lingula anatina Lamarck

Lingula anatina Lamarck, 1801, p. 141. Davidson, 1888, p. 206. Emig, 1977b, p. 102.

Patella unguis Linnaeus, 1758, p. 783.

Lingula unguis: Rowell, 1964, p. 223.

Lingula murphiana Reeve, 1859, pl. 1. Davidson, 1888, p. 215. Johnston and Hirschfeld, 1920, p. 58. Emig, 1977a, p. 402.

Lingula lepidula Adams, 1863, p. 101. Davidson, 1888, p. 220. Hatai, 1940, p. 179.

Lingula smaragdina Adams, 1863, p. 101. Davidson, 1888, p. 220. Hatai, 1940, p. 179.

?Lingula nipponica Hayasaka, 1931, p. 364. Hatai, 1940, p. 181.

?Lingula hirundo Reeve, 1859, pl. 2. Davidson, 1888, p. 220. Johnston and Hirschfeld, 1920, p. 53.

MATERIAL EXAMINED

Moreton Bay: G5483 (Toorbul Point); G5207 (Sandgate); G2126 (Sandgate); G1084 (Wellington Point); G5118 (Dunwich); G11668 (Amity Point); G2305, 2306 (Nudgee Beach); G2100 (Traviston) (Queensland Museum). Southport: G2304, G12058–60, G2872 (Queensland Museum). Burnett Heads: G5373, part G5487/1 (one specimen of 3 paratypes of *L. bancrofti*) (Queensland Museum). Northeast Queensland: G2283–5 (Proserpine); G11666 (Cardwell) (Queensland Museum). Port Curtis: AM C59917, C107138 (dried valves) (Australian Museum). Singapore, Senegal: material listed as *L. anatina* by Emig 1977a, b. Madegascar: material listed as *L. murphiana* by Emig 1977a.

All the Queensland Museum specimens previously assigned to *L. bancrofti* and *L. murphiana* have been compared with *L. anatina* (see above). No significant differences could be found between most specimens. The syntypes of *L. bancrofti* (AM C43925) are unquestionably synonymous with *Lingula rostrum*. However, of the three paratypes of *L. bancrofti* (QM G5487), two are assigned to *L. rostrum* and one to *L. anatina*. Johnston and Hirschfeld (1920) considered *L. rostrum* as a synonym of *L. anatina* while they regarded *L. bancrofti* as closely related to *L. anatina*. This confused later workers, and most of the specimens that were subsequently

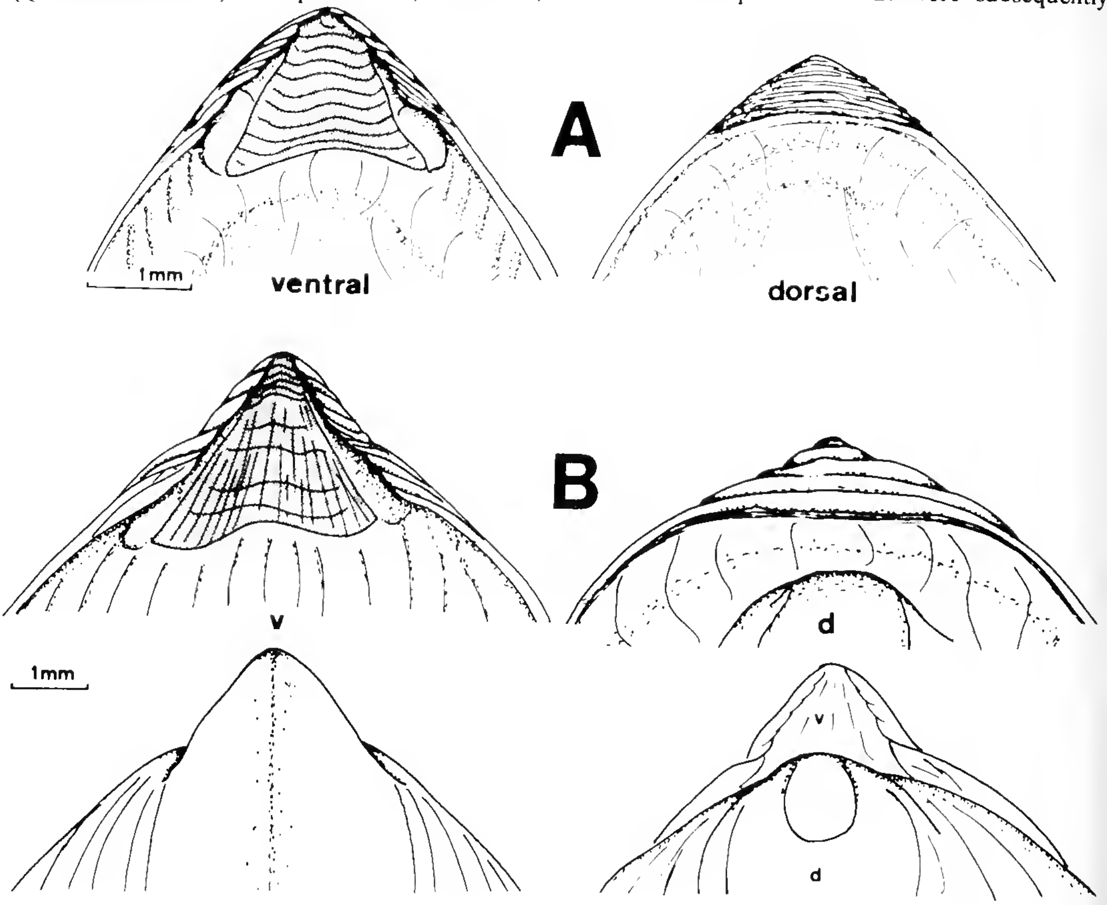

FIG. 1: Deltidial regions of A, *Lingula anatina* (interior view); B, *L. rostrum* (interior and exterior views).

assigned to *L. bancrofti* actually belong to *L. anatina*.

On the other hand, *L. murphiana* Reeve (type-locality: Moreton Bay) is without doubt a synonym of *L. anatina*. In his original description Reeve (1859) states 'this *(L. murphiana)* should be regarded as an Australian form of *L. anatina* or as a distinct species, it is certain that the differences are obvious and constant'. The first assertion is confirmed. Johnston and Hirschfeld (1920, p. 58) correctly named Australian specimens *L. anatina*, and so did Hedley (1909) whose dried valves (AM C59917 and C107138) were examined and his identification confirmed.

The characteristics of *L. anatina* from Queensland waters are as following:

The shell is oblong-elongate, has parallel lateral margins, sometimes slightly concave in large specimens. The anterior edge is nearly straight, or slightly convex, with a median angular projection; frontal margins are almost equal (Plate 1a). The deltidial region of the ventral valve possesses a longer beak than the dorsal one and, on the inner surface, a shallow pedicular groove. The beak of the dorsal valve has a somewhat flattened inner face (Fig. 1A, Plate 1a, c).

The external surface of the shell valves is rather smooth, but growth lines are distinct (Plate 1a, b). Three low-siphonal ribs extend from beak to the anterior margin of the shell in the direction of the three clusters of setae (Plate 1a, d). Internally, the surface is smooth. The dorsal valve shows a well-marked median ridge (Plate 1c) that is only outlined on the ventral valve. The degree and extent of calcification is variable, as is the colour, which is generally greenish to dark-greenish.

In side view, the shell of *L. anatina* is slightly elliptical (Plate 1b).

The peduncle, fleshy in colour, is once to twice the length of the shell. No pallial pigmentation is observed. The arrangement of musculature (Fig. 2A) is comparable in all points with previous data (Emig 1977a, 1977b). Measurements of dorsal larval valve are similar to those given by Chuang (1962): width 574–651 μ ; length 667–853 μ . The ratio w/l is 0·763–0·897. The two main mantle canals are generally elongate and only a little incurved (Fig. 2A).

L. lepidula Adams and *L. smaragdina* Adams are generally considered as juvenile forms of *L. anatina* (Davidson 1888, Hatai 1940). Hatai (1940) believed that *L. nipponica* probably also belonged to *L. anatina* from which it is distinguished only by the outline of the shell. Hatai's description however could also agree with *L. rostrum*. *L. hirundo* Reeve (type locality Port Curtis) is another possible synonym of *L. anatina*, as some dried valves from Port Curtis (Australian Museum collection) suggest a close resemblance with *L. anatina*. This view is supported by Johnston and Hirschfeld (1920) who point out that the form and the proportion (of *L. hirundo*) do not agree with *L. bancrofti* (< *L. rostrum)*.

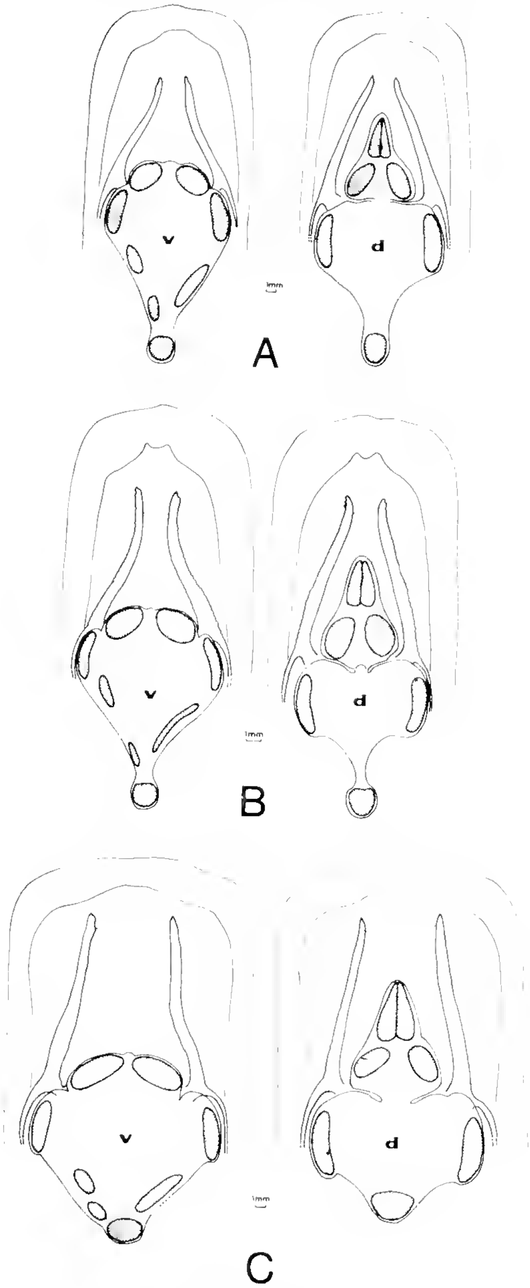

FIG. 2: *Lingula rostrum:* arrangement of the musculature and disposition of the two main anterior mantle canals of A, *Lingula anatina;* B, *L. rostrum;* C, *L. adamsi*.

The view of Hammond and Kenchington (1977) that *L. bancrofti, L. exusta, L. hians, L. murphiana* should all be assigned to the type species *L. anatina* is not supported by the present observations.

Lingula rostrum (Shaw)

Mytilus rostrum Shaw, 1797, pl. 315.
Lingula hians Swainson, 1823, p. 401. Sowerby, 1846, p. 338. Davidson, 1888, p. 216. Johnston and Hirschfeld, 1920, p. 54.
Lingula exusta Reeve, 1859, pl. 2. Davidson, 1888, p. 217. Johnston and Hirschfeld, 1920, p. 63.
Lingula bancrofti Johnston and Hirschfeld, 1920, p. 67.
?*Lingula affinis* Hancock, 1858, p. 791. Davidson, 1888, p. 215.

MATERIAL EXAMINED

Burnett Heads: G5487/2, 3 (2 specimens of 3 paratypes of *L. bancrofti*) (Queensland Museum); AM C43925 (syntypes of *L. bancrofti*) (Australian Museum). Moreton Bay: G5298 (Redland Bay); G984, G1056 (Sandgate) (Queensland Museum). Port Denison: AM C43684 (Australian Museum). Dunk Island: G11667 (Queensland Museum); AM C45047 (Australian Museum). Amboina (type-locality): material listed as *L. rostrum* by Cals and Emig 1979.

A comparison of *L. rostrum* from Amboina (type-locality) with the Queensland material, indicates that many individuals belong to *L. rostrum*, but that some specimens have been wrongly assigned to that species. Examinations of the syntypes and paratypes of *L. bancrofti* indicate that it is undoubtedly a synonym of *L. rostrum*. However Johnston and Hirschfeld (1920) were wrong in designating *L. rostrum* as a synonym of *L. anatina*. *Lingula hians* and *L. exusta* are also synonyms of *L. rostrum*. *Lingula hians:* Johnston and Hirschfeld (1920) was described from dried valves, rather distorted. Several specimens from the Australian Museum collection were previously referred either to *L. hians* or *L. exusta*, but they could not be distinguished in any way from *L. rostrum*. *Lingula exusta*, from its type-locality, Moreton Bay, closely resembles *L. rostrum* from its type-locality (see also Sowerby, 1846, and Davidson, 1888). Further, Reeve (1859) adds 'If *L. murphiana* is an Australian form of *L. anatina*, this *(L. exusta)* might be regarded as the representative in the same locality of *L. hians*'. Specimens from Dunk Island have been determinated by Johnston and Hirschfeld (1920) as *L. exusta*, but several individuals occurring in this locality (QM G11667; AM C45047) are referred to *L. rostrum*. Under the name *L. affinis*, Hancock (1858) describes and figures a species agreeing either with *L. rostrum* or *L. reevii*, while his other species has been correctly identified as *L. anatina*.

The characteristics of *L. rostrum* from the Queensland waters are described below:

The shell is oblong-ovate. The lateral margins are subparallel, often broadest posteriorly, rarely anteriorly. The anterior front is slightly convex with a small median projection; the frontal angles are rounded. The anterior edges are almost superposed (Plate 1e). *Lingula rostrum* is characterized by the possession of a posterior 'rostrum' (= deltidial beak of ventral valve), largely projecting over the dorsal valve and distinct from the continuity of posterior margins, that is visible on the external face (Fig. 1B, Plate 1f). The pedicular groove is deep and almost continuous with the inner surface of the valve (Fig. 1B), as in *Lingula reevi*.

The external surface of the shell is rather smooth with visible lines of growth (Plate 1e, f). The inner surface is smooth and only the dorsal valve shows a short internal median ridge. The degree of calcification is variable. The shell colour varies from yellow to reddish beige with some vivid green lines of growth. Generally the front is bright green. In transverse section, the shell of *L. rostrum* is elliptical, slightly flattened (Plate 1f).

The peduncle, brownish in colour is about one and a half the length of shell. No strong pallial pigmentation is observed. The muscle arrangement is shown in Fig. 2B; it is somewhat different from that of *L. anatina*, but very similar to *L. reevii* (Emig 1978). The two main mantle canals are more incurved to the middle than in *L. anatina* (Fig. 2B). Measurement of the dorsal larval valve has been performed on three specimens: width 654–711 μ ; length 842–887 μ . The mean w/l ratio is 0·804.

Lingula adamsi Dall

Lingula tumidula: Adams, 1863, p. 100. Davidson, 1871, p. 310. (non *L. tumidula* Reeve 1841).
Lingula adamsi Dall, 1873, p. 202. Davidson, 1888, p. 218.
Lingula shantungensis Hatai, 1937, p. 322; Hatai, 1940, p. 177.

MATERIAL EXAMINED

Moreton Bay: G5659. Yeppoon: QM G5486 (Queensland Museum); AM C2476 (Australian Museum). Queens Beach, Bowen: QM G5879 (Queensland Museum). Formosa: B12561 (figured by Davidson 1888, pl. 28, fig. 19) (British Museum).

A careful comparison of a single specimen in the Museum National d'Histoire Naturelle de Paris with the descriptions of Reeve (1841, 1859), Sowerby (1846), Dall (1873), and Davidson (1888), and the Queensland specimens, has indicated that *L. tumidula* Reeve and *L. adamsi* Dall are two distinct species. This is corroborated by the examination of the probable holotypes of these two species, deposited in the British Museum (*L. adamsi:* B12561, Formosa; *L. tumidula:* ZB 338–340, Moreton Bay). Thus the assertion of Dall (1873) that *L. adamsi* is distinct from *L. tumidula,* that was accepted by Davidson (1888), is confirmed. The single specimen of MNHN-Paris could be referred without hesitation to *L. tumidula.* It is very similar to the holotype and true to the original description of Reeve (1841), and the accounts of Sowerby (1846) and Davidson (1888). On the other hand, all examined specimens with a large quadrate shell in the Queensland Museum are identical with *L. adamsi* holotype and original description, rather than with *L. tumidula* (despite the fact that Australian specimens have generally been referred to the latter species). This confusion has arisen because *L. tumidula* type-locality is Moreton Bay, accordingly all quadrate shell individuals on the Queensland coasts have been assigned to that species rather than to *L. adamsi.* Davidson (1888) indicates that he fell at first into the same mistake.

The Queensland Museum material contains only *L. adamsi* which has the following characteristics:

The Australian specimens are characterized by the possession of a very large shell, quadrate in outline. The anterior edge is straight to gently concave without a projection in the middle; its lateral corners squarely rounded. The lateral margins are subparallel (Plate 2). The deltidial regions are very different from those of the other lingulid species. The deltidium of the dorsal valve shows a rounded margin, with ill-defined beak; the ventral valve possesses a small, sharply, median beak, slightly overlapping the dorsal valve, and a small groove, on the inner surface, for the pedicle passage (Plate 2e).

The external surface of the shell is marked with several rude equidistant growth lines (that become more distinct as the shell grows: Plate 2) and numerous small concentric lines of growth. The shell sculpture looks and feels rough. Two longitudinal ridges extend from the highest point of the valve to each frontal corner, especially on the ventral valve. In lateral view, the dorsal valve becomes more flattened than the ventral. The colour is yellowish brown to dark brown with reddish brown to darkest brown distally. The pedicle, flesh in colour, is almost twice as long as the shell. No pallial pigmentation has been observed. The setae of the frontal angles are conspicuously long (Plate 2c). The muscle attachment is not visible through the shell; its arrangement is different from that of the other lingulids that have the same quadrate body shape (Plate 2 b, e). The two main mantle canals are subparallel anteriorly (Plate 2b, e).

The characteristics of *L. shantungensis* described by Hatai (1937, 1940) seem to be similar to those of *L. adamsi,* and these species are probably synonymous. A comparative study on *L. tumidula* and *L. adamsi* is now in preparation by C. C. Emig and L. Hammond.

CONCLUSIONS

In the present study the distribution of *Lingula* species in Queensland waters has been largely modified according to new specific criteria (one of the characters, disposition of the two anterior mantle canals has been used for the first time). The examination of species types and specimens from the type-localities has demonstrated that *L. anatina, L. rostrum* and *L. adamsi* are the most commonly occurring Queensland species. Several synonymies have been established and the species are considered to be true taxa in the studied geographical area. *Lingula murphiana* is now referred to *L. anatina. Lingula hians, L. exusta, L. bancrofti,* and *L. anatina:* Johnston and Hirschfeld, 1920, are synonyms of *L. rostrum. Lingula tumidula:* Johnston and Hirschfeld, 1920, is a synonym of *L. adamsi.* The true *L. tumidula* has not been rediscovered in its type locality (Moreton Bay) or in the Queensland Museum collection.

The taxonomy of all species of *Lingula* needs revision, for, as with the species discussed above, confusion has been created owing to the previous lack of taxonomic characters that could be used to establish species identity.

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PLATE 1

a-d: *Lingula anatina.* a, dorsal view of a complete animal; b, side view; c, interior view of a dorsal valve showing the median ridge (arrow); d, dorsal view of a shell of a Singapore specimen.
e, f: *Lingula rostrum.* e, ventral view of shell; f, side view.

Scale lines = 1 cm.

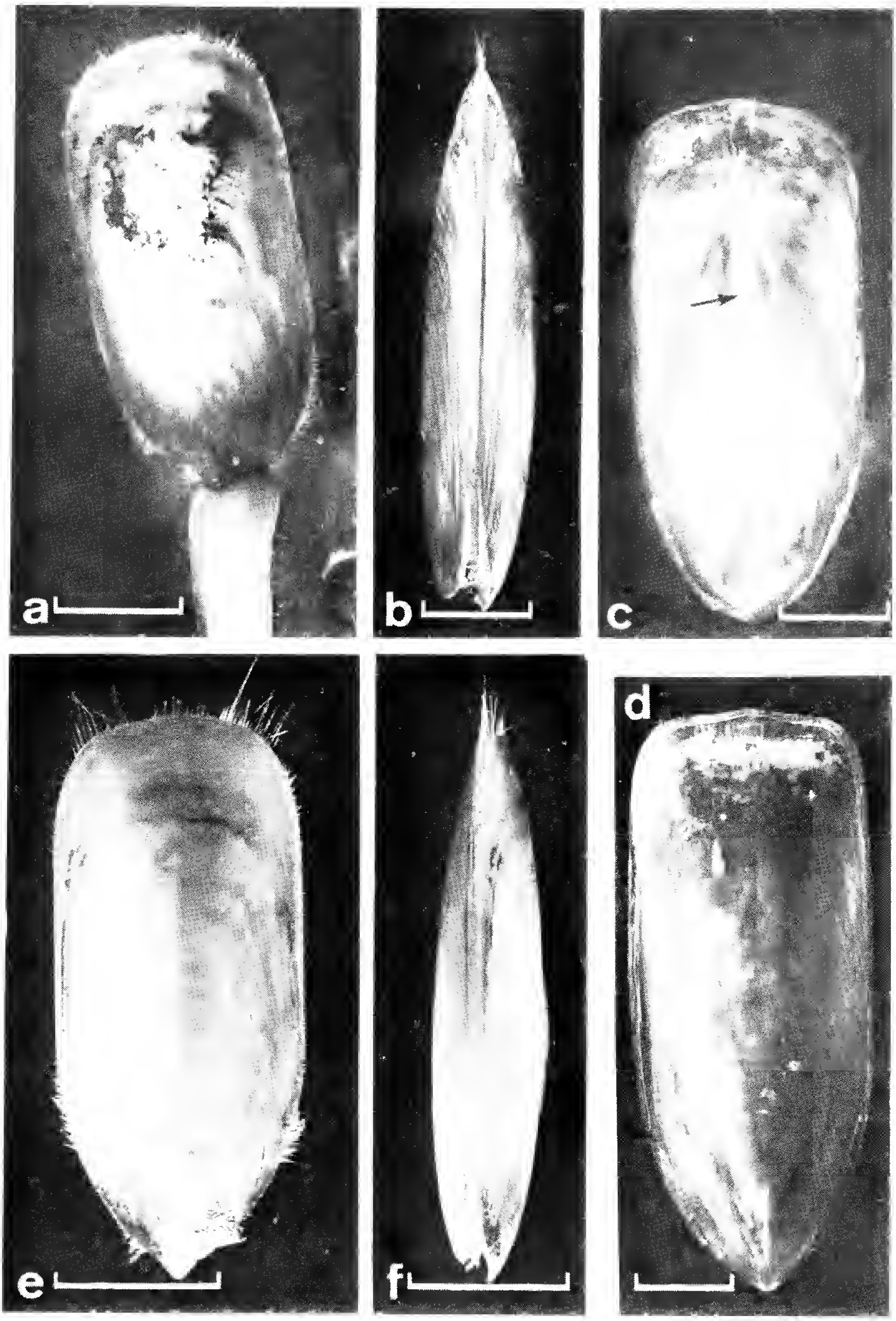
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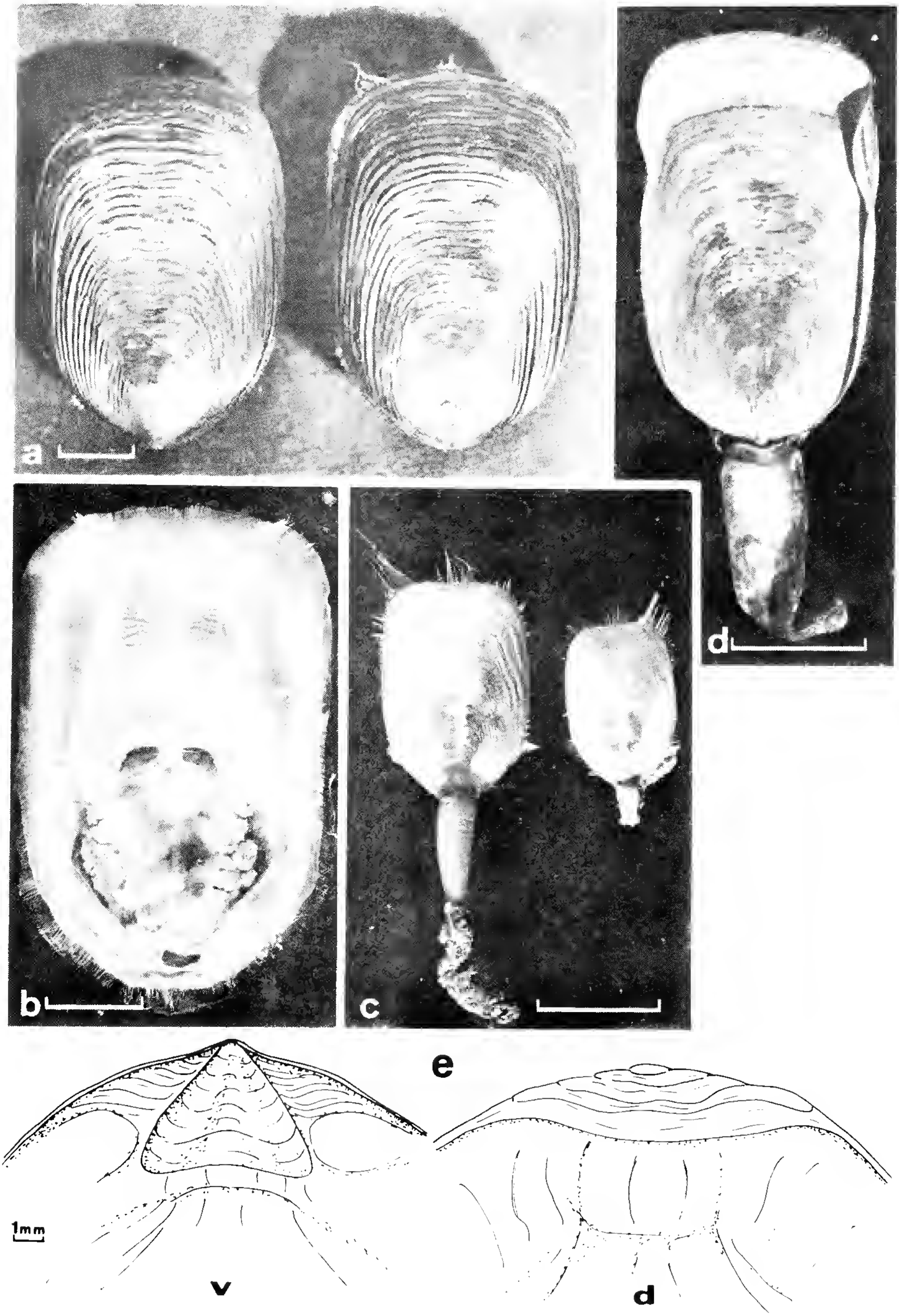
PLATE 2

a-d: Shell characters of *Lingula adamsi*. a, ventral and dorsal valve; b, ventral side of body showing the muscle arrangement and the mantle canals; c, two complete young specimens in dorsal view; d, specimen from the British Museum (B12561) figured by Davidson (1888, pl. 28, fig. 19) (by courtesy of Dr H. Brunton, British Museum). Scale lines = 1 cm.

e: Deltidial region, *Lingula adamsi*, interior view.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NEMATODES FROM PAPUA NEW GUINEAN SNAKES

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ABSTRACT

The nematodes *Kalicephalus enygri*, *K. novaebritanniae*, *Abbreviata oligopapillata* and *Abbreviata kaulensis* n.sp. were recovered from snakes collected on Karkar Island, Papua New Guinea. The coexistence of two *Kalicephalus* species within the oesophagus of the same host is reported for the first time, and their differentiation and the probable means by which they ensure reproductive isolation are described. The snakes *Enygrus asper*, *Acanthophis antarcticus* and *Stegonotus modestus* are new host records for *K. novaebritanniae*, and *A. antarcticus* is a new host record for *A. oligopapillata*.

There have been few reports of the parasites of reptiles from Papua New Guinea. This paper reports the nematodes recovered from 16 snakes collected around Kaul village, Karkar Island, Madang Province, in January 1970, viz., *Stegonotus modestus* (2), *Enygrus asper* (6), *Enygrus carinatus* (4), *Acanthophis antarcticus* (1), *Boiga irregularis* (1) and *Dendrelaphis punctulatus* (2). These were killed with ether and preserved in 70% alcohol. Removed worms were stored in 70% alcohol with glycerine and transferred to chlorolactophenol for examination.

RESULTS

Order: STRONGYLIDA

Superfamily: DIAPHANOCEPHALOIDEA

Kalicephalus enygri Kreis 1940

MATERIAL EXAMINED: 42♂ 54♀, QM G11771; 7♂ 9♀, QM G11772; 12♂ 17♀, QM G11773; 44♂ 52♀, QM G11774; 38♂ 39♀, QM G11775, from oesophagi of *E. asper* QM J28755, J28758, J28751, J28756 and J28757 respectively; 10♂ 17♀, QM G11776; 4♂ 5♀, QM G11777; 1♂ 4♀, QM G11778; 1♂ 2♀, QM G11779, from oesophagi of *E. carinatus* QM J28752, J28753, J28754 and J28760 respectively.

Worms were recovered from the oesophagus, usually the upper 5 cm, of five of the six *E. asper* ($\bar{x} \pm s = 63 \pm 17$ worms per snake) and all four *E. carinatus* ($\bar{x} \pm s = 11 \pm 4$ worms per snake). Females were slightly more common than males, but no size differences from the two hosts were detected.

Kalicephalus novaebritanniae Baylis 1927

MATERIAL EXAMINED: 13♂ 6♀, QM G11780; 1♂ 3♀, QM G11781; 10♂ 9♀, QM G11782; 13♂ 5♀, QM G11783; 22♂ 33♀, QM G11784, from oesophagi of *E. asper* QM J28755, J28758, J28751, J28756, and J28757 respectively; 1♂ 4♀, QM G11785, lower oesophagus *A. antarcticus* QM J28764; 1♂ 5♀, QM G11786, upper small intestine *S. modestus* QM J28761.

Worms were recovered from five of the six *E. asper* ($\bar{x} \pm s = 23 \pm 9$ worms per snake), from the *A. antarcticus* (five worms) and from one of two *S. modestus* (six worms). Worms from *E. asper* were found in the oesophagus, mainly in the anterior region with *K. enygri*, whereas those from *A. antarcticus* were in the lower oesophagus and those from *S. modestus* in the upper small intestine. Females were slightly more common than males, but no marked size differences from these three hosts were detected.

In the series measured from *E. asper* (QM J28757) the maximum body width and head capsule diameter were less than in either Schad's (1962) or Maplestone's (1931) measurements, whereas all other measurements were intermediate between theirs. The vulval ratio was greater in this series than in Schad's, probably a reflection of the generally greater length of these specimens.

Both *K. enygri* and *K. novaebritanniae* were recovered from the same hosts. Comparative measurements of the species were made on 131 worms recovered from *E. asper* (QM J28757), Table 1, and these show that *K. novaebritanniae* were consistently larger than *K. enygri*, significantly so in lengths of spicules, vagina and tail and in the vulva ratio. In *K. novaebritanniae* the vulva was on a retractable peduncle and was consistently further posterior than in *K. enygri*, where it was on a slight elevation. All *K. enygri* females were amphidelphic, whereas in all *K. novaebritanniae* the uteri were opposed as they left the ovijectors, but the posterior uterus then turned anteriorly, extending far past the anterior end of the anterior ovijector. Overlap was apparent in the shape of the anterior chitinoid ridge, and worm lengths, maximum head diameter, buccal capsule depth, and ratio of oesophagus length to oesophagus bulb diameter.

DISCUSSION

Schad (1956) showed that the *Kalicephalus* species *K. agkistrodontis*, *K. parvus* and *K. rectiphilus* occupied different sites within the host *Coluber constrictor*. The shape of the posterior ventral chitinoid plate, disposition of the uteri, position of the vulva and length of the spicules and vagina made differentiation of the two species within New Guinea snakes simple. The greater vaginal length and spicule length in *K. novaebritanniae* without any overlap between the two species must preclude interbreeding, and are assumed to be the mechanism by which genetic isolation is ensured. Sprent (1977) has recently reported a similar situation where pairs of species of ascaridoid nematodes exist together in the same organ in the same python hosts; spicule and vagina lengths are the features precluding hybridization.

K. enygri was described by Kreis (1940) from *E. asper* collected from New Britain, and it has since been reported from *E. carinatus*, *A. antarcticus*, *Denisonia superba* and *Varanus indicus*. The measurements of *K. enygri* from *E. asper* in the present study were, in almost all respects, similar to those from *E. carinatus* from the Solomon Islands and those from *A. antarcticus* and *D. superba* from Australia (Schad 1962). All the worms found in this study, however, were amphidelphic (with a similar vulval ratio to those from *E. carinatus*). Specimens from Australian hosts were prodelphic with the vulva further posterior and consequently a higher vulval ratio.

K. novaebritanniae has previously been recorded from *Boiga irregularis*, *Ptyas mucosus* and *Naja naja* from New Britain and India. The three hosts recorded in this paper are therefore new host records. The measurements of this species recorded by Schad (1962) from *B. irregularis* from New Britain and Maplestone's measurements from *P. mucosus* and *N. naja* in the Calcutta Zoo (Maplestone, 1931) indicate that this is a species which shows much geographical or host-dependent variation. In the present study the posterior ventral chitinoid plate was less markedly triangular than in Schad's description, although distinctive from the lunate plate of *K. enygri* in almost all individuals. Further studies on specimens from other areas, and from other hosts, would be valuable in elucidating the systematics in this species.

The position of *K. novaebritanniae* in the three hosts varied: those from *E. asper* were from the upper oesophagus, from *A. antarcticus* from the lower oesophagus and from *S. modestus* from the upper small intestine. The presence of this worm in five of six *E. asper*, but its absence from all four *E. carinatus* (all of which were infected with *K. enygri*) from the same neighbourhood, suggest

TABLE 1: MEASUREMENTS (IN MM) OF *KALICEPHALUS ENYGRI* and *K. NOVAE-BRITANNIAE* FROM *ENGYRUS ASPER*.

	K. enygri 38♂ and 38♀ $\bar{x} \pm s$	*K. novae-britanniae* 22♂ and 33♀ $\bar{x} \pm s$	P
Maximum width, male	0·17 ± 0·015	0·19 ± 0·017	<0·1
Maximum width, female	0·21 ± 0·017	0·24 ± 0·020	<0·1
Oesophagus length, male	0·32 ± 0·020	0·34 ± 0·010	<0·1
Oesophagus length, female	0·34 ± 0·020	0·39 ± 0·028	<0·05
Oesophagus width, male	0·13 ± 0·010	0·14 ± 0·007	<0·1
Oesophagus width, female	0·15 ± 0·010	0·17 ± 0·010	<0·1
Spicules	0·24 ± 0·020	0·37 ± 0·03	<0·001
Vulva ratio	2·45 ± 0·20	4·59 ± 0·39	—
Vagina length	0·08 ± 0·007	0·15 ± 0·01	<0·001
Tail length	0·29 ± 0·030	0·42 ± 0·05	<0·001

that the latter snake may not be a suitable host for *K. novaebritanniae*.

Order: SPIRURIDA

Superfamily: PHYSALOPTEROIDEA

Abbreviata kaulensis n.sp.
(Table 2; Fig. 1)

MATERIAL EXAMINED

HOLOTYPE: QM G11787, male, from stomach of *Enygrus asper*, QM J28755, collected by H. I. Jones from Kaul village, Karkar Island, Madang Province, PNG, January 1970.

ALLOTYPE: QM G11788, female, from stomach of *E. asper*, QM J28757, same data as Holotype.

PARATYPES: Six specimens in poor condition from rectum of *E. asper*, QM J28758, same data as above; one male, QM G11789, same data as Holotype.

DIAGNOSIS

Blunt apical tooth on each lip. Bifid internal apical tooth, and on internoventral and internodorsal surface of each lip; eight very small denticles near the corner of each lip, and a row of about ten very small denticles between the external and internal apical teeth. Ridge bearing variable very small denticles internal to dorsal and ventral bifid teeth. Spicules dissimilar, left five times length of right, finely pointed.

DESCRIPTION

Cylindrical worms, cuticular striations transverse, males to 24 mm in length and females 42 mm with cervical collarette. Anterior end with two lateral lips, each bearing a large blunt external apical tooth with, at its internal base, a row of about 10 very small denticles and, internal to these, a single bifid tooth. Two small bifid teeth, one ventrally and one dorsally on internal surface of each lip and internal to these a roughened ridge with two inconstant minute denticles. A row of 7 or 8 small, blunt denticles extend to the mouth corners, ventrally and dorsally. Two sessile papillae and an amphid on exterior of each lip. Short muscular oesophagus, surrounded near its posterior end by a nerve ring, clearly demarcated from the wider glandular oesophagus about nine times as long. Excretory pore conspicuous, with wide excretory canal passing posteriorly towards it, posterior to origin of glandular oesophagus. Cervical papillae inconspicuous, spiked, anterior to excretory pore. Glandular oesophagus widens slightly in passing posteriorly.

TABLE 2: BODY MEASUREMENTS OF *ABBREVIATA KAULENSIS* N. SP. (IN MM)

	Holotype	Allotype
Length	21·37	28·12
Maximum width	0·37	0·49
Muscular oesophagus length	0·27	0·36
Muscular oesophagus width	0·12	0·15
Glandular oesophagus length	2·45	3·76
Glandular oesophagus width	0·20	0·32
Oesophago-intestinal junction*	3·00	4·26
Nerve ring*	0·27	—
Cervical papillae*	0·42	—
Excretory pore*	0·55	—
Vulva*	—	6·37
Eggs	—	50 × 28–31µ
Left spicule	1246 µ	—
Right spicule	252 µ	—

* distance from anterior end.

MALE: Bursa extends just beyond tip of tail, supported by four pairs of long, pedunculated, pericloacal papillae. Three pairs of short, pedunculated, caudal papillae, approximately equally spaced. Bursa lined by rows of small tuberculations anteriorly and laterally; on the tail they are replaced posterior to cloaca by a rugose area extending as far as the central, caudal papillae; on the alae they extend beyond the fourth long papillae, decreasing in size, the rows spaced at 14 µ intervals. Two small lateral and one central sessile papillae anterior to cloaca, and two pairs of postcloacal sessile papillae.

Spicules unequal. Left about five times length of right, originating anterior to junction of seminal vesicle and ejaculatory duct, thin and sinuous, terminating in a very fine point, 1246 µ long; right stout and well chitinized, alate near tip, terminating in a blunt point.

FEMALE: Vulva situated about one quarter along the length of the body, flush with body wall. Muscular oviduct leads posteriorly to a reservoir; uterus with four branches. No uterine branches anterior to vulva. Tail pointed. Eggs elongated, smooth thick shells, embryonated, 50×28–31µ .

DISCUSSION

A. kaulensis has similar eggs and spicules to *A. oligopapillata*, but is a longer worm, with seven to eight small corner lip denticles instead of the four larger ones in *A. oligopapillata*, and postcloacal bursal tuberculations replaced by a rugose area. The conformation of the lip denticles distinguishes this species from the three other species recorded from New Guinean reptiles: *A. multipapillata*, a much larger worm with considerably longer spicules; *A. natricis*, which has no corner mouth denticles; and *A. heterocephala*, which is also without corner denticles (Kreis 1940). The distinct row of small denticles between the external and internal apical teeth distinguishes this from all recorded Australian species; in addition, *A. confusa* has a spatulate tip to the left spicule (Johnston and Mawson 1942), *A. physignathi* has larger eggs and a considerably longer left spicule (Baylis 1924), and *A. antarctica* has less inequality in the spicule lengths (Irwin-Smith 1922a). It most closely resembles *A. bancrofti*, but this species has more elongated eggs, and five pointed mouth corner denticles, instead of 7–8 small ones (Irwin-Smith 1922b).

Abbreviata oligopapillata Kreis 1940

MATERIAL EXAMINED. 1♂ 1♀ immature (stomach), 6♂ 5♀ (rectum), QM G11790, from *A. antarcticus*, QM J28764.

The worms varied from 9 to 12 mm in length, and corresponded with the description given by Kreis (1940) of specimens recovered from *Sphenomorphus jobiensis* from New Britain, although the eggs were larger, 28×51μ compared with 37×22μ in Kreis' specimens. This snake had the remains of an unidentifiable lizard in the stomach, and this infection may have been a spurious one.

ACKNOWLEDGMENTS

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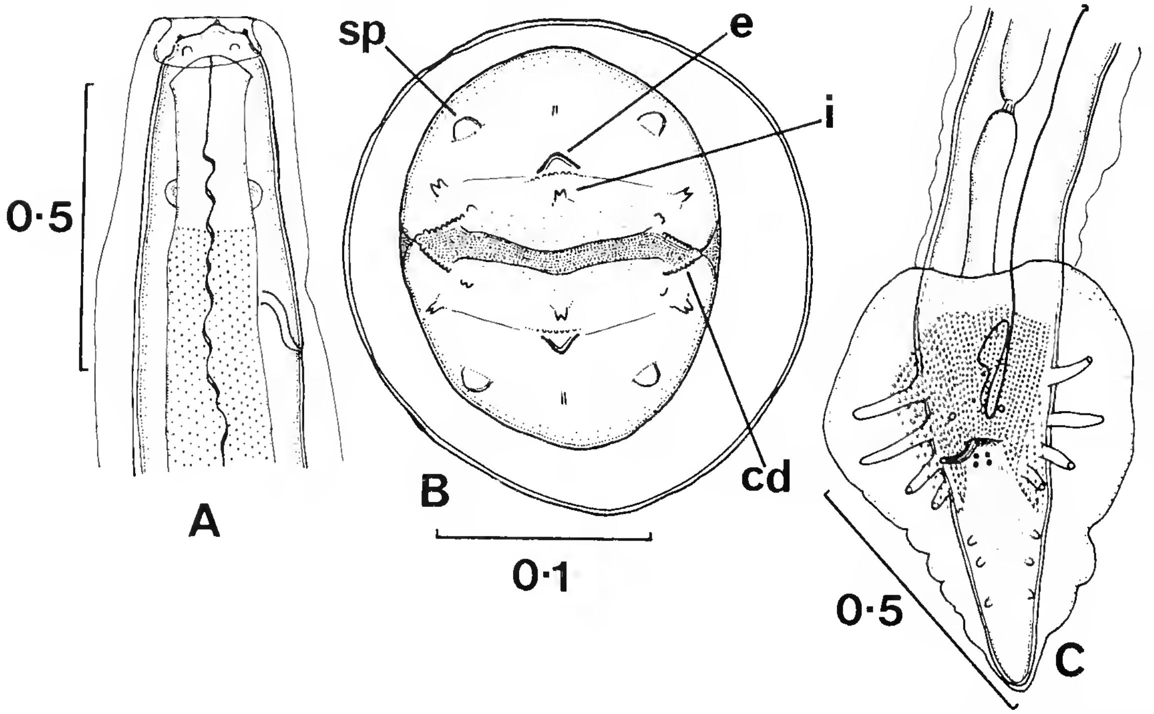

FIG. 1: *Abbreviata kaulensis*. Holotype, QM G11787. A, anterior end, lateral; B, anterior extremity, *en face* showing lateral lips; C, male bursa, ventral. (cd = mouth corner denticles, e = external apical tooth, i = internal apical tooth, sp = sessile papilla.) Measurements in mm.

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THE SUBTIDAL FOULING ORGANISMS OF THE CALLIOPE RIVER AND AUCKLAND CREEK, CENTRAL QUEENSLAND

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J. MOVERLEY*

ABSTRACT

The fouling organisms of Calliope River and Auckland Creek have been investigated to determine the most abundant and recurrent macrofouling species, and their succession on newly exposed surfaces. Short- and long-term test plates have been used at three localities since May 1975, and data to May 1977 are analysed here.

Forty-seven species were found on the short-term plates. Thirteen were sessile and used in numerical analyses. Sites 2 and 3 (Calliope River) differed from Site 1 (Auckland Creek) by: the number of species; paired *t*-tests of species occurrence; and the mean number of individuals of each species. These differences are presumed to reflect physical disturbance at Site 1. Only three species *(Balanus, Ficopomatus* and *Electra)* occurred consistently on the short-term plates. Optimal wavelengths of the 5 species which showed significant periodicity in settlement were determined and compared with periodicities in temperature, chlorinity and rainfall. All had significant relationships with temperature, 3 with chlorinity and 0 with rainfall. Algal biomass also showed a much closer relationship to temperature than to chlorinity.

The long-term plates indicated that a 'pioneer' phase is gradually (after 3–11 months) replaced by a 'climax' phase, characterized by *Crassostrea, Modiolus, Balanus* and *Ficopomatus.* A mosaic of the 'pioneer' and 'climax' phases is the common condition found on old plates and on naturally occurring substrates in the study area.

Apart from their obvious economic importance, fouling organisms provide a measure of the extent of pollution for they must remain exposed to the physical conditions which surround them (McCain 1975). Since April 1975, three sets of artificial-substrate samplers have been placed in the Calliope River (2) and Auckland Creek (1) to determine (a) the most abundant and recurrent macrofouling organisms, their settling periods and factors associated with settlement, and (b) the natural sequence of colonisation and development on newly exposed surfaces.

Various numerical techniques have been used to analyse the data, and a novel technique has been developed by one of us (W.S.), which allows the rapid determination of optimal wavelengths of periodic species.

THE STUDY AREA

The study area (Fig. 1) comprises the Calliope River and Auckland Creek which flow into Port Curtis. Draining an upland of mostly argillaceous rock, the Calliope River carries a large stream sediment load of predominantly mud (Conaghan 1966).

Climatically the area is subtropical with a mean annual rainfall (81 years) of 1011 mm falling mostly during December to March. Mean monthly rainfall and mean monthly river flow volume in the Calliope River are given in Fig. 2 for the duration of the study period.

Water temperatures in the Calliope River during the study period ranged from 16·2°C in July 1976 to 31·2°C in December 1976. Salinities for the same period showed concentrations of 37·94°/oo during winter and 6·53°/oo during the wetter months. Turbulent flow in the rivers (the tidal range is up to 4·2 m) results in generally mixed water and stratification is slight.

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SAMPLING METHODS

Each artificial-substrate sampler consists of a stainless steel rod (diameter 9·5 mm) on which are placed six sandblasted glass plates 30 × 30 cm. The plates are separated by PVC spacers 6 cm long. The entire sampler is weighted by a small drum filled with concrete and it is held 1·5 m above the bottom by a small buoy attached immediately above the uppermost plate. A second buoy at the surface ensures relocation.

Glass plates were originally used but breakages were frequent. After preliminary tests, these were replaced by roughened white perspex plates of identical dimensions.

SHORT-TERM PLATES

At least one plate was renewed on each sampler at approximately monthly intervals. Each surface of the fouled plates was divided into 25 cm^2 squares and in eight selected squares on each surface, all organisms were counted. Of the eight squares counted, two included one or two edges while the remaining six were away from edges. Plates from Site 2 with algae on the upper surface were air-dried, and the dried algal biomass was determined.

LONG-TERM PLATES

Long-term plates, lifted at various irregular intervals, were transported to the laboratory in water-proofed containers and all organisms were counted on both surfaces of each plate.

RESULTS

SHORT-TERM PLATES

During the 24 months of this study, a total of 47 species were found on these plates (Table 1). Of these species, thirteen were algae growing on the

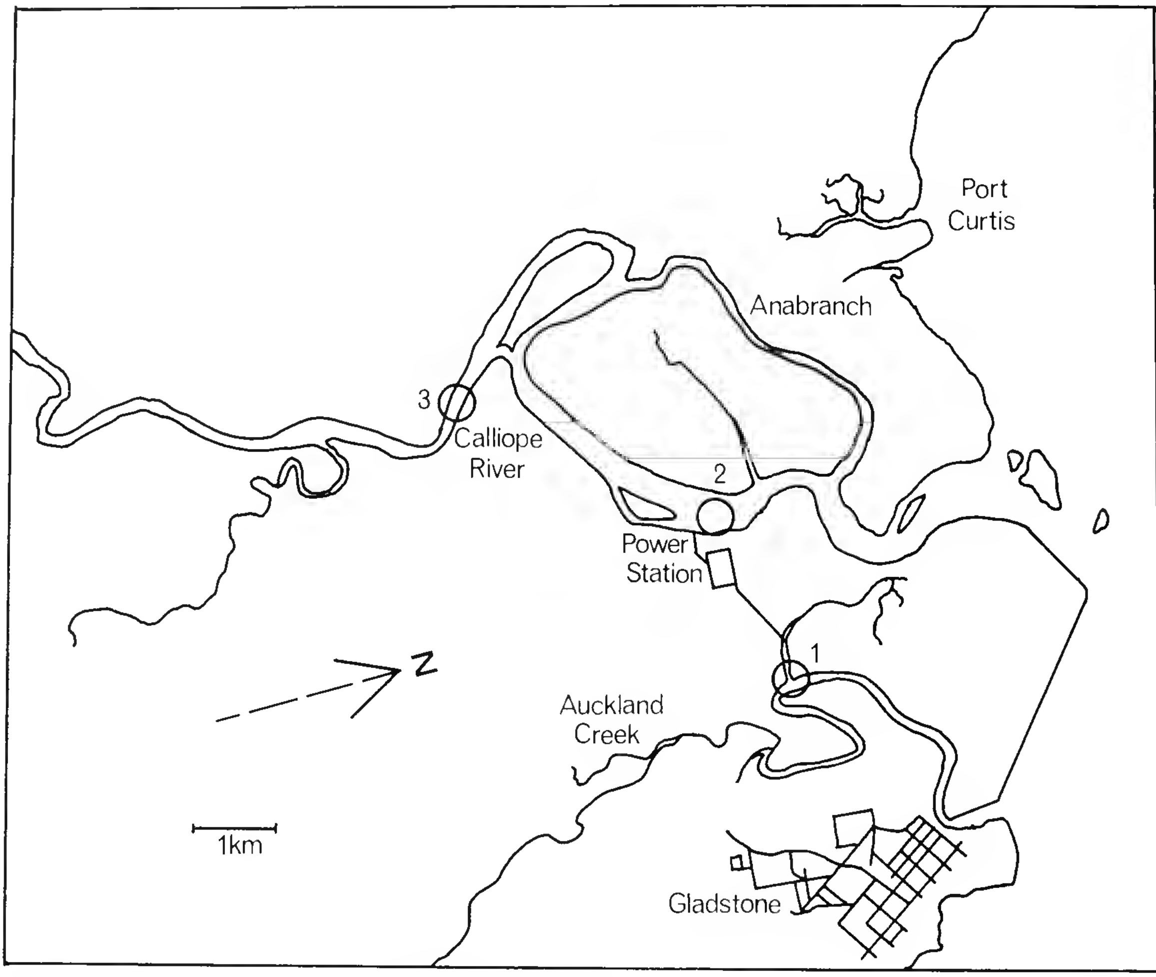

FIG. 1: Location of artificial-substrate samplers: Sites 1, 2 and 3.

upper surface of the plates at Site 2, one *(Obelia longicyatha)* was found only once on the upper surface of the plates at Site 3, and twenty-one were non-sessile species. The remaining twelve sessile species were used in the numerical analyses. Subsequent reference to species is generally by generic name where known, or by code number (Table 1).

TABLE 1: SPECIES LIST. SHORT-TERM PLATES

Species	Systematic Position	Code No.
SESSILE SPECIES		
Balanus amphitrite Darwin	Cirripedia, Crustacea	1
Ficopomatus uschakovi Pillai	Serpulidae, Polychaeta	2
Bugula cf. *stolonifera*	Bryozoa	3
Dryopoides sp.	Amphipoda, Crustacea	4
Electra cf. *anomala*	Bryozoa	5
Hippodiplosia sp. A	Bryozoa	6
Crassostrea cucullata (Born.)	Ostraedia, Bivalvia	7
Ascidia sydneyensis Stimpson	Tunicata	8
Tubularia crocea (Agassiz)	Hydrozoa, Coelenterata	9
ascidian I	Tunicata	10
ascidian III	Tunicata	11
Plumularia sp.	Hydrozoa, Coelenterata	12
Obelia longicyatha Allmann	Hydrozoa, Coelenterata	
Bryopsis indica Gepp and Gepp	Bryopsidaceae, Chlorophyta	
Hormidium subtile (Kuetz.) Heering	Ulotrichaceae, Chlorophyta	
Rhizoclonium sp.	Cladophoraceae, Chlorophyta	
Giffordia mitchellae (Harvey) Hamel	Ectocarpaceae, Phaeophyta	
Sporochnus comosus C. Agardh	Sporochnaceae, Phaeophyta	
Callithamnion sp.	Ceramiaceae, Rhodophyta	
Ceramium cliftonianum J. Agardh	Ceramiaceae, Rhodophyta	
Hypoglossum sp.	Delesseriaceae, Rhodophyta	
Polysiphonia variegata (C. Ag.) Zan.	Rhodomelaceae, Rhodophyta	
Ptilocladia sp.	Ceramiaceae, Rhodophyta	
Lophocladia harveyi (Kuetz.) Schmitz	Rhodomelaceae, Rhodophyta	
Soliera robusta (Grev.) Kylin	Solieriaceae, Rhodophyta	
Spermothamnion sp.	Ceramiaceae, Rhodophyta	
ASSOCIATED SPECIES		
Ceradocus sp.	Amphipoda, Crustacea	
Paraphoxus sp.	Amphipoda, Crustacea	
amphipod II	Crustacea	
amphipod V	Crustacea	
caprellid I	Amphipoda, Crustacea	
Macrobrachium sp.	Macrura, Crustacea	
Parapandalus sp.	Macrura, Crustacea	
Rhynchocinetes sp.	Macrura, Crustacea	
Hippolytidae sp. III	Macrura, Crustacea	
Alpheus sp.	Macrura, Crustacea	
Paracerceis sp.	Isopoda, Crustacea	
Xanthidae sp. I	Brachyura, Crustacea	
Hyastenus sp.	Brachyura, Crustacea	
Charybdis helleri (M.-Edwards)	Brachyura, Crustacea	
Lutjanus fulviflamma (Forskal)	Lutjanidae, Pisces	
Prionobutis microps (Weber)	Eleotridae, Pisces	
Drombus palackyi (Jordan and Seale)	Gobiidae, Pisces	
Omobranchus punctatus (Valenciennes)	Blenniidae, Pisces	
Omobranchus ?germaini (Sauvage)	Blenniidae, Pisces	
Redigobius chrysosoma (Bleeker)	Gobiidae, Pisces	

Data on species from monthly plates comprised estimated numbers of individuals, except for: algae (estimated by dry weight); bryozoans (counted as colonies); and colonial, prostrate organisms. Ascidian III and *Plumularia* were given a surface cover rating (3 = dense; 2 = medium; 1 = sparse; 0 = absent) which was summed and averaged. To bring all data to an equivalent form, these ratings were multiplied by ten and the resultant regarded as numbers of individuals. Hence the data which were analysed are all in meristic (whole number) form. A copy of these raw data has been deposited with the editor.

These data comprise a 12 species × 3 sites × 24 times (t_{1-24}) matrix, although for Site 3, data for t_2, t_{18}, t_{19} and t_{24} were missing due to vandalism and flooding.

In recent analyses (Stephenson and Campbell 1977, Stephenson *et al.* 1977) 3D matrices have been converted into three separate 2D matrices and these have then been classified and/or ordinated. With only three sites, a site

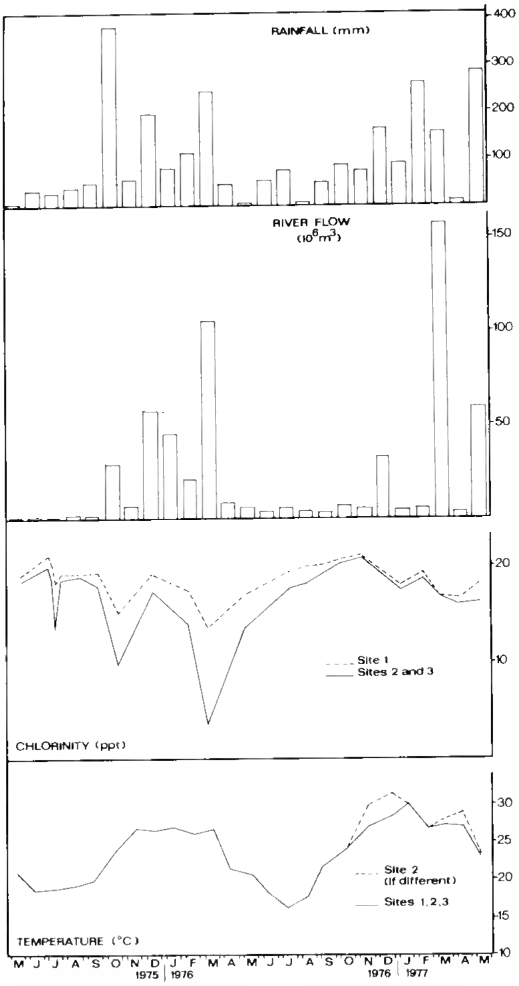

FIG. 2: Hydrologic data for the Calliope River and Auckland Creek, May 1975 to May 1977.

classification is somewhat trivial and differer approaches were used.

INTERSITE COMPARISONS

The following were calculated for each plate: — the number of species present; N — th number of individuals of all species; G — Gleaso diversity; H' — standardised Shannon diversity base 2 and J' — Shannon equitability. Perusal the data suggested that intersite differences wou be most clearly revealed on the S and N valu Using times at which all sites were sample paired t tests were performed using the three pai of sites. Only the S values showed any significa differences as follows: between Site 1 (mean 5·8 and site 2 (mean 4·60) significant at 0·01 lev between Site 1 and Site 3 (mean 4·55) aga significant at 0·01 level. Since these tests we performed on raw values without regard f normality of distribution, they should be regard as rough tests only. However they set Site 1 apa from the others.

The data suggested that the most effecti method of comparing sites would be to opera with individual species using paired t tests. F these tests to be entirely satisfactory, data shou be normally distributed and there should similar variance in the two sets under compariso Attempts were made to normalise the data (most cases) by using fractional power transform tions, plotting histograms and making visu judgements. Results suggest a 4·5th root as t most suitable overall transformation and this w used in the t tests and also for later analyses.

TABLE 2: SIGNIFICANCE TESTS OF SPECIES OCCURRENCES AT PAIRED SITES

Species	Pairs of sites compared 1 and 2 Δ	1 and 2 t	1 and 3 Δ	1 and 3 t	2 and 3 Δ	2 and 3 t
Balanus	–0·158	0·473	–0·183	0·538	–0·025	0·130
Ficopomatus	0·633	1·766	–0·350	1·451	–0·983	2·706*
Bugula	1·737	6·271***	1·966	8·861***	0·229	2·249*
Dryopoides	–1·157	4·098***	–1·054	4·541***	0·103	0·560
Electra	0·548	2·069	0·268	1·210	–0·280	2·179*
Hippodiplosia	0·824	4·461***	0·931	6·469***	0·107	0·725
Crassostrea	0·244	1·375	0·432	1·648	0·188	1·041
Ascidia	0·502	2·578*	0·502	2·578*	—	—
Tubularia	–0·331	1·863	–0·155	0·802	0·176	0·832
ascidian I	0·223	2·164*	0·223	2·164*	—	—
ascidian III	0·478	2·782*	0·478	2·782*	—	—
Plumularia	–0·819	4·240***	–0·648	3·469***	0·173	0·616

* Significant at 0·05 level
** At 0·01 level
*** At 0·001 level

Results of the *t* tests, given in Table 2, show that only three species (*Balanus*, *Crassostrea* and *Tubularia)* fail to show significant differences between any of the pairs of sites. Table 2 also shows that Sites 2 and 3 have the smallest number (3) of significantly different species viz. *Electra* and *Ficopomatus* which are both lower in Site 2, and *Bugula* which is higher in Site 2. Sites 1 and 2 and Sites 1 and 3 have seven significantly different species.

Further comparisons between sites were made using the mean number of individuals of each species (averaged over the 20 'common' times) — these are given in Table 3. The most useful comparisons involve correlation coefficients which are amenable to significance testing. Spearman rank correlation coefficients between pairs of sites are given in Table 4 together with the Pearson product–moment correlation coefficient based on normally transformed data. From Table 4 it is apparent that there is highly significant similarity between Sites 2 and 3. Based on this, it would be legitimate to fuse Sites 2 and 3 for intertime comparisons but this was not done for three reasons: (a) three species have significantly different populations in the two sites (Table 2), (b) data in Table 3 are averaged over times and hence eliminate possible phase differences between periodic changes and (c) there are difficulties due to the incomplete data at Site 3.

TABLE 3: MEAN NUMBER* OF INDIVIDUALS PER SPECIES PER SITE

Species	Site 1	Site 2	Site 3
Balanus	72·35	164·25	132·60
Ficopomatus	109·85	107·55	241·80
Bugula	68·40	3·90	0·15
Dryopoides	1·75	25·70	13·20
Electra	12·00	4·05	10·75
Hippodiplosia	10·75	3·45	0·70
Crassostrea	17·35	1·00	0·80
Ascidia	7·95	4·15	0
Tubularia	0·90	4·20	1·85
ascidian I	0·35	0	0
ascidian III	3·05	0	0
Plumularia	0	5·55	1·85

* Averaged over 20 times

TABLE 4: INTERSITE COMPARISONS USING CORRELATION COEFFICIENTS DERIVED FROM TABLE 3

Coefficient	Sites compared 1 and 2	 1 and 3	 2 and 3
Spearman	0·257	0·385	0·827**
Pearson	0·499	0·441	0·886**

** Significant at 0·01 level

INTERTIME COMPARISONS

CLASSIFICATION: Stephenson, Williams, and Cook (1974) have noted that hierarchical classification of times by species is likely to give confusing results with time-groups, giving mixtures of seasonality and annuality. Nevertheless a species × times matrix was classified hierarchically for each of the three sites. Those species absent from a given site were eliminated first and one species *(Plumularia)* was also eliminated because it occurred at a single time.

Bray-Curtis dissimilarities were used because these are moderately abundance sensitive, and the data was transformed to avoid giving undue stress to occasional high values. In the past, choice of the transformation has been arbitrary, and the same transformation (usually log $(n+1)$) has been applied prior to entity classification and to attribute classification. Here a series of root transformations from n to $n^{1/8}$ were used on the columns of data (entities = times) and modal root transformations which reduced the moment coefficient of skewness to a predetermined level were sought. Using a coefficient of 0·50 gave an entities transformation, and repeating with rows of data (attributes = species) gave an attribute transformation. It should be noted that the latter was less stringent.

For Site 1 the entity transformation was a 4th root and the attribute transformation a square root. Entities were classified by using the Bray-Curtis dissimilarity on 4th rooted data followed by group-average sorting and the dendrogram is given in Fig. 3a. Attributes were classified by using the Bray-Curtis on square rooted data, followed by standardisation by attribute totals, then group-average sorting. The resultant dendrogram is shown in Fig. 3b.

Considering attributes first, six species groups were selected, shown X on Fig. 3b. The only sizeable and moderately coherent group contains *Balanus, Ficopomatus, Bugula, Electra* and *Hippodiplosia*. The entity dendrogram was resolved into eight time groups shown as X in Fig. 3a. With the exception of three times (t_{12-14}) all groups contained sequential times; the only grouping with any hint of seasonality is the right one in Fig. 3a which groups April to May 1976 with Jan. to April 1977.

Dryopoides and *Ascidia* characterise $t_{18,19}$; *Tubularia* $t_{15,16}$; *Crassostrea* $t_{12,13,21-24}$; and ascidian II t_{9-14}. In other words five of the eleven species are best regarded as intermittents. The

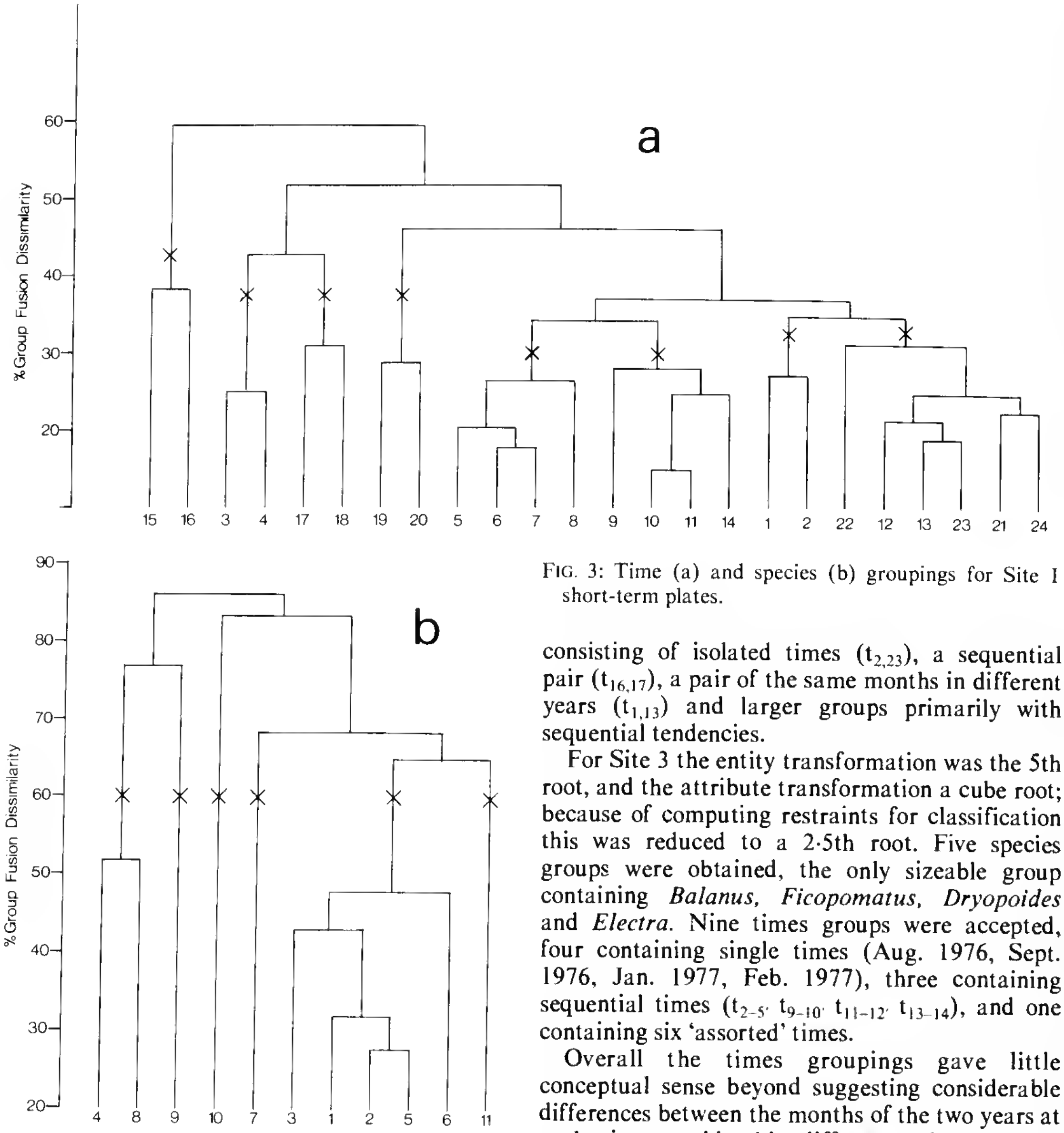

FIG. 3: Time (a) and species (b) groupings for Site 1 short-term plates.

more abundant species — the five listed earlier — are best regarded as recurrents and the clustering technique fails to distinguish any marked times changes in these species.

Results on the other sites were broadly similar and the dendrograms are omitted. For Site 2 the entity transformation was *ca.* 4·5th root, and the attribute transformation a square root; for classification 4th root and square root were used respectively. Six species groups were obtained, with the only sizeable group containing *Balanus, Ficopomatus, Dryopoides, Electra* and *Plumularia.* Eight times groups were accepted consisting of isolated times ($t_{2,23}$), a sequential pair ($t_{16,17}$), a pair of the same months in different years ($t_{1,13}$) and larger groups primarily with sequential tendencies.

For Site 3 the entity transformation was the 5th root, and the attribute transformation a cube root; because of computing restraints for classification this was reduced to a 2·5th root. Five species groups were obtained, the only sizeable group containing *Balanus, Ficopomatus, Dryopoides* and *Electra.* Nine times groups were accepted, four containing single times (Aug. 1976, Sept. 1976, Jan. 1977, Feb. 1977), three containing sequential times (t_{2-5}, t_{9-10}, t_{11-12}, t_{13-14}), and one containing six 'assorted' times.

Overall the times groupings gave little conceptual sense beyond suggesting considerable differences between the months of the two years at each site, considerable differences between the different sites and an overall tendency to group sequential times. Only three species are consistently in the same group and these are the three most abundant species — *Balanus, Ficopomatus* and *Electra.*

ANALYSES OF PERIODICITY: Stephenson (1978) has previously used autocorrelation coefficients to determine the wavelength of the optimal cycle in the data, and multiple regression to quantify the importance of a selected wavelength. This was felt to be preferable to the more standard approach using power-curve spectra for the following reasons: (a) power-curve spectra available through standard computer programmes have frequency as the dependent variable; hence wavelength is scaled reciprocally, giving wide spacing in areas of interest and (b) quantification of the variance is not readily effected and in effect, requires multiple regression.

Given any wavelength (T), the proportion of the total sum of squares accounted for by the regression (R^2), can be derived by multiple regression. If the chosen wavelength is the predominant one in the system then R^2 will be maximal. By 'scanning' through a series of wavelengths and plotting values of R^2, a different form of spectrum — here called a variation spectrum — can be obtained, the advantages being: (a) wavelength not frequency is the dependent variable. This gives the desired equal spacing when wavelength is the main interest. (b) scanning intervals can be adjusted to give fine resolution in wavebands of especial interest, an important advantage over autocorrelations. (c) R^2 values and F values for significance testing are readily interchangeable. Thus R^2 for 0·05 significance is $F'/[(\frac{N-k-1}{k}) + F']$ where F' is the F value for 0·05 significance with k and N–k–1 degrees of freedom. For a two stage regression as in the present case, $k=2$ and with N the number of cases, the previous expression becomes $F'/\,(\frac{N-3}{2} + F')$. Hence it is possible to scale the variation spectrum and determine immediately whether there is any significant periodicity. (d) incomplete data sets can be used without recourse to substituted values. This is an important advantage over autocorrelations in the case of Site 3. (e) as lags increase, autocorrelations involve fewer determinations and are consequently prone to increasing inaccuracies; this does not apply to R^2 determinations. Trials with the present data showed that autocorrelations and R^2 determinations gave different optimal wavelengths, and for the above reasons, R^2 was preferred.

Computations are not difficult and present results were obtained by a programme written for the Texas Instrument TI 59 with printer. This gave the regression parameters of the following equation:

$$y=\tfrac{1}{2}A^{\circ} + A\cos(2\pi t/T) + B\sin(2\pi t/T).$$

In this equation $\tfrac{1}{2}A^{\circ}$ is the estimated mid point of the oscillating curve; also from this equation C the half amplitude of the curve $(= \sqrt{A^2 + B^2})$ is obtained and also the estimated time of maximum values.

Based on early calculations, species data were given a 4·5th root transformation; this approximates to that required to give zero moment coefficients of skewness. For all species-in-sites which show significant periodicities, results are given in Table 5. Optimal wavelengths are to the nearest 0·1 month and three broad groups are apparent; much greater than 12 months (*Balanus* and *Bugula* in Site 1, and *Dryopoides* in Site 3); about 12 months (range 9·3–15·0) with ten cases; much smaller than 12 (*Electra* and *Ascidia* in Site 1 and *Tubularia* in Site 3).

If a roughly annual cycle is regarded as normal, then four of the 'abnormal' cases are in Site 1. Hints of abnormality in Site 1 were also obtained when ordinating the times, the data for the first year showing a particularly heterogeneous picture. This site is in a creek which was being deepened and widened to serve as the cooling water intake canal for the power station. This dredging activity was in progress until January 1976, and it is likely that the physical disturbance, change in hydrology and increased turbidity, contributed to biotic 'abnormality'. Results of the analyses conducted on the data from the second year (13 times, $t_{12\text{-}24}$) are given in Table 6. Comparison with Table 5 shows that now only two species (*Bugula* and *Hippodiplosia*) are 'abnormal'; in particular *Balanus* and *Electra* now show periodicities of about 12 months. The significance of the R^2 values has also been increased. Subsequently Site 1 data from $t_{1\text{-}11}$ have been disregarded.

Two species-in-sites have short wavelengths: *Hippodiplosia* in Site 1 (4·5 months) and *Tubularia* in Site 3 (6·1 months). At this stage no further relationships to abiotic factors have been explored; possibly tidal amplitudes would repay attention. Most of the remaining species approximate to twelve monthly cycles.

To apply the present approach to abiotic data, these should be normally distributed. Perusal suggested normality for all except rainfall data where a 4th root transformation was required (and established via moment coefficients of skewness and kurtosis).

In Table 7 the results of the R^2 approach to data on temperature, chlorinity and rainfall are given. Temperatures for all sites were identical up to t_{18}; thereafter at Site 2 mostly higher temperatures (due to the thermal output from the Power Station) were recorded.

The R^2 values in Table 7 show significant cycles in order of significance with temperature > chlorinity > rainfall. Apart from chlorinities in Sites 2 and 3, there are approximately annual cycles throughout. Comparison of estimated times of maxima in Table 7 with those of Tables 5 and 6 would permit estimates of phase lag between abiotics and the species showing cyclical phenomena.

However the method here used is based on correlation coefficients, using appropriately transformed data and involved shifting the time base to obtain maximal agreement. Calculations were restricted to species with significant cycles and began on Site 2 since the data for this site is complete and the most extensive. Results given in Table 8 show 5/5 significant relationships with temperature, 3/5 with chlorinity and 0/5 with rainfall. Because of the low R^2 values for cyclical regressions using rainfall data (Table 7), no further correlations with rainfall were attempted.

Results from t_{12-24} for Site 1 are given in Table 9. Because of difficulties in shifting the time base when data are missing, data for Site 3 are restricted to t_{1-17} inclusive, with values substituted for those missing at t_2; for these the means of t_1 and t_3 were used. Results for Site 3 are also given in Table 9.

From Tables 8 and 9 collectively, it is clear that correlations with temperature are more significant than those with chlorinity — of 16 cases studied, 13 gave higher r values with temperature.

TABLE 5: SIGNIFICANT SPECIES PERIODICITIES, SITES 1, 2, AND 3

Species	Opt. W.L.	R^2	C	½A^0	Est. time of maxima (months)
SITE 1 (all times)					
Balanus	17·5	0·2950*	0·7170	2·0770	6·6, 24·1
Ficopomatus	11·1	0·5159***	1·2142	2·1163	5·7, 16·8
Bugula	19·9	0·6926***	1·2815	2·0005	9·8
Dryopoides	12·6	0·3287*	0·6234	0·4671	6·0, 18·6
Electra	5·7	0·3136*	0·5224	1·4205	1·3, 7·0, 12·7, 18·4, 24·1
Ascidia	5·0	0·3983**	0·7697	0·5067	2·5, 7·5, 12·5, 17·5, 22·5
SITE 2 (all times)					
Balanus	11·9	0·3857**	1·2974	2·2687	7·6, 19·5
Ficopomatus	12·3	0·6356***	1·6894	1·4654	9·2, 21·5
Bugula	12·7	0·3795**	0·6566	0·3601	5·2, 17·9
Electra	14·6	0·4864**	0·6963	0·8944	11·5
Tublaria	12·2	0·6523***	0·8774	0·5644	4·8, 17·0
SITE 3 (no data for t 2, 18, 19, and 24)					
Ficopomatus	11·9	0·6409***	1·4594	2·4570	4·3, 16·2
Dryopoides	18·3	0·4260**	0·6349	1·4486	9·2
Electra	15·0	0·5713***	0·9462	1·2508	11·8
Tubularia	6·1	0·3643*	0·5701	0·3762	6·0, 12·1, 18·2
Plumularia	13·3	0·4629**	0·7064	0·5897	7·7, 21·0

* Significant at 0·05 level
** at 0·01 level
*** at 0·001 level

TABLE 6: SIGNIFICANT SPECIES PERIODICITIES, SITE 1, TIMES 12–24

Species	Opt. W.L.	R^2	C	½A^0	Est. time of maxima (months)
Balanus	13·8	0·9227***	0·9992	2·0392	22·2
Ficopomatus	10·7	0·7879***	1·5939	1·7310	21·4
Bugula	ca 18	0·6419***	(not calculated W.L. "too long")		
Dryopoides	11·1	0·6933***	0·9176	0·7435	19·2
Electra	10·8	0·7375***	0·7002	1·4855	22·6
Hippodiplosia	4·5	0·5038*	0·7918	1·5361	12·6, 17·1, 21·6
Crassostrea	10·3	0·6546**	1·3351	0·9665	20·6

* Significant at 0·05 level
** at 0·01 level
*** at 0·001 level

TABLE 7: PERIODICITY OF ABIOTIC DATA, SITES 1–3

	Opt. W.L.	R^2	C	$½A^0$	Est. time maxima (mths)
Temperature Site 1*	13·1	0·9481	5·7178	25·2595	9·5, 22·6
Site 2†	12·1	0·8369	5·5865	23·5027	9·3, 21·4
Site 3†	12·1	0·9188	5·2060	23·0998	9·2, 21·3
Chlorinity Site 1*	11·4	0·8509	2·0086	18·7836	10·3, 21·7
Site 2†	18·5	0·5200	4·0574	15·4178	0·9, 19·4
Site 3†	18·5	0·5227	3·4236	12·9209	0·9, 19·4
Rainfall‡ Sites 2&3†	13·3	0·4745	0·7301	2·7846	12·2
Site 1*	12·9	0·4491	0·7000	2·7496	9·7

* Times 12–24
† all times
‡ 4th root transformation

TABLE 8: CORRELATION BETWEEN CYCLICAL SPECIES AND ABIOTIC FACTORS, SITE 2

Species	Temperature r	Time shift	Chlorinity r	Time shift	Rainfall r	Time shift
Balanus	0·6092	3	–0·4722	0	0·2984†	0
Ficopomatus	0·8165	2	–0·4195	–1	0·3448†	0
Bugula	–0·5151	4	0·2701†	5	0·4091†	–1
Electra	0·5390	2	–0·3798†	–1	0·2860†	–4
Tubularia	–0·7271	3	0·4253	2	0·1858†	0

† Non significant correlations

In general there are positive correlations with temperature, with *Bugula* and *Tubularia* in Site 2 the only exceptions. Again with two exceptions (*Dryopoides* in Site 1 and *Tubularia* in Site 3) there is a positive shift i.e. species reach their maximum populations some months after the temperature maximum. The average shift for the significant cases in 2·43 months. The average time of the first temperature peaks being 9·33 (Jan. 1976) gives the 'average species' peak at $t_{11·76}$ (April 1976). Using the average time of the second temperature peaks (i.e. 21·77, Jan. Feb. 1976) an 'average species' peak at $t_{24·20}$ (April 1977) is obtained.

Comparing shifts in sites using the two cyclical species common to all sites (*Ficopomatus* and *Electra*) gives average shifts of 3 months for Site 1, 2 months for Site 2 and 3 months for Site 3; these differences are negligible. Comparing the two species occupying the three sites, gives averages of 2·7 for both *Ficopomatus* and *Electra*.

Of the 10 cases with significant *r* values with chlorinity, 8 have negative correlations, the exceptions being *Dryopoides* in Site 1 and *Tubularia* in Site 2. Disregarding these two species, the average time shift in significant cases is 0·63 months, implying that population peaks approximately coincide with salinity minima.

ANALYSIS OF ALGAL BIOMASS DATA

The algal biomass data from the upper surface of the plates at Site 2 are given in Table 10. Because of the considerable variation in the data, monthly means of the biomass were used to determine whether any relationship to abiotics could be detected. Initially a linear relationship between algal biomass and aboitics was assumed and regression analyses indicated that for chlorinity the relationship was not significant (*r* = 0·50) and no other relationship could be detected.

TABLE 9: CORRELATION BETWEEN CYCLICAL SPECIES AND ABIOTIC FACTORS, SITES 1 AND 3

Species	Temperature r	Time shift	Chlorinity r	Time shift
Site 1 (*t*12–24)				
Balanus	0·8795	3	–0·6000	1
Ficopomatus	0·8085	3	–0·7395	1
Dryopoides	0·8346	–1	0·6860	1
Electra	0·7018	3	–0·3942†	2
Hippodiplosia	0·5314	3	–0·2090†	2
Crassostrea	0·7844	2	–0·6202	–2
Site 3 (*t*1–17)				
Ficopomatus	0·8195	3	–0·5765	2
Dryopoides	0·6043	1	–0·6411	1
Electra	0·6089	3	–0·6203	3
Tubularia	0·3664†	–2	–0·4202†	1
Plumularia	0·3960†	0	0·1381†	1

† Non significant correlations

TABLE 10: ALGAL BIOMASS FROM UPPER SURFACES OF PLATES, SITE 2

Month	Biomass*			
	1975	1976	1977	Mean
January	—	49·0	206·2	127·6
February	—	150·3	0	75·2
March	—	133·3	36·5	84·9
April	—	48·9	0	24·5
May	963·6	108·2	78·6	383·5
June	615·0	387·2	419·3	473·8
July	444·2	301·8	824·6	523·5
August	222·1	304·1	936·2	487·5
September	225·5	336·0	355·4	305·6
October	96·8	0	717·5	271·4
November	118·5	228·9	—	173·7
December	92·3	111·6	—	102·0

* grams dry weight/m^2

For temperature r = -0·91, significant at 0·001 level, and the regression was biomass (g) = -3·50 (temperature) + 105·3. These data show a much closer relationship of algal biomass to temperature than to chlorinity. The generally greater variation in chlorinity may be responsible for the low r values.

LONG-TERM PLATES

Two sets were available from Auckland Creek and the Calliope River respectively, and analyses of each follows the techniques for the short-term plates except that no species were eliminated. Times were coded 1–6, species were coded 1–14 for Auckland Creek and separately 1–6 for the Calliope River.

TABLE 11: SPECIES GROUPINGS AND ABUNDANCE ON LONG-TERM PLATES, SITES 1 AND 2

Species	Code Number	Species Group*	Age of plates in months					
			1(t_1)	7(t_2)	8(t_3)	9(t_4)	10(t_5)	11(t_6)
Auckland Ck								
Tubularia crocea	4	I	16	8				
Balanus amphitrite	1		3		1			
Bugula neritina	3		44	4			2	
Electra cf. *anomala*	6		12					
Microcosmus australis	12	II			1			
Plumularia sp.	7	III		1		3		2
Ascidia sydneyensis	9			5	1	3	2	2
Polyandracarpa rhizoma	8			65	69	106	82	308
Bugula cf. *stolonifera*	2		5	1	5	13	7	13
sponge I	11			2	11	8	3	8
Hippodiplosia sp. A	5	IV	6		6	9	21	6
Branchiomma sp.	10				1	2	2	1
ascidian sp.	13					3	2	
Crassostrea cucullata	14	V						4
Calliope R.			1(t_1)	3(t_2)	4(t_3)	11(t_4)	12(t_5)	23(t_6)
Plumularia sp.	3	I	10					
Balanus amphitrite	1	II	173	24	22	13	5	12
Ficopomatus uschakovi	2		190	11	7	5	23	17
Electra cf. *anomala*	5		3	1				
Crassostrea cucullata	4	III	6	23	10	10	16	20
Modiolus auriculatus	6	IV					14	20
BIOMASS (g)			73·2	180·0	416·8	468·8	516·8	244·1

*From heirarchical classification

AUCKLAND CREEK DATA (SITE 1)

To obtain moment coefficients of skewness of 0·5, the modal transformation for times was a 5th root and for species a 1st root (ie. untransformed data). Results of the classifications are given in Figs. 4 and 5 respectively. The former shows 'chaining', no groupings and suggests successive and sequential changes. The latter was resolved into five groups (I–V) of which two are isolated species (*Microcosmus* and *Crassostrea*). In Table II the results are given as a two-way coincidence table, with inclusion of species and code numbers.

Considering the species classification (Fig. 5) species group I contains species present in largest numbers at t_1 (the biotically most isolated time) and either not present later (*Electra*) or present at only the first two times (*Tubularia*) or intermittently present later (*Balanus*, *Bugula neritina*). They can be regarded as the 'pioneer' community. Species group II can be neglected. Species group III contains species present from t_2 onwards and can be regarded as the 'stable' community. Species group IV attains maximum values in t_{4-5}; they may be either seasonal species or may indicate a seral stage to a later 'climax'. Species group V (*Crassostrea*) occurred only at t_6, and on the basis of other observations in the area, is considered to be an important climax species.

The difficulties caused by the absence of groupings in the times classification (Fig. 4) were partly resolved by determining inter-time coefficients (using 5th root transformations). There are significant correlations between all pairs of t_{3-6}. These times can be regarded as delimiting the climax state.

CALLIOPE RIVER DATA (SITE 2)

To obtain moment coefficients of skewness of 0·5, the modal transformation for times and for species is a 1st root transformation (i.e. no transformation). Results of classifications gave groupings in both cases — these are shown X on Figs. 6 and 7.

The two-way table (Table II) shows that species group I (*Plumularia*) is an early transient or pioneer species; species group II contains species present in greatest numbers in t_1, and they either drop out soon (*Electra*) or persist (*Balanus* and *Ficopomatus*); species group III (*Crassostrea*) is present throughout in substantially similar numbers while species group IV (*Modiolus*) only appears in later plates.

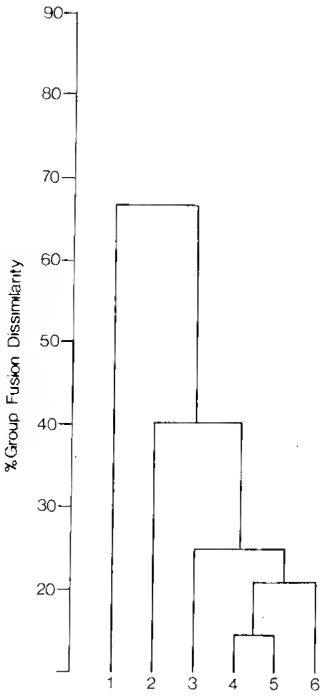

FIG. 4: Dendrogram of times classification from Auckland Creek long-term plates.

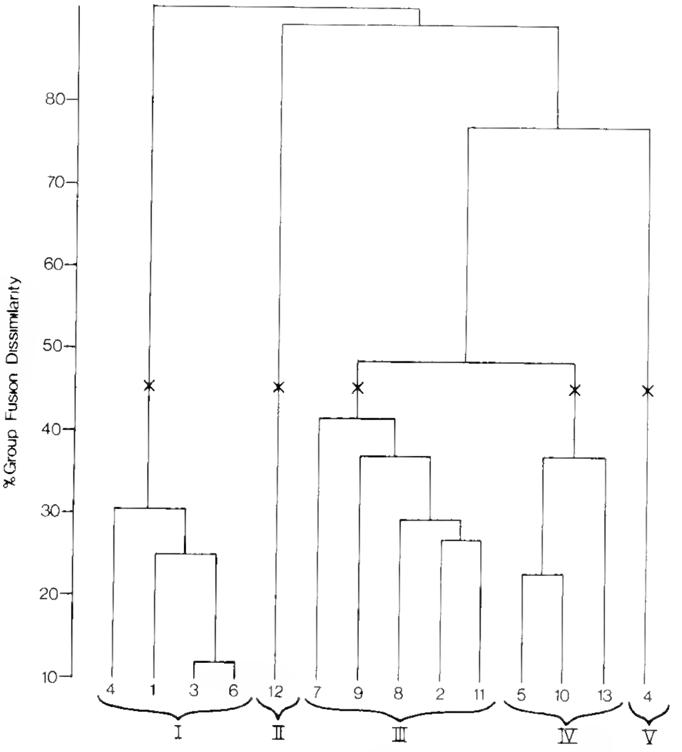

FIG. 5: Dendrogram of species classification from Auckland Creek long-term plates. X indicates species-groups accepted.

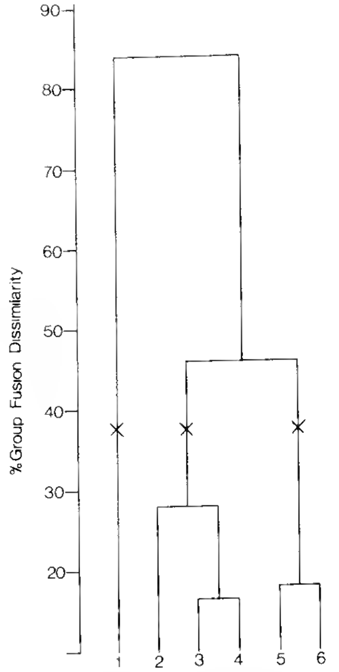

FIG. 6: Dendrogram of times classification from Calliope River long-term plates. X indicates times-groups accepted.

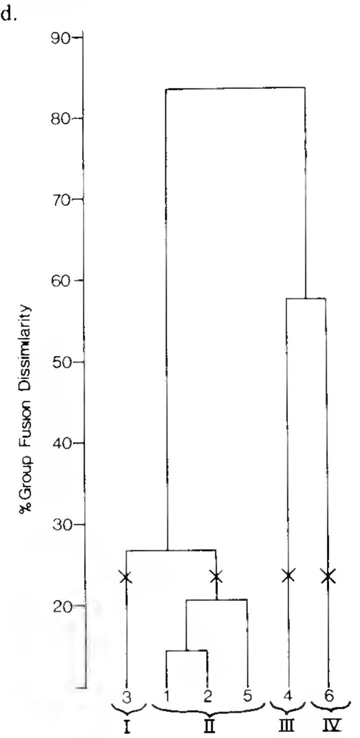

FIG. 7: Dendrogram of species classification from Calliope River long-term plates. X indicates species-groups accepted.

The first time group (t_1) is biotically the most isolated, the second (t_{2-4}) is characterised by *Balanus, Ficopomatus* and *Crassostrea,* while the third group (t_{5-6}) is additionally characterised by *Modiolus.*

Intertime correlation coefficients showed significant positive correlations between pairs of t_{2-4} and also between t_{5-6}. On this basis, t_{2-4} delimits a seral stage and t_{5-6} the climax.

Differences between the Auckland Creek and Calliope River will be noted; these are commented on below.

DISCUSSION

Little data on fouling organisms in Australasian waters is available and this is mostly from temperate waters (Allen and Wood 1950, Allen 1950, Skerman 1960, Straughan 1968, Wisely 1958a, b, 1959). While considerable overseas data is available on subtidal fouling organisms (Aleem 1957, Graham and Gay 1945, Haderlie 1968, Scheer 1948), most of these studies have not used detailed numerical analysis, or have used only binary data (e.g. McCain 1975).

Despite the subtropical estuarine setting of the present study, considerable generic similarity is found with the fouling organisms in Sydney (Wisely 1959) and Auckland (Skerman 1959). However caution must be exercised in comparing such areas for as the present data show, considerable variation exists from one sampling station to another. Site 1, situated in Auckland Creek (Fig. 1), significantly differs from Sites 2 and 3 in the Calliope River on the basis of (i) the number of species, (ii) the paired *t*-tests of individual species occurrence (Table 2) and (iii) the mean number of individuals of each species (Tables 3 and 4). Whether these differences result from abiotic factors or the proximity of mature adults is not known; however there are indications in the data (Tables 5 and 6) that physical disturbance at Site 1 is responsible for obscuring otherwise periodic settlement.

Nevertheless a group of species emerges which regularly occupies the short-term plates i.e. *Balanus, Ficopomatus* and *Electra.* These three species are the most numerous on the short-term plates and occur throughout the year. Other accompanying species do so only for certain periods of the year (Fig. 8).

The relationship between settlement and abiotic factors indicates the correlations are strongest with temperature, less so with chlorinity and are further reduced with rainfall. The algal biomass data from Site 2 shows identical relationships. This order of correlation is not unexpected since in an estuary with a large catchment area, chlorinity will be more variable in the short-term than temperature, and the relationship of chlorinity and rainfall will be modified by the intensity and duration of rainfall, especially where extensive salt flats occur (Saenger and Robson 1977). Of those species showing approximately twelve monthly cycles (Tables 8 and 9), maximum settlement occurs about 2·7 months after the temperature maximum i.e. around April. In relation to chlorinity, maximum settlement in significant species occurs around the salinity minimum.

Classification of short-term plates gave time-groups that made little conceptual sense. It did emphasise that three species (*Balanus, Ficopomatus,* and *Bugula*) are regular colonisers of the short-term plates. Classification of the long-term plate data however indicated that these three species together with other less numerous ones, formed the 'pioneer' phase using one set of data (Auckland Creek) and were also present in largest numbers in the one month plates at the second (Calliope River). The two sets gave different 'climax' communities and two points require emphasis. Firstly, the time of initiation and collection has a bearing on the 'pioneer' species composition. For example, the 1-month old plate from Auckland Creek represents a winter plate and consequently *Ficopomatus* is absent and *Tubularia* is present in relatively large numbers (Fig. 8). Similarly the 1-month old plate from the Calliope River is an autumn plate and consequently *Crassostrea* is present (Fig. 8). Secondly, while the 23-month old plate from the Calliope River is termed a climax, it is only partly so. When the fouling community matures on a plate, it attains a thickness of approximately 2·5 cm, and with water movement and the death of underlying organisms, small patches of the entire community break off (with the consequent reduction in biomass — Table 11). The 'pioneer' species colonise these newly-formed, almost bare patches and a mosaic of different aged growth results. Consequently 'pioneer' species are found on mature plates although not strictly in the 'climax' phase. This type of 'patch-climax' is the common covering on natural substrates in the study area.

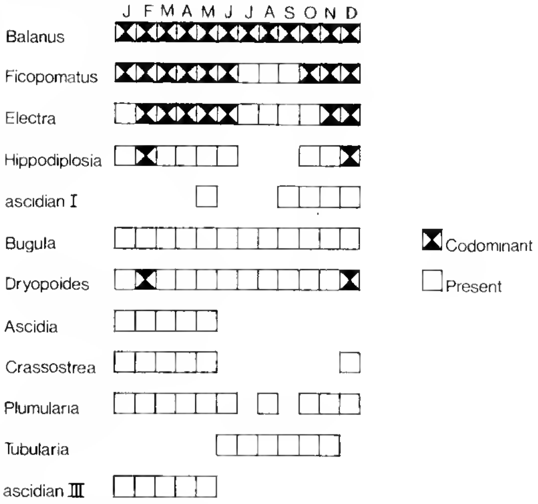

FIG. 8: Seasonal occurrence of sessile colonisers from short-term plates at all sites from May 1975 to May 1977.

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BEHAVIOUR IN CAPTIVE INDIVIDUALS OF THE DASYURID MARSUPIAL *PLANIGALE MACULATA* (GOULD 1851)

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ABSTRACT

Common Planigales *(Planigale maculata)* from coastal Queensland and New South Wales were maintained for three years in captivity. They were found to have relatively poor eyesight compensated by acute senses of hearing and smell. Their activity phases consisted of periods of intense activity followed by torpor-like rest periods. They constructed ball-shaped compact nests only when with young and at other times occupied small depressions under grass, logs or rocks. Their postures were similar to those seen in other dasyurids, although a number of grooming actions involving the cleaning of vibrissae, pinnae, or matted tail hairs, appear to be uncommon in other genera. Animals defaecated and urinated both deliberately and randomly throughout their enclosures. They also rubbed their cloacas and sternums on objects in the cage. They preyed voraciously upon insects and small vertebrates and exhibited a 'fanning' response to mucous-covered or unpalatable prey. At least five specific vocal calls were made, females being more vocal than males. Aggression between animals was most commonly observed during a female's oestrus and also after food thieving, but threat and appeasement calls usually inhibited serious fighting. Oestrus females attracted potential mates by calling for a period of two or three days. Copulation lasted approximately two hours, and was characterised by males using a neck grip and 'scratching' with the hind feet throughout the entire copulatory procedure. Females were generally passive throughout copulation. The gestation period was approximately twenty days, the young first detached from the teats between twenty-four and twenty-eight days and were independent at seventy-two days.

It is proposed that wild Common Planigales are most probably polyoestrus and socially intolerant.

Small dasyurids studied in detail in captivity include: *Sminthopsis crassicaudata* [Ewer 1968], *Dasycercus cristicauda* [Ewer 1969], *Dasyuroides byrnei* [Aslin 1974], *Antechinus stuartii* [Marlow 1961; Braithwaite 1970], *Dasycercus cristicauda* and *Dasyuroides byrnei* [Sorenson 1970], *Dasycercus cristicauda* [Mitchener 1969], and *Dasyuroides byrnei* [Eisenberg and Leyhausen 1972].

The only comparable studies of species of *Planigale,* are some general observations of captive specimens of *P. ingrami* (McKay 1974), recordings of particular aspects of reproduction in *Planigale maculata sinualis* (Aslin 1975), and the emergence of pouch young in individuals of *P. maculata* (Morrison 1975). Other reports of behaviour and reproduction in Planigales (e.g. Fleay 1965, 1967; Van Deusen 1969) have been confused by uncertainty in specific identifications (Archer 1976).

This study reports behaviour in individuals of *Planigale maculata maculata* (Plate 1a) from various east coast Australian localities. Identifications have been based on the revision of the genus by Archer (1976). *Planigale maculata* (the Common Planigale) is a non-arid-adapted species inhabiting grasslands (e.g. *Imperata*) associated with a variety of habitat types. It is common east of the Great Dividing Range in Queensland. Because of their aversion to standard mammal trapping techniques (Van Deusen 1969), their ecology and behaviour in the wild is undocumented. The present study on captive animals was undertaken to provide preliminary information on aspects of behaviour which may in the future be checked in wild situations.

METHODS AND STOCK

Live Common Planigales were obtained from Condong in northern New South Wales and

Gympie, Townsville, Ingham and Coen in Queensland. These animals were studied from 1973 to 1976 with most of the detailed observations taking place during 1975. Animals were housed individually or in pairs in glass-fronted cages measuring 90 × 100 × 80 cm. These cages contained numerous hiding places and pathways formed by hollow logs, tree boughs, rocks, grasses, and litter on a dirt and sand floor. They were left uncleaned for as long as possible in order to minimise disturbance. The animals were studied under either an eight watt fluorescent tube covered with blue cellophane, a red forty watt bulb, or a combination of both. Under these conditions the animals did not appear to register disturbance while being quietly observed. There was no reversal of light, and animals were subject to Brisbane ambient temperatures throughout the study.

A typical weekly diet for each Planigale consisted of: one or two baby House mice four times per week; mealworms and other insects four times per week; and meat mixture (minced meats, brawn, grated cheese, vitamin E oil, hard boiled egg, ground dog kibble) six times per week. Water was always available in small dishes and was supplemented with Pentavite Infant Drops once weekly.

RESULTS OF OBSERVATIONS

SENSORY RESPONSES

The Common Planigale has small eyes compared with many other dasyurids e.g. *Sminthopsis* and *Dasyuroides*. In contrast to the senses of hearing and olfaction, sight appeared to be of minor importance. During scuffles with prey, Planigales were unable to relocate dropped food by sight. It would seem that in the absence of sufficient olfactory or aduitory clues, dynamic visual signals are necessary before animals respond.

In *Antechinus godmani* natural disease can cause blindness (pers. obs.). The ease with which blind individuals move around the rainforest floor, catch insects, and enter traps (pers. obs.) suggests that in this small-eyed *Antechinus*, eyesight is not vital. This supports the supposition that eyesight in the Common Planigale is also a non vital sense.

Olfactory and auditory perceptions appeared to be well developed although it was not always possible to establish which stimulus animals were responding to, because sniffing nearly always accompanied auditory perception.

When meat was introduced into the cage with Common Planigales, the animals left their nests where they were sleeping, sniffed the air, jerked the head up and down rotating it at the same time, and followed the scent to its source. This sniffing behaviour is much more developed in Common Planigales than in spp. of *Smithopsis* (pers. obs.). Pieces of handrubbed string or paper brought sleeping animals from their holes often within fifteen seconds after introduction. Some scents, and in particular human breath, disturbed the animals. If subjected to slow human breathing from about 30 cm above their nests, the animals would flee to various hiding places in the cage, emitting a wheezy call similar to the 'possession call' (described later).

They responded to gentle scratching on their cage walls by tracking the sound to its source. Insects moving in the cage were always investigated and tracked down prior to the investigation of similar dead insects, and they dug up litter and soil to reach live insects they detected underground.

It seems that olfaction and hearing are acute over a longer range than sight. Close range activities involving sight are probably aided by stimuli received through the very long vibrissae.

ACTIVITY RHYTHM

Common Planigales emerged at, or slightly before dusk. In some cases they emerged up to two hours before sunset. Activity continued throughout the night, interspersed with rest periods.

During the day animals slept in regular sleeping sites: in nests under logs, rocks, or in the bases of grass clumps.

During the night, rest periods were not confined to regular sleeping nests but often occurred in diverse areas around the cage. Male Planigales often rested on branch tops or lodged themselves between a branch and the cage wall. The actual time of night that animals returned to their nest was variable.

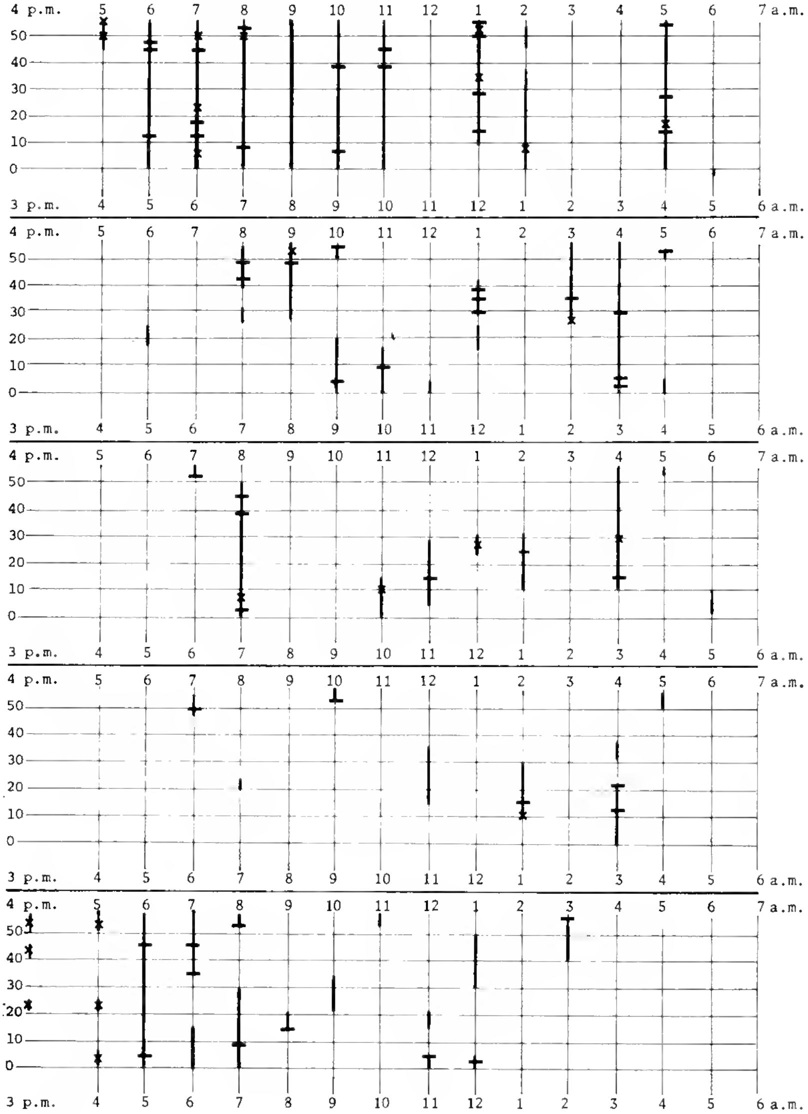
Reversed light was not set up, and few all night watches were kept. One is summarized in Figure 1. Total time out of nests varied from 9 hours in a maturing male to 1·5 hours in an adult female. Feeding and drinking times usually took place soon after emergence at night, again during the subsequent activity periods, and again before dawn in the last activity phase. The Planigales rarely extended their activities beyond sunrise. Most animals returned to nests at least one to two hours before sunrise. This contrasts with individuals of *Sminthopsis macroura* which often extend their early morning phases up to an hour or more after sunrise (pers. obs.).

During the day animals were often seen grooming themselves, yawning and 'sleeping'. In describing the behaviour of *Planigale ingrami*, McKay (1974, p. 5) states '. . . they alternate between periods of intense activity and periods of quiescence. Within the resting periods there are times when respiratory movements are rapid and shorter periods of slow respiration, presumably sleep'. For the purpose of this paper 'sleeping' was regarded as a marked reduction in breathing rate and body activity, whether the eyes were open or closed. Normal alert breathing rate in adults is approximately 350 breaths (intakes) per minute, whereas during 'sleep', this rate drops to as low as 80 per minute, (all counts were made at 22° C). This phase of very low breath rate may be torpor.

During nocturnal rests animals yawned, groomed and slept, but because they were often hidden from view it was not possible to quantify these aspects of behaviour.

NESTING ACTIVITIES

The Planigales did not dig tunnels, although superficial 'tunnels' were formed by pushing through surface material such as leaf litter and



Male 1
Total time of activity:
9 hours.
Number of separate
activity phases: 4.

Female 1
Total time of activity:
3 hours 40 mins.
Number of separate
activity phases: 11.

Male 2
Total time of activity:
2 hours 50 mins.
Number of separate
activity phases: 8.

Female 2
Total time of activity:
1 hour 30 mins.
Number of separate
activity phases: 8.

Group of 7 juveniles
Total time of activity:
4 hours 50 mins.
Number of separate
activity phases: 14
(combined totals).

FIG. 1: Activity rhythms for Common Planigales, 6 June 1975. x = times at which animals drank; — = times at which animals fed.

grass-cuttings. These often terminated in small cup-like depressions (nests) in which they slept. Heinsohn (1970) reports a captive male Ingram's Planigale *(P. ingrami)* pushing through grass and forming a 'covered runway' at the end of which was a hollow chamber used for nesting. The same type of tunnelling has been recorded for the Dusky Marsupial Mouse *(Antechinus swainsonii)* (Van Dyck and Ogilvie 1977).

Adult females with pouch young carried nesting material including grass, leaves and insect wings, in order to construct compact 'tennis-ball shaped' nests in hollow logs. Fleay (1965, p. 196) records that his female Planigale, with seven young, maintained '. . . a small neat saucer-shaped nest of dry grass beneath concave shells of wood and bark'. He describes one nest as being similar to those made by Blue Wrens (*Malurus* spp.).

Juvenile Common Planigales, after leaving the pouch permanently, always slept together in a crude saucer-shaped nest originally constructed by their mother. This nest they shaped with the mouth and attempted to maintain with grass cuttings and leaves.

Each individual in unmated pairs had its own nest in a separate corner of the cage and each showed consistent agonistic behaviour when another individual appeared at its nest entrance. All diurnal and most nocturnal sleeping was done in these nests. The animals regularly took large prey back to within a few centimetres of the nest entrance to eat.

Nests of Common Planigales examined in the wild contained single animals. On one occasion an adult male caught in Ingham was found sleeping with a juvenile *Melomys burtoni* in a small grass and leaf nest under corrugated iron (pers. obs.). Most nests constructed under sheets of iron or wood were simple tea-cup-like structures made of leaves and grass, and lined with insect wings and small leaves.

Mated pairs in captivity consistenly slept together under or in small logs and rearely changed the position of their nests.

POSTURES AND EXPRESSIONS

The terminology used here is that given by Ewer (1968).

BIPEDAL STANCE: This is a common dasyurid posture (also called 'Investigatory Upright' by Aslin 1974) and occurs when animals investigate sounds or objects above them. In this position Planigales rest much more of the tail on the ground than do individuals of either *Sminthopsis macroura* or *S. crassicaudata*. The posture can vary from a vertical upright position with only the hind toes and tip of the tail touching the ground, to a semi-bipedal stance where the whole surface of the foot rests on the ground (Plate 1b-c). The ears are turned forward and the forepaws are held out in front of the animals (see Plate 1b).

INDECISION ALERT: In this common posture the ears are turned forward, one forepaw raised, and the tail held horizontally without touching the ground (Plate Id). This position closely resembles that seen in individuals of *Antechinus* spp.

The position of the ears can change rapidly from a forward direction when investigating, to tightly folded back when the animals are subject to sudden noises, aggression from other animals, or when attacking prey.

EATING AND GROOMING: The animals adopt a squatting-on-the-haunches position with the ears turned back and out. The whole of the tail

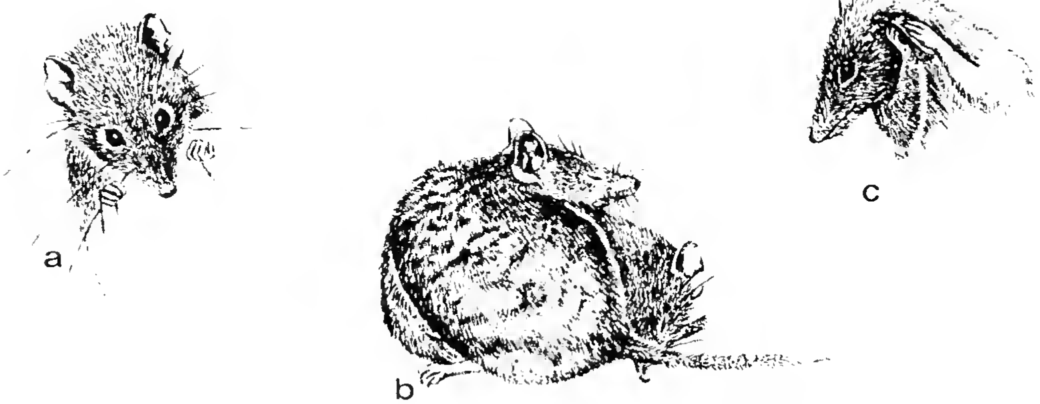


FIG. 2: Common Planigale postures. a, cleaning vibrissae; b, sleeping; c, cleaning an ear.

contacts the ground and the hind legs are stretched out in front. This posture provides considerable stability (Plate 1e). Both forepaws are generally used in holding even very small prey.

SLEEPING: Common Planigales adopted a variety of 'tight' sleeping positions with the limbs usually kept close to the body. When pairs slept together they often lay over one another (Fig. 2b). Juveniles slept on top of and across one another, but generally all animals lay with the dorsal side up.

'FREEZING': Planigales frequently 'froze' after noise or disturbance. They would remain completely motionless for as long as two minutes. Usually another sound or movement 'snapped them out'. They then continued with the activity engaged in before the disturbance.

This 'freezing' is very common in other dasyurids, e.g. *Sminthopsis* spp., *Phascogale tapoatafa* and *Dasyurus hallucatus* (Fleay 1962), and probably protects them from nocturnal predators (e.g. owls) that rely on movement for detection of their prey.

GAITS: Common Planigales are splay-footed (their hind feet point out and away from the sides of the body). Leg sequence during walking is right front, left rear, left front, right rear. Much activity involves running, or hurdling over objects, as well as jumps of up to 10–15 cm between branches and rocks. The hind legs often remain together during hops from a slightly higher position to a lower one, or over leaves. This is reminiscent of the gait in sick individuals of *S. murina* and *S. crassicaudata*. All Common Planigales hold the tail high when walking or running so that no part of it comes in contact with the ground. Characteristic movements while carrying prey are discussed under 'Feeding behaviour'.

ARBOREAL ACTIVITIES

Planigales appear well adapted for arboreal activities (Plate 1f). A young male spent 30% of a one-hour evening activity phase amongst branches in his cage. This accounts for most time not otherwise spent in eating, grooming, or running on an exercise wheel. Both males and females actively and expertly climb using the same gait and speed in descending and ascending as they use on ground. After eating large meals, some individuals climbed onto branches in order to groom or rest.

The palm of the manus and the sole of the pes have enlarged striated pads aiding in arboreal activities. The hind limbs are turned out, and while walking on small twigs (2–4 mm diam.) the toes of the hind feet wrap completely around the twig.

EXPLORATORY BEHAVIOUR

A cloth bag saturated with House mouse urine was introduced by a string into the cage. Planigales responded with the investigatory sniffing of the air; a slow approach; an inspection and sometimes a clawing of the bag; and finally ignored it.

Planigales were cautious of unfamiliar food bowls placed in the cage. The slightest noise from other animals in the cage would cause them to instantly abort an initial approach to an unfamiliar item.

Individual differences in exploratory behaviour are high, and male Planigales appear to take greater initiative in investigation of new objects and are less wary of new situations (also see later in regard to olfactory signals), than females.

GROOMING

Mutual grooming between adult individuals of *Planigale maculata* was never observed.

During one all-night watch, hourly records were made of the total time that an adult male spent grooming. During the thirteen-hour period, 19 minutes 35 seconds (19:35) were spent in grooming and there were 34 separate periods of grooming activity. The times spent in grooming for each hour from 4 p.m. to 6 a.m. were: 1:20, 2:00, 4:55, 1:05, 0:20, 2:15, 2:25, 0:00, 3:25, 0:45, 0:00, 0:00, 2:05, 0:00.

Animals were also observed grooming during the day, and before emerging at night.

Grooming invariably followed mouse meals and generally followed those of mealworms. Some elements of a typical grooming sequence observed after eating consisted of:

(1) Licking the paws together (6–10 sec) and working them along under the snout together, the hands being drawn over the whiskers; the hands work in opposition around the snout, along under the chin, down from the eye to the mouth, behind the ears, and back over the closed eyes to the mouth (20 sec).

(2) Licking the upper arm of forefeet while the forefeet stretch downward; the tongue then licks below the animal's chin on the chest while the neck is stretched; the animal holds the right leg with the left paw and licks the right forearm, before reversing the posture in order to clean the left leg (15 sec).

(3) Cleaning the belly and body by licking the fur that is held between or below the forepaws as they pull the skin to the mouth and simultaneously comb the fur after licking. The animal then licks and nibbles the cloacal region and testes (30 sec).

(4) Left hind foot scratches between the ears and is returned to the mouth where it is licked. It then scratches under the mouth and is again returned to the mouth to be licked. This process of scratching and returning the paw to the mouth continues — flank, to mouth; neck, mouth; left ear, mouth; belly, mouth; middle of the back and under the flank, mouth; behind the left ear and under the front foot, mouth; left ear, mouth (30 sec).

Grooming lasted up to three minutes and generally started with face and paw cleaning, progressed through forearm, body and tail cleaning, and ended with the body being scratched with the hind leg.

The occasional scratch with the hind foot generally resulted in the foot being licked. When the interior of the pouch was cleaned, it was not forced open with the forepaws but lay open by muscular relaxation.

Some grooming actions seen in these Common Planigales have not been noticed in other related dasyurids such as species of *Sminthopsis:* (1) straightening of matted hairs on the tail by using the upper incisors to comb the tail hairs; (2) cleaning the vibrissae using simultaneous action of the left forefoot to left vibrissae and right forefoot to right vibrissae (Fig. 2a). The vibrissae are pulled through the closed paws; (3) slowly running a single pinna in sandwich fashion between the two forepaws, licking the paws and repeating (Fig. 2c).

OTHER MOVEMENTS: Shaking of the body was not observed (this is common in individuals of *S. crassicaudata* and *D. byrnei).*

Sandbathing and rolling was never observed, although facilities existed for these activities.

Stretching occurred mainly on emergence from nests. Forelegs extended singly with wide-stretched fingers and then back legs were stretched together with a general lowering of the body.

Yawning occurred after sleeping; when awake during the day; or while stretching.

DEFAECATION AND MICTURITION

Animals did not soil their nests and 'deliberate and casual' defaecation and micturition took place. ('Deliberate' refers to the regular deposition of faeces or urine in a selected spot whereas 'casual' deposition takes place at random throughout the enclosure; see Ewer 1968).

In unmated pairs, deliberate defaecation occurred in each corner of the cage nearest to the animal's day nest and about 10 cm away from the next entrance. The cloaca was generally wiped on the substrate after defaecation. Micturition was only observed to occur in association with defaecation. Following deliberate and casual defaecation the faeces were usually smelt and then ignored. The average toilet was five drops of urine followed by a 1 cm dropping.

Adult mated pairs and pregnant females deliberately deposited faeces in two corners of the cage. The pregnant females mostly used the corner nearest the nest (<10 cm from it). This behaviour continued through lactation. Juvenile animals made a communal pile in one corner and casual defaecation was common.

It would also seem that Common Planigales use urine and faeces in scent marking.

If an individual had difficulty in evacuating a faecal pellet from its cloaca by rubbing it along the ground, it picked the pellet out with its incisors and either flicked it away with a sudden toss of its head, or brushed it from its mouth with its paw.

FEEDING BEHAVIOUR

Foraging took place with forepaws digging alternately on either side of the head, as the nose thrust into areas where prey was possibly concealed. In locating prey, the animals either ran around the enclosure, stopping to investigate sounds or smells, or they sat quietly — mainly near branches, nests, or cover — and responded quickly to any sounds.

Small innocuous prey such as mealworms were normally grabbed with the incisors and immediately transferred to the cheek teeth with the use of the forepaws. However when taking mealworms from a dish, the animals often reached down and snatched the mealworm out with the hand. When stealing food from another animal the forepaw was generally used to snatch food from the owner. When taking mealworms from my hand, a female always smelt the worm, grabbed it, and ran off to the eating corner.

Common Planigales usually adopted one of two eating postures: a 'secure' eating posture (shown in Plate 1e and g) when unharassed and in a suitably private spot; or an 'insecure' position with one forepaw on the ground when eating in haste or when being harassed by other animals.

When in possession of food and under threat, Common Planigales uttered a 'possession call' (described later) and ran to a 'safe' spot in the cage with the food, using a hopping gait with head held high, reminiscent of that used by most rodents when retrieving young. (I have not seen this gait in individuals of the genus *Sminthopsis*). The animals adopted a hunched eating posture and used the hands to transfer the worm from one side of the mouth to the other. While one hand held the food in the mouth, the other made grabbing movements and 'air-clutches' near the mouth, corresponding with those of the hand that was holding the food. It takes c. 300 chews and 1·25 minutes to eat a fully grown mealworm larva. No particular end is started at and no 'killing bites' are administered. As in most other dasyurids, hands were used extensively for grabbing and restraining flying prey such as moths and beetles.

Large lumps of meat-mix held in the incisors were broken into small pieces by quick sideways flicks of the head. These small pieces were then searched out and eaten.

Very small grasshoppers (<2 cm) were quickly killed by bites into the thorax and head and then eaten entirely except for the wings.

In dealing with larger grasshoppers (<7·5 cm), adults closed their eyes on contact with the insect. They did not stalk with closed eyes as do individuals of *Sminthopsis macroura*. Attacks were generally ineffectively directed at the large hind legs although one female consistently pushed her snout up between the abdomen and wings and bit into the soft abdomen. Persistent biting prevented the grasshopper's escape and it was ultimately injured or worn down by the perseverence of the planigale rather than being quickly killed. The abdomen was eaten and the head, thorax and wings discarded. Young Planigales also closed their eyes on contact with grasshoppers but were unable to kill those over 5 cm, which were usually sniffed and ignored.

Inexperienced Planigales were generally very poor killers of mouse pups. After grabbing the pup, they 'hopped' with it to an appropriate spot and commenced eating it at any part of its body, often from the hind feet or tail. In this way the pup was often still squirming and squeeking three or four minutes after the initial attack. It generally took a Planigale about fifteen to twenty minutes to devour a pup, and considering the relative sizes of the two animals, this reflects the incredible appetite of the Common Planigale (see Plate 1g for comparions of size).

Juvenile animals were at first very poor killers and although their jaws were strong enough to crush the skull, they often bit at random, chewed on limbs, and left mouse pups maimed and bleeding. Their technique improved with experience. The most efficient killers were old adults, which always administered neck and head bites, and increased biting if the mouse pup squeeled. This ensured quick deaths and was followed by the pup being eaten from the head-end first.

Food stealing was prevalent and resented by other individuals. Thieves snatched with paws and often made an open attack on the owner of the food. Juveniles were observed diving for the owner's neck and wrestling with him without reference to the prey. Attacks of stealing were generally met with threat calls and 'boxing', or the owner would utter the possession call and run away with the food. Some of the worst fights observed in juveniles occurred over thieving.

A Brown-orange Bug *(Musgraveia sulciventris* (Stal)), was introduced into a cage. It was sniffed out and immediately bitten by a female Common Planigale. After being sprayed by the insect she retreated and rubbed her chin on the ground while walking in a circle. After two more mouth attacks, the forepaws were used to administer attacks, scratching the bug towards itself using alternate paws. During the attack the female vigorously bit a leaf lying nearby. After being sprayed in the eye, she rubbed that side of the head in a circle on the ground. She continued to make paw attacks accompanied by 'fanning' (rapid lateral movements of both paws — reminiscent of hands clapping, but without ever meeting). This behaviour has been seen in the Darling Downs Dunnart (*Sminthopsis macroura*) when dealing with witchety grubs, and in Ingram's Planigale (*Planigale ingrami*) when trying to eat worms (pers. obs.). It was also seen in Common Planigales when the animal had trodden on and squashed ants. The purpose of this behaviour is not known, but it is always associated with irritating substances such as mucous on prey. Eventually the female dislodged the bug's head, discarded it, and ate the body.

VOCALIZATION

Common Planigales have an audible repertorire of at least five calls:

(1) A 'possession-call', a soft 'rhitt rhitt rhitt . . . with each 'rhitt' repeated about three times per second, was uttered when retreating with food, even if unchallenged by potential thieves. This often aroused sleeping animals who came out to look for the food.

(2) The threat call of the female consisted of a sharp 'ssstt' and was in defence of space or in

attack. The male call consisted of a soft 'tit tit tit. . .' uttered when attacking and retreating.

(3) When struggling with large grasshoppers and when breathed on by humans, Common Planigales uttered a soft, short, 'sss sss sss . . .' each 'sss' of which is repeated about four times per second.

(4) A 'mate-attracting' call was uttered by females approximately three days before mating. This is a wheezy loud 'tsz tsz' uttered while sitting high on a rock or log. This was sometimes answered by the male with similar call.

(5) An appeasement call was generally uttered by a male while being attacked by a female. This call resembled 'fitt zitt' and 'fitt fitt'. The eyes were usually closed.

OLFACTORY SIGNALS

Common Planigales appear to recognise each other by mouth smell (Ewer 1968, noticed this for the Common Fat-tailed Dunnart *(Sminthopsis crassicaudata)*. Two animals approach one another front-on, with ears pressed back, each sniffing the other's mouth along the lower jaw. One may open its mouth slightly and utter a threat call or both may ignore each other. Sniffing occurred more frequently in Common Planigale encounters than in encounters between Darling Downs Dunnarts (*Smithopsis macroura*) under similar conditions (pers. obs.).

Individuals of *S. macroura* react to foreign odours (pieces of string or paper rubbed on the hand or body) by dropping urine, rubbing the cloaca, depositing faeces upon, or spreading saliva near the source of the odour. Common Planigales, however, sniffed the string and paper and ignored it (except for one young female who, after sniffing the paper, grabbed it in her mouth, 'hopped' with head in the air to her usual eating corner where she then ignored it).

STERNAL GLAND MARKING

In early June, young males which had been born the previous September began actively rubbing the chin and chest over food bowls, leaves, branches, and their exercise wheels. During the second hour of an eight-hour activity phase one individual marked 39 times.

A leaf marked by a young male was placed in a cage containing a pair of adults. The adult female sniffed and immediately 'attacked' it, bit it for one or two seconds, sniffed it for forty-five seconds, then bit it again for a few seconds; after another five minutes of mild interest she finally ignored it. The same leaf was sniffed and ignored by the adult male. Alternately, grass transferred from an adult pair's cage to an unmated pair's cage induced sniffing by the young male and extra marking of food bowls, but after that the grass was ignored.

Braithwaite (1973) notes that in the Brown Antechinus *(Antechinus stuartii)* males and females move in June to areas where they usually remain until death. During this month the sternal gland of males increases in size. Marking activity increases, and testosterone levels rise. The testes also increase in size, and aggression between males becomes greater.

AGGRESSION

In all instances, when an unfamiliar female (either in or out of oestrus) was placed in an adult male's cage, it was the female who initiated threats, bites, and vocalization. In most cases the male would turn the head exposing the chin, raise the forepaw, and accept bites to the neck and face by the female, and 'retaliate' only by scratching at her. Females would generally sniff the mouth of the male and direct bites around his face. During this activity females' mouths were opened and they kept calling. The ears of both animals would be tightly folded against the head and the eyes half closed. The male would follow the female and sniff her cloaca, which usually either brought her swinging around to direct a few more bites at the male, or sent her scurring off.

During 'copulatory fights' where the male made advances to an oestrus female, the two would have sparring confrontations lasting up to a few minutes each time. In such instances the female would make consistent quick bites at the male, often catching him briefly on the nose. Her eyes and mouth would remain wide open while his eyes would stay squinted. Eighty such 'jabs' by the female sometimes occurred within a single minute. These appeared to be 'soft-mouthed' until the male's advances become more intense, when the female often bit the male hard on the nose. At this time the male would utter a constant appeasement call (see previously). The most interesting feature of these confrontations is the definite inhibition on the male's part to bite the female or to force his attentions. Morrison (1975) records similar dominance by the female.

Little aggression was seen in unmated pairs before June. The male would frequently displace the female from the exercise wheel with no bodily contact. If the male poked his head into the females' nest-hole she would utter a few threat calls, and he would slowly enter after initial mouth smelling.

From the beginning of June the young males' aggression increased. One frequently attacked the female in the activity wheel and actively sought her out during the first few hours after emergence at night. When she ran from the wheel the male often ran after her, dived onto her back, bowled her over, and tried to bite her neck. Alternatively he would chase and grab her and then bite her tail. In most cases a few loud threat calls uttered by the female would cause the male to retreat. Braithwaite (1973) suggests that in the Brown Antechinus, *A. stuartii,* the endogenously arisen appetitive behaviour for aggression results from variation in corticosteroid production. The same probably applies to aggression in maturing male Common Planigales.

Flights were also seen in juveniles (as described above for food thieving). The animals frequently rolled around while limb-locked. Most bites were directed to the back of the head or neck.

Tail thrashing in adult males was common after scuffles. This behaviour is very common in many kinds of dasyurids and appears to be a form of displacement activity.

REPRODUCTIVE BEHAVIOUR

Observations were recorded from the matings of three pairs of Common Planigales (23 Aug. 1974, 19 Nov. 1974, 6 Jan. 1975) and two raised litters.

BIRTH TIMES: Fleay (1965) records summer births for his Planigales, but Aslin (1975) records breeding in individuals of *Planigale maculata sinualis* in all seasons. Juveniles of *P. maculata maculata* in the Queensland Museum collections were measured, the dates of their captures recorded, and an approximate date of birth assigned to each individual or litter (this date is assumed from comparisons with series of captive bred juveniles of *Planigale maculata sinualis* preserved in spirit in the Queensland Museum). Probable birth dates, presented in Table 1, suggest that *P. maculata maculata* also reproduces in all seasons.

Lactating females J21325, J8244, J3093 were captured on 9 Sep., 20 Feb., 27 Nov., respectively.

Although births may occur throughout the year in Queensland and northern New South Wales, there is insufficient data available to predict in which seasons (if any) most litters are produced. This is further complicated by the possibility that preferences in breeding seasons may vary with latitude. It is also not known if individuals of this subspecies are polyoestrus. Animals held in captivity bred only once during the year.

MATE CALLING: At the onset of oestrus, females usually became more active, calling persistently throughout the night. Typically females stopped running, lifted their heads and uttered a wheezy, husky but loud 'tsz' call, and then ran off again. More often they called from a high vantage point in the cage. At this time their cloacas appeared to be swollen and they actively rubbed sternum and cloaca on objects in the cage, in particular on such items as clean food trays.

This activity is almost identical to that seen in the Common Dunnart *(Sminthopsis murina)* which, when without a mate, may call for a period of approximately ten days (pers. obs.). By about the fifth day, Common Dunnart females even call throughout the day and the call changes to a succession of sharp 'ts-ts-ts-tsst' sounds. By the sixth and seventh days this activity slows down and the calls are made from sitting positions on, for example, favourite rocks in the cage.

TABLE 1: PROBABLE MONTHS OF BIRTHS OF JUVENILE COMMON PLANIGALES

Registration No. (QM) and sex	Head-Body Length (mm)	Capture Date	Probable month of births
J22041 undet.	8	12 January	January
J4268 ♂	16	9 March*	February
J8070 ♂	47	26 June*	March
J4534 ♀	50	23 July*	April
J21324 undet.	45	11 October	July
J21326 ♂	46		
J21327 ♂	41	(one	
J21328 ♂	41	litter)	
J21330 ♂	51		
J17621 ♂	17	September	August
J7559 undet.	7	14 September*	September
J578 ♂	11	26 November*	October
J17914 undet.	9	26 November	November
J3345 undet.	10	20 November	November

* Date of entry into register, probably close to capture date.

Male Common Planigales became more interested in the females at the onset of oestrus and made frequent unsuccessful low-key attempts to mount. Although the females' behaviour at this time was directed towards mate finding, they at no time accepted copulation passively, but fought with and hid from pursuing males. On the second day of calling, the males' interest was more aroused. They sniffed the females' cloacas, and between unsuccessful attempts to copulate, they licked their erect penises and rubbed and thrust them on rocks and other objects in the cage. Males made leaps of up to 25 cm in attempts to spring on to escaping females.

COPULATION: When males finally caught females, they gripped them very firmly behind the ribs and in front of the hind legs with their forefeet and then bit the skin between the ears, high on the females' necks.

Ewer (1968) notes no use made of a neck bite by male Common Fat-tailed Dunnarts *(Sminthopsis crassicaudata)*. The behaviour however is common to many species of *Antechinus* (Marlow 1961) and is common in initial stages of copulation in the Kowarie *(Dasyuroide byrnei)* (Aslin 1874). Archer (1974) notes use of the neck grip in the Western Native Quoll *(Dasyurus geoffroii)* and cites the observation of Miss V. Bristow that the necks of female Western Native Quolls become swollen when they are reproductively receptive.

In Common Planigale males, the penis always erected very quickly and underwent an independent 'thrashing' motion until in contact with the female's cloaca. After about two minutes of active copulation males began a hind-foot 'scratching' that resembled a standing dog trying to scratch its belly with its hind foot. Marlow (1961) termed this a 'scratching reflex' after observing it in the Brown Antechinus *(Antechinus stuartii)*.

This behaviour has been noted by Archer (1974) in *Dasyurus geoffroii*. Aslin (1975, p. 200) records a male *Dasyuroides byrnei* 'scratching the female's cloacal area with his hind leg'.

Scratching in Common Planigales alternated from left to right foot every second, and each foot 'scratched' about four times per second. The activity appeared continuously throughout the copulatory sequence and after about one and a half hours the scratching appeared to be directed at the neck of the scrotum, so that the leg did not come to rest on the ground but on the top of the scrotum. The male's forefeet constantly grabbed and clutched the female's skin. Any resistance on the part of the female was now countered by a male taking a bigger mouthful of the female's neck.

After 15 to 20 minutes, males made a series (up to 30) of very powerful thrusts, which often twisted the pair in circles or caused them to topple over on their sides. Marlow (1961) records Brown Antechinuses *(Antechinus stuartii)* rolling over after a single coital thrust made by the males.

Males frequently lifted up females and turned them in the opposite direction. Sometimes the males would give the female's head a vigorous lateral shaking every 5 to 10 seconds, taking fresh and deeper bites of the neck at every shake.

During most of the copulation period, the females remained so passive that they appeared dead. They remained motionless with eyes closed, and only occasionally struggled or dragged the male around. Their only consistent activity was a slight upward jerking of the head which occurred approximately once every two seconds throughout the sequence. Copulation usually ended with a struggle. The two separated and both appeared very active with no visible signs of fatigue. Females showed no sign of damage from the male's neck grip. In three separate instances, copulation lasted 1·75, 2·5, and 2 hours respectively.

The males showed continued interest in the females for one or two days following copulation, and sometimes copulated again during this time. After these two days no more sexual interest was shown. During the two days following copulation females became increasingly aggressive towards males. It is probable that in the wild this aggression would drive males away. For this reason the male was removed from the cage about a week after copulation.

GROWTH OF YOUNG: Births of the young occurred after gestation periods of twenty and twenty-one days respectively.

On about the sixteenth day after birth, females constructed a tight grass-ball nest in a log.

By the seventeenth day, the pouch no longer always remained tightly closed, and a rear view revealed four young, positioned anteroposteriorly inside the pouch. By this stage the pouch had greatly enlarged, and a thin flap of muscular skin had spread out over the young and almost covered them, except for the posterior end near the cloaca. Females frequently licked the young in the pouch by relaxing the pouch muscles, sitting in a squatting position with the head between the legs, and pushing in with the snout. After fright, any excreta spilt on the young was licked off. Seventeen-day young are covered with minute transparent hairs; the ears are pressed down and flat; the eyes are undeveloped, but the limbs and tails are well-developed; the skin on the back is grey to black but pink in other areas. Their breathing rate was approximately 148 intakes per minute.

At approximately seventeen days after birth the diets of the females changed. They rejected mouse pups and ate only live insect food. They responded to a human finger near the glass cage wall with partly opened mouth and a wheezing high-pitched whistle. Females continued to add grass to their nests, making them so tight that by two weeks after birth, the interior of the nests could not be seen without demolition.

In two litters, the young ceased to be permanently attached to the teats and were left in the nest for the first time at twenty-four and twenty-eight days. Morrison (1975) reports a litter of five being released at six weeks. Fleay (1965) reports release after five to six weeks and Aslin (1974) noted release after twenty-eight days. As Morrison (1975) points out, these differences may be due to different litter sizes.

Females now ventured out only to defaecate (four to six drops urine and two large faecal pellets) and eat. Over a three to four day interval, they may be seen only once or twice outside the nest.

First emergences from the nest by the young were noted at forty-five days. They strayed about 6 cm from the nest walked around in circles for about three minutes, and then returned. A wheezing call was uttered by females as they entered the nest and this was returned by the young. It appeared to be a 'gathering contact' call. Females' appetite increased at this time and an average of thirty mealworms each were taken nightly.

At fifty-seven days, the young took solid food (mealworms) but continued to suckle from the female who lay 'spread-eagle' above them as they lay under her in a variety of positions — on the side, back, with eyes closed and feet generally in contact with her body though not grasping. There was no 'kneading' of the teats by juveniles while sucking.

At this age a variety of interactions could be seen in the family groups. The females appeared to be very volatile in temperament toward the young. It seems as if weaning is hastened by the increased aggression of the female toward the young. When a joey approached, the female would rush to 'attack' it with a jabbing lunge directed to the head. The young would utter a threat call which would bring all the other young to the immediate vicinity. The joey that had initially approached the female always remained motionless during the initial 'attack'. The female would calm down after the young's threat call. She would accept each baby after a small scuffle involving a rush and a mouth smell, whereupon the young, after remaining perfectly still, would rush over onto her back and cling on and climb over her. Young then jostled on the mother's back, clinging to her, jumping over her, grabbing one another and scuffling. As soon as she moved they grabbed the neck behind the ears with the incisors and lowered their bodies (resembling the male's position during copulation). All bites delivered to the young by the female at this time were open mouthed and soft.

At sixty-one days the young fed on insects after the pattern of behaviour seen in adults. When young encountered the female at this time they approached with ears back, mouth open and threat calling — but no struggles were ever seen.

At seventy-two days the young were independent of their mother; mouse pups were accepted but not cleanly killed.

They continued to sleep together in a tight bundle until about five months old, at which time the animals became more aggressive to each other and started sleeping in separate nests.

Aslin (1975) reports that reproductive maturity in females occurred at about ten months. Related information was not determined from this study.

DISCUSSION

Common Planigales have been collected from savannah woodland and grassland (Heinsohn 1970); stacked posts, neighbouring blady grass, partially flooded and generally soggy areas of peat swamp, dense forests of coarse, high grass beneath Swamp Mahogony Gums (Fleay 1965); and from debris at the base of Pandanus Palms and Melaleucas (Parker 1973). Most Common Planigales that I have collected have come from rubbish dumps in *Imperata* grasslands. Here the animals constructed small grass and leaf nests under iron and wood heaps. One adult male caught in Ingham (north Queensland) was found sleeping with a juvenile Little Melomys *(Melomys burtoni)* in a nest under corrugated iron. J. Covacevich (pers. comm.) has also observed Common Planigales nesting with Little Melomys and constructing their nests under sleepers on disused railway lines.

In the wild, Common Planigales are most probably unspecialized predators on insects (mainly), other invertebrates, and in some cases small invertebrates. Their arboreal abilities increase their hunting range and allow access to additional types of food (e.g. small nestling birds). Their relatively poor eyesight is compensated for by a keen sense of smell and hearing as well as agility, sensitivity to stimulation of the vibrissae, and well developed snatching abilities. Their shrew-like appetite and determination to tackle prey larger than themselves has been demonstrated on many occasions. Van Deusen (1969) records a specimen of Ingram's Planigale *(Planigale ingrami)*, from Karumba (north Queensland) that fed mainly on geckos, skinks, spiders and beetles but showed little interest in grasshoppers. However he notes (p. 617) '. . . my individual thrived on *Leggadina* (a small murid) which he killed and ate completely'. It is possible that *P. maculata* also takes a significant number of nestling and juvenile rodents in the wild.

In captivity, despite the presence of ample meat-mix food in familiar surroundings, the animals still exhibited persistent searching behaviour. If this active searching is appetitive behaviour, then perhaps the stimulus needed to bring about other action patterns and thereby stop the appetitive behaviour is not the act of eating, but the act of catching, struggling with, and killing prey. This idea may be supported by the tendency of these Planigales and other dasyurids to exhibit sterotyped boredom behaviour (where most of their activity consists of monotonously following a regular path) in dull environments and when fed on meat mixtures. The animals probably scavage in the wild, but this activity may normally be secondary to active predation. 'It seems that dead bait does not attract them and for that reason *Planigale* is not commonly taken' (W. Hosmer in Van Deusen 1969, p. 617).

Common Planigales fall prey to many animals. Their remains have been found in owl pellet deposits (e.g. from Burleigh, S.E.Q., J13526). The high frequency with which they appear in the Queensland Museum as 'cat-kills' leaves no doubt about their vulnerability throughout their entire range of feral and pet cats. Covacevich and Archer (1975) record one collected from a Cane Toad *(Bufo marinus)* stomach. One specimen in the Queensland Museum (JM1180) is labelled as having died from the bite of a black house spider *Ixeuticus robustus*. Heaviest predation probably takes place on juvenile animals just after leaving the nest (see Buchmann and Guiler 1977 for cannibalistic tendencies in *Sarcophilus harrisii)*, and on mating animals which advertise their positions with persistent calling.

In young Common Planigales raised on mealworms and other insects, the methods of handling and killing mouse pups, large grasshoppers, and other intimidating prey improved with experience. In addition food preference appeared to be learned by picking food from the mother's mouth while she ate near the young. Braithwaite (1973) states that from mid-January juvenile Brown Antechinuses *(A. stuartii)* catch food, but the young seemed to learn to feed from the female by hunting together, feeding on the female's scraps, and by stealing food. The Common Planigale's generalized diet probably necessitates the rapid development of efficient killing techniques and the ability to revise past experiences.

Wild Common Planigales are probably socially intolerant. The repetoire of calls may serve to inhibit aggression when animals come in contact.

The high degree of aggression inhibition that results from threat calls has been demonstrated in male–female interactions, mother–young interactions, and juvenile–juvenile interactions. The 'mate-finding' call initiated by females is almost certainly further evidence of this intolerance under non-breeding conditions. It is interesting that even though the animal is socially intolerant, and the female never accepts copulation without violent struggles and vocal threats, she nevertheless advertises her reproductive condition by calling and attracting potential mates. Buchmann and Guiler (1977, p. 167) note that Tasmanian Devils *(Sarcophilus harrisii)*, although essentially solitary animals, are extremely vocal '. . . and their loud and rather eerie noises enable them to effect efficient long range communication'. They note that broadcasting tape recorded calls readily drew the elusive animals from cover and caused them to vocalize in response. Perhaps similar use may be made of recorded Planigale calls in an attempt to study them in the wild.

Male Common Planigales are generally larger than females. Braithwaite (1973) suggests that in *Antechinus stuartii* marked size difference between male and female creates less food competition between the two and thereby enhances the species' chances of survival in the same habitat. However it is also possible that it may have arisen in response to problems associated with reproduction between essentially socially intolerant animals. It is apparent that in such intolerant animals as Common Planigales, where the female is usually more vocal and aggressive than males, greater strength and weight is advantageous in males, enabling them to mate effectively and ensure that successful implantation takes place. This dimorphism could be produced by selection for the larger more persistent males who finally overcome and mate with females. The uncooperative nature of the females ensures that genetically desirable males are selected. The aggressive behaviour exhibited by male Common Planigales during copulation as well as the extended period over which copulation takes place may further ensure conception in females.

Common Planigales marked their cages with scents recognizable at least to their own kind; cloacal rubbing was observed in both sexes and sternal rubbing took place in maturing males and oestrus females. As the rubbing by males increased, so did their aggressiveness toward the female sharing their cage. Braithwaite (1973) examines the same actions in the Brown Antechinus *(A. stuartii)* and notes that cloacal rubbing chemically marks sites of victory and possibly functions as a threat for some time. Wood (1970), studying the same animals, reports them to be strongly site attached and possessive of their territories. Johnson (1973, p. 531) points out that in many cases marking makes the habitat familiar — a sort of proximity orientation. 'In many species it is found that common marking sites are used by several individuals and marking points may be sought out and appear to elicit marking behaviour. This may be interpreted as indicating that scent marks act as sites for general exchange of information.' Johnson also suggests that marking may be involved in regulating population densities.

The concept of familiarization of the habitat seems more acceptable in the case of the Common Planigale. The animal marks its surroundings with cloacal smears, sternal rubs and faecal piles. New objects such as food trays are quickly investigated and may be marked. In such familiar surroundings more energy can then be devoted to activities such as food finding and reproduction rather than to regular assessment of the surroundings.

The reproductive cycle of *Planigale maculata* is poorly understood. Data collected from specimens in Queensland show a possible preference for summer parturition. There is no data that definitely shows the animal to be either monestrus or polyoestrus. *P. maculata sinualis* from Northern Territory is polyoestrus (see Aslin 1975). The incidence of births throughout the year in Queensland suggests that *P. maculata maculata* may follow a similar strategy.

In contrast, the Little Northern Quoll *(Dasyurus hallucatus)*, and all species of *Antechinus*, breed in the spring months. The accepted explanation for this is that the increase of invertebrates during the summer provides abundant food for the lactating females and weaning young (Braithwaite 1973, Wood 1970, and Freeland 1972). Because the grassland habitat of the Common Planigale is periodically destroyed by fire, usually in summer, large litters and extended breeding seasons would impart an adaptive advantage.

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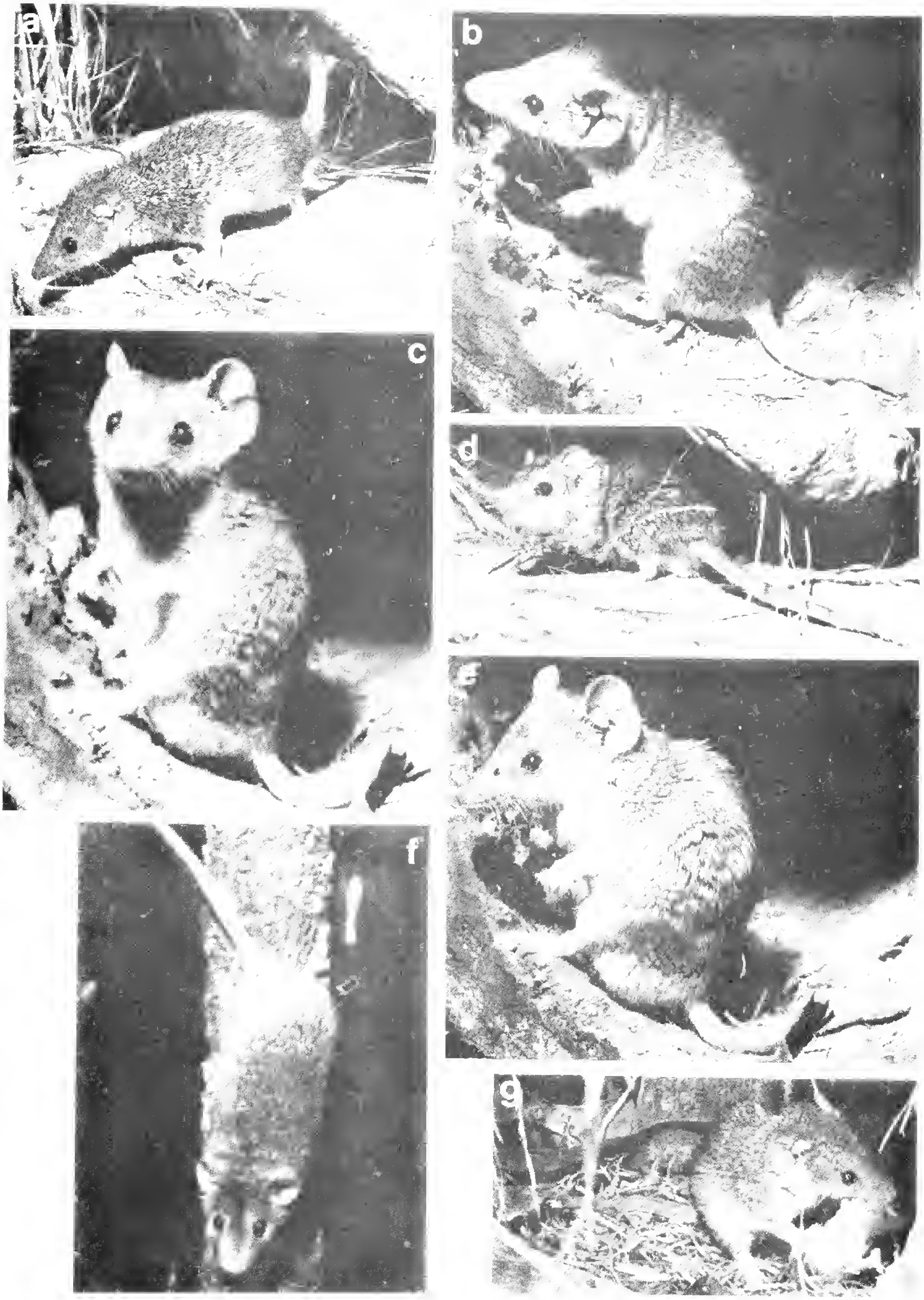
PLATE 1

a: Adult female Common Planigale (*Planigale maculata*).
b, c: Investigatory upright postures.
d: Indecision-alert posture.
e: Typical eating or grooming posture.
f: Typical arboreal posture.
g: Adult female eating a mouse pup.

PLATE 1



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THE OCCURRENCE OF LIZARDS OF THE GENUS *EMOIA* (LACERTILIA, SCINCIDAE) IN AUSTRALIA

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ABSTRACT

The presence of the genus *Emoia* in Australia is confirmed. Two taxa — *E. cyanogaster longicauda* (Macleay) and *E. atrocostata irrorata* (Macleay) — occur on the islands of Torres Strait and mainland Queensland.

The literature on *Emoia* in Australia is confusing. Macleay (1877) described five new species of what is currently regarded as the genus *Emoia* from Australia and New Guinea, but his descriptions were not diagnostic (Boulenger 1887; Loveridge 1948; Brown 1953, 1954; Arnold 1966). All that could be extracted from Macleay (1877) was that at least two species of *Emoia* occurred on the Torres Strait Islands. Boulenger (1887) listed a specimen of *E. cyanogaster* from Murray Island, Torres Strait; he included Cape York in the distribution of *E. atrocostata* but listed no material from there. Barbour (1914) recorded *E. cyanogaster* from Murray Island, and Brown (1954) recorded it from Prince of Wales Island, Torres Strait. Worrell (1963) describes both species as occurring on the Australian mainland, and Arnold (1966) recorded a specimen of *E. atrocostata* in the Australian Museum from Cape York Peninsula, but as Cogger (1975) noted 'Australian mainland records are few and uncertain'.

Goldman, Hill, and Stanbury (1969) examined the reptile types in the Macleay Museum. Using Boulenger's (1887) key and following Loveridge (1948) they decided that Macleay's *Mabouia irrorata* and *M. marmorata* were synonyms of *Emoia atrocostata; Euprepis simillimus* and *E. longicaudis* were synonyms of *Emoia cyanogaster;* and *Euprepis submetallicus* was a synonym of *Emoia baudinii pallidiceps.* Brown (1953, 1954) earlier had placed *E. longicaudis* in *E. cyanogaster;* he considered *E. submetallicus* a good species, separating it from both *E. baudinii* and *E. pallidiceps.* The Macleay types are now housed in the Australian Museum, and I have examined the types of *M. irrorata, M. marmorata, E. simillimus,* and *E. longicaudis,* and the species *E. cyanogaster* and *E. atrocostata* across their range. As a result of my examination of these specimens I concur with Brown (1954) and Goldman *et al* (1969) in the allocation of these Macleay names.

The two forms of *Emoia* recognized here as occurring in the Torres Strait and on the Australian mainland have been aligned with *E. cyanogaster longicauda (sensu* Brown 1954) and *E. atrocostata irrorata (sensu* Loveridge 1948). This does not signify confirmation of the status of these subspecies. These names are used merely as conveniences to place the available names in the Australian-Papuan region. A final decision on what subspecies should be recognised awaits a revision of these island-inhabiting lizards across their whole range from southeast Asia to Polynesia.

Specimens examined are housed in the following museums QM — Queensland Museum, AM — Australian Museum, NMV — National Museum of Victoria, BMNH — British Museum of Natural History. I thank J. Covacevich, H. G. Cogger, J. Coventry and A. Stimson respectively, for allowing me access to the specimens under their care.

Genus Emoia

DIAGNOSIS AND DESCRIPTION: See Greer (1974).

The Australian *Emoia* may be distinguished from all other Australian genera by the combination of the following characteristics: large (snout–vent lenth up to 100 mm) aboreal or rock-dwelling pentadactyl skinks with a moveable lower eyelid bearing a transparent disc; supranasals present; frontoparietals fused; parietals in contact behind interparietal; no postnasal scale; upper labials 7 or 8; and oviparous with a clutch size of 2 eggs.

DISTRIBUTION: The islands of the southwest and south Pacific from southeast Asia east through the Indo-Australian Archipelago, the Philippines, New Guinea, the Bismarks and north into Micronesia, south into Melanesia and east into Polynesia (Greer 1974). In Australia, the Torres Strait Islands and eastern Cape York Peninsula.

Emoia cyanogaster longicauda (Macleay)
(Plate 1, Fig. 1)

Euprepis longicaudis Macleay, 1877, p. 86. Darnley Island, Torres Strait, Queensland (Chevert Expedition). Lectotype AM R31859.

Euprepis simillimus Macleay, 1877, p. 69. Katow, Papua New Guinea (Chevert Expedition). Lectotype AM R31855.

Emoia cyanogaster longicauda: Brown, 1954, p. 264.

SPECIMENS EXAMINED

Queensland: Saibai Island (AM R48351–2); Darnley Island (AM R31856–60, 42621, 42563); Murray Island (BMNH 78.10.16.76; AM R4503, 9676, 42489–90, 42554, 42571–2, 42643–5, 42647, 42649, 44260–7, 44927–9, 45970); Torres Strait (NMV D3383); Lake Boronto (QM J24730); Lockerbie (QM J24731); Heathlands (QM J29126); Dulhunty River Crossing (QM J24600); Claudie River, Iron Range (NMV D674; QM J24601, 27872, 28028); Mt Tozer, Iron Range (QM 31833); Leo Creek, McIlwraith Range (QM J32480); Cape York (NMV D565).

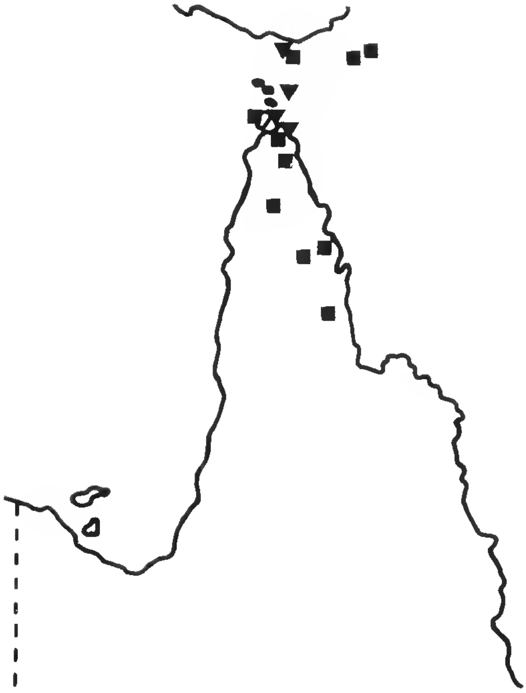

FIG. 1: Distribution of *Emoia* in Queensland. ■ = *E. cyanogaster*, ▲ = *E. atrocostata*.

Papua: Trobirand Island (BMNH 95.10.17.26); Woodlark Island (BMNH 96.7.8.3); Fergusson Island (BMNH 95.4.26.33–4); Haveri (BMNH 97.12.10.64); Karimui (NMV D12055); Katow (AM R31853–8); Myal Sinbif (NMV D38580); Oriomo Station (NMV D38574–6, 38578–9); 48 km above D'Albertis Junction, Fly River (AM R12158–61 A, B); Fly River (BMNH 86.5.20.8).

DIAGNOSIS: See Brown (1954).

Differs from *E. atrocostata* the only other Australian species of *Emoia* in colour (mainly tan with a lemon-yellow belly *vs* black or blackish-grey with a bluish-white belly), in more numerous subdigital lamellae (63–82 under fourth toe *vs* 29–36), fewer scales between nuchals and base of tail (51–58 *vs* 61–67), and in habitat (rainforests, and plantations, *vs* rocks and mangroves in the littoral zones).

DISTRIBUTION IN AUSTRALIA: Torres Strait Islands and eastern Cape York Peninsula from Lockerbie south to 13° 33′ S in the McIlwraith Range (Fig. 1).

DESCRIPTION: Snout-vent length (mm): 43–98 (N=22, mean 76·9). Head width (%SVL): 12–18 (N=22, mean 15·0). Tail (%SVL): 194–268 (N=10, mean 222·2).

Prefrontals separate, very rarely forming a suture. First loreal not contacting supranasal. Supraciliaries mostly 7 or 8, rarely 6 or 9 (N=38, mean 7·6). Palpebral disc small. Ear opening round, equal in size to palpebral disc, with one or two large lobules on anterior edge, and smaller ones on other margins. Midbody scale rows 24–30 (N=22, mean 26·5); number of scales from nuchals to base of tail 51–58 (N=22, mean 54·8). Lamellae under fourth toe 63–82 (N=20, mean 70·7).

Dorsally and laterally tan coloured with body, legs, and tail with or without white and black spots; sometimes a thin dark line from nostril to eye, continuing backwards for varying distances. Upper and lower labials pale, sometimes outlined in black. Ventrally lemon-yellow in life, sometimes blue in preservative; distal three-quarters of tail speckled with brown.

REMARKS: From the type series of *Euprepis longicaudis* (AM R31856–60), R31859 has been selected as lectotype; from the type series of *E. simillimus* (AM R31853–5), R31855 has been selected as lectotype. Loveridge (1948) noted that *Emoa cuneiceps* De Vis (1890) agreed in every respect with *E. cyanogaster* except for the midbody scale rows. He suggested the 33–36 rows may have been a misprint for 23–26. Scott, Parker, and Menzies (1977) however, gave *Emoia cuneiceps* full species status.

HABITAT: Rainforest and its edges, wet scrub along creeks, and nearby gardens. Fred Parker *(in litt.)* notes that it is common on mainland New Guinea from sea level to about 1500 m, where it is found in all habitats as well as gardens and plantations.

Emoia atrocostata irrorata (Macleay)
(Plate 1, fig. 1)

Mabouia irrorata Macleay, 1877, p. 66. Hall Sound, Papua New Guinea. (Chevert Expedition) Holotype AM R31851.
Mabouia marmorata Macleay, 1877, p. 65. Long Island, Torres Strait, Queensland. (Chevert Expedition). Holotype AM R31852.
Emoia atrocosata irrorata: Loveridge, 1948, p. 372.

SPECIMENS EXAMINED

Queensland: Dauan Island (AM R48561); Long Island (AM R31852); Horn Island (QM J25423–6, 25786, 25800); Somerset (QM J24732); West Cape York Peninsula (AM R9600).

Papua New Guinea: Fly River (BMNH 85.6.30.4); Hall Sound (AM R31851); Ela Beach, Port Moresby (J32826, 32828); Fergusson Island (BMNH 95.4.26.43).

DIAGNOSIS: See Loveridge (1948), and diagnosis of *E. c. longicauda*.

DISTRIBUTION IN AUSTRALIA: Islands of Torres Strait and tip of Cape York Peninsula at Somerset and Naru Point (Fig. 1).

DESCRIPTION: Snout-vent length (mm): 46–85 (N=10, mean 73·3). Head-width (%SVL) 14–16 (N=10, mean 14·8). Tail (%SLV): 103 (N=1).

Prefrontals separate. First loreal contacting supranasal. Supraciliaries 7, rarely 6, 8 or 9 (N=19, mean 7·2). Palpebral disc small. Ear opening round, equal in size to palpebral disc, with or without a small lobule on anterior margin. Midbody scale rows 34–39 (N=10, mean 35·5); number of scales from nuchals to base of tail 61–71 (N=10, mean 67·5). Lamellae under fourth toe 29–36 (N=10, mean 32·9).

Dorsally grey-brown with body, legs, and tail spotted with black. Laterally black with or without pale speckling; side of head sometimes grey brown. Ventrally cream with dark throat and toes.

HABITAT: Mangroves and rocks in the inter-tidal zone.

REMARKS: This lizard was very common on the trunks and branches of mangrove-trees on Horn Island. The first specimens collected during January, 1975 were flushed from holes in dead mangroves by the rising tide. They made their way higher up the tree as water filled the occupied holes. During low tide many individuals were basking in small patches of sunlight that penetrated the thick canopy. At Somerset and Naru Point they were common on the rocky shore, even in the splash zone, where they often hid in holes amongst oysters. At all localities individuals when hard pressed would jump into the water, then swim strongly with their robust tails.

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PLATE 1

Above: *Emoia atrocostata,* Horn Island, Torres Strait. (Photograph R. Sadlier).

Below: *Emoia cyanogaster,* Heathlands, Cape York. (Photograph A. Easton).